Chapter 2
The Neuroscience of Action and Perception

The visual cortex of humans and other primates is composed of two main information pathways, called *ventral stream* and *dorsal stream* in relation to their location in the brain, depicted in Fig. 2.1. The traditional distinction put forth by Ungerleider and Mishkin (1982) and detailed by Goodale and Milner (1992) talks about the ventral "what" and the dorsal "where/how" visual pathways. In fact, the ventral stream is devoted to perceptual analysis of the visual input, such as in recognition, categorization, assessment tasks. The dorsal stream is instead concerned with providing the subject the ability of interacting with its environment in a fast, effective and reliable way. This second stream is directly involved in estimating position, shape and orientation of target objects for reaching and grasping purposes.

The two cortical systems related to the visual streams were previously considered to act nearly independently (Milner and Goodale 1995). However, although recent studies confirm that the dorsal stream is more oriented toward action-based vision, whilst the ventral one is more suitable for categorization, their interaction seems to be extremely important for allowing both of them to function properly (Goodale and Milner 2004).

The tasks performed by the two streams, their duality and interaction, constitute the neuroscientific basis of the research described in this thesis, and this chapter is devoted to a detailed explanation of the related concepts.

2.1 The Two Cortical Streams of Visual Elaboration, Fundamental Roles and Proofs of Dissociation

Looking at an object with grasping purposes activates a neural pathway which is not active when grasping actions are not involved. This activation seems to represent a potential grasping action, and is reinforced when the action is actually performed. Some neurons in the *anterior intraparietal area* (AIP) of posterior parietal cortex in monkeys are found to be active when grasping some particular objects, but also

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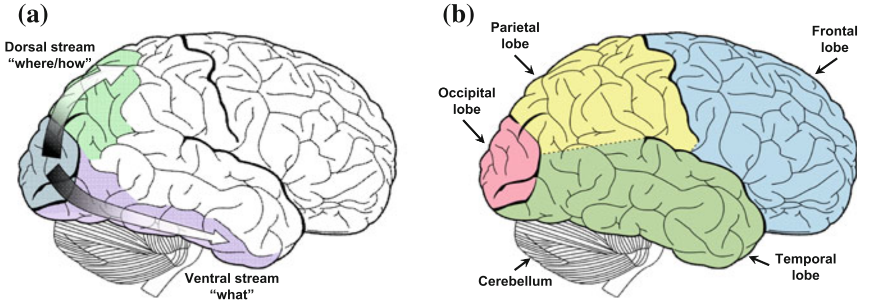

Fig. 2.1 Visual streams and cortical lobes of the human brain. **a** Dorsal and ventral streams. **b** Cortical lobes and cerebellum

when looking at them with the purpose of grasping (Sakata et al. 1998). Some other neurons of the same area are sensitive to the size or orientation of objects, and to hand postures. Area AIP is not activated when the task is to recognize or classify objects and no practical interaction is required. A very similar pattern has been found in humans as well (Culham 2004; Cohen et al. 2009; Hoeren et al. 2013), thanks to *fMRI* and *TMS* research (see boxes below).

fMRI is a non-invasive neuroimaging technique that infers the activity of brain areas from their hemodynamic response. The most common type of fMRI, called BOLD (Blood Oxygen Level Dependent), measures regional differences in oxygenated blood. BOLD-fMRI is by far the most used neuroimaging technique due to its very high spatial and temporal resolution, although the exact relation between neuronal activity and blood oxygenation is still a matter of debate (Culham 2001; Logothetis et al. 2001; Heeger and Ress 2002; Snow et al. 2011).

Transcranial magnetic stimulation (TMS) is a non-invasive brain study technique that creates localized, completely reversible lesions to the brain cortex through the induction of weak currents by rapidly changing magnetic fields (Pascual-Leone et al. 2002). The technique allows to study the functionality and connectivity of brain areas by inactivating them during the execution of certain tasks. The advantage of TMS over imaging methods is that an observed disruption implies the direct involvement of the stimulated area in the tested function. On the other hand, TMS spatial resolution is lower than in fMRI, and the results are strongly dependent on the exact stimulation, in space and time, of the target area.

In the dorsal visual stream of the primate brain, there is thus an area especially dedicated to encode the 3D features of objects in a format suitable to be used for planning and executing grasping actions. Similarly, a large part of the human brain close to the lateral-occipital sulcus (the *lateral-occipital complex*, LOC) is dedicated to recognize visually-presented stimuli, such as objects or faces, but is not directly involved in action execution toward them (Kourtzi and Kanwisher 2001). LOC is probably the most typical ventral stream area.

2.1.1 A Dual Mechanism for Vision

The dualism between "vision for action" and "vision for perception" had been hypothesized long time before neuroimaging research (Goodale et al. 1991; Milner and Goodale 1993). Studies with neurally-impaired people, especially on two categories of brain damages, *visual agnosia* and *optic ataxia* (see box), suggested such dualism.

Visual agnosia (from Greek: *a-gnosis*, lack of knowledge) is the name given to a number of different disorders and syndromes in which visual object recognition is impaired (Farah 2004). Of particular interest for the two streams research is *visual form agnosia*, a type of agnosia that affects identification of shapes even though the subjects have preserved visual acuity, color vision, tactile recognition, and are able to move correctly and properly grasp objects presented in their peripersonal space (Milner et al. 1991; Rice et al. 2006a).

Optic ataxia (from Greek: *a-taxis*, lack of order) occurs when the patient has a deficit in visually-guided arm movements that cannot be explained by motor, somatosensory, or visual acuity deficits (Buxbaum and Branch Coslett 1997; Glover 2003). People affected by optic ataxia are unable to grasp common objects if not very clumsily and unreliably, although their recognition and classification skills are totally spared (Milner and Goodale 1995).

The apparent complementarity of the two impairments have been of great help for the elaboration of the two streams theory. Recent neuroimaging studies revealed that visual agnosia is caused by damages to the LOC and nearby areas, whereas damages to the dorsal stream around AIP provoke optic ataxia. For example, the brain of patient DF, suffering from visual form agnosia, does not show activation related to object identification, because her ventral stream is damaged (James et al. 2003; Whitwell et al. 2014). Nevertheless, she is able to correctly perform grasping actions, and her parietal activation is rather similar to control subjects, including in the anterior intraparietal sulcus during grasping. The opposite behavioral patterns are observed in optic ataxic patients (Goodale and Milner 2004).

Evidence for the different role and processing mechanisms of the two pathways has been provided during the last two decades by plenty of studies following different research approaches and techniques. Recent fMRI research showed the complementary responsiveness of the two streams in identification and spatial analysis of visual stimuli (Valyear et al. 2006; Thoma and Henson 2011). Such dissociation is confirmed for situations in which the action is observed and not directly performed by the subject (Shmuelof and Zohary 2005), or only pantomimed Makuuchi et al. (2012). Considering two of the most representative areas of the streams, AIP for the dorsal, and LOC for the ventral stream, the former shows differential activity during grasping movements with respect to reaching, whilst the latter does not. On the other hand, LOC activates whenever a recognizable object is visible (compared to scrambled images), whilst AIP only when a potentially graspable object is in view (Culham et al. 2003).

Behavioral studies based on optical illusions, distractor stimuli and concurrent tasks suggest that visual information is analyzed and processed differently by the streams (Winkler et al. 2005; Plewan et al. 2012). According to Westwood and Goodale (2003a), explicit object perception in the ventral stream is “scene-based” and the size and location of an object is represented contextually with the size and location of nearby objects. The control of object-directed actions by the dorsal stream follows instead an “actor-based” frame of reference, in which object location and size are represented with respect to the subject body, and especially to hand and arm. Dorsal visual analysis is driven by the absolute dimensions of the target object, and other objects in the environment are likely to be considered and hence taken into account only as potential obstacles (Ansuini et al. 2007b). Another distinction talks about holistic and analytical visual representations (Ganel and Goodale 2003; Red et al. 2012): object dimensions that are perceived globally by the ventral stream are, in the same situation, processed locally by the dorsal stream if a visually-guided action is directed at the object.

Several studies (see e.g. Grill-Spector et al. 1999; James et al. 2002) demonstrated that ventral stream areas such as LOC show adaptation for different views of the same object, denoting viewpoint invariance. On the contrary, areas of the intraparietal sulcus do not exhibit such invariance, and respond to different views as they were different objects. This suggests a more “pragmatic”, action-oriented on-line processing along the dorsal stream, focused on the actual situation of the environment rather than on objects’ implicit quality. Even access to memory seems to be different for the two streams, and working memory related to spatial location and visual appearance is probably located in different subsystems (Darling et al. 2006; Kawasaki et al. 2008).

The streams dissociation has thus been confirmed, but also criticized, by the neuroscientific community, and the original theory is constantly being revised and updated. The trend is toward a more integrated view of the functioning of the two streams, that have in many cases complementary tasks (Goodale and Westwood 2004; Zachariou et al. 2014).

2.1.2 Brain Pathways for Vision-Based Grasping

The anatomy of the visual and motor cortices of human and closer superior primates is well known. Although the knowledge regarding associative regions of the brain, such as the posterior parietal or the inferior temporal cortices, is less established, it is possible to outline a simplified schema of the brain areas more directly involved in vision-based grasping actions. Those areas more thoroughly considered in this work are depicted in Fig. 2.2. A longer list of brain areas, with acronyms or short names and references to the sections in which they are described is provided in Table 2.1. Here, only an overview of the two pathways is given, and more details are provided in the rest of this chapter.

Visual data in primates flows from the retina to the lateral geniculate nucleus (LGN) of the thalamus, and then mainly to the primary visual cortex (V1) in the occipital lobe. The two main visual pathways go from V1 and the neighbor area V2 to the posterior parietal cortex (PPC) and the inferior temporal (IT) cortex. Through the dorsal pathway, object related visual information flows through area V3A and the caudal intraparietal area (CIP), which extracts action-related spatial visual properties of objects. Visual data then reaches the anterior intraparietal sulcus (AIP), in which visual features are analyzed in order to plan and monitor the execution of suitable grasping actions. Area AIP projects mainly to the ventral premotor area (PMv), that selects and composes motor primitives (see box on motor primitives) to form complete grasping actions, which execution signals are released by the primary motor cortex (M1).

Object information flowing through the ventral pathway passes through V3 and V4 to the lateral occipital complex (LOC), that is in charge of object recognition. According to recent interpretations of the two streams hypothesis (Goodale and Milner 2004; Ellison and Cowey 2009), the LOC itself is implied in some action-related processing, although the way the two streams communicate is still mostly unknown.

The neuroscience concepts most relevant for the current research are described in the next sections, separated in early visual processing, dorsal, and ventral stream areas. Exhaustive reviews of grasp-related research are Castiello (2005) and Culham et al. (2006). For details regarding visual areas, fundamental studies are Felleman and Essen (1991) and Chalupa and Werner (2003). Most brain regions cited in the text can be localized in Fig. 2.2.

Fig. 2.2 Brain areas involved in vision-based grasping actions

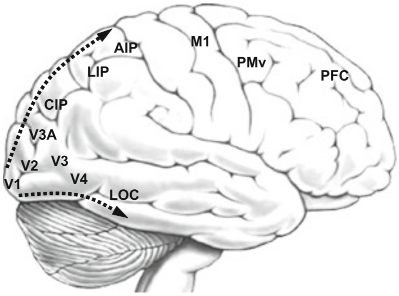

Table 2.1 Principal cited brain areas, with acronym and reference to the section in which they are described

Brain area	Acronym	Sections
Visual areas		
Primary visual cortex	V1	2.2
Visual area 2	V2	2.2
Visual area 3	V3	2.2
Middle-temporal area	MT/V5	2.2
Dorsal stream areas		
V3 Accessory area	V3A	2.2
Intraparietal sulcus	IPL	2.3
Caudal intraparietal sulcus	CIP	2.3.1
Anterior intraparietal sulcus	AIP	2.3.2
Lateral intraparietal sulcus	LIP	2.3.4
Ventral intraparietal sulcus	VIP	2.3.4
Parietal reach region	PRR	2.3.4
Ventral stream areas		
Visual area 4	V4	2.4
Lateral occipital complex	LOC	2.4.1
Ventral occipital temporal area	vTO	2.4.1
Lateral occipital cortex	LO	2.4.1
Motor areas		
Primary motor cortex	M1	2.3.3
Ventral premotor cortex	PMv/F5	2.3.3
Dorsal premotor cortex	PMd	2.3.3
Other areas and structures		
Lateral geniculate nucleus	LGN	2.2
Posterior parietal cortex	PPC	2.3
Somatosensory cortex	SI/SII	2.4.2
Prefrontal cortex	PFC	2.4.2
Basal ganglia		2.4.2
Cerebellum		2.4.2

Differences between humans and other primates are discussed in the text

2.2 Visual Areas and Stream Separation

The *retina* is the visual receptor of the human body. Visual information gathered by the retina is sent through ganglion cells to the *lateral geniculate nucleus* (LGN) of the thalamus. Ganglion cells are of two types: *parvocellular* (P) and *magnocellular* (M); the former are smaller, slower and carry many details such as color, the latter are larger and faster, and rather rough in their representations. Although these two types of cells seem to correspond nicely to the ventral and dorsal stream distinction,

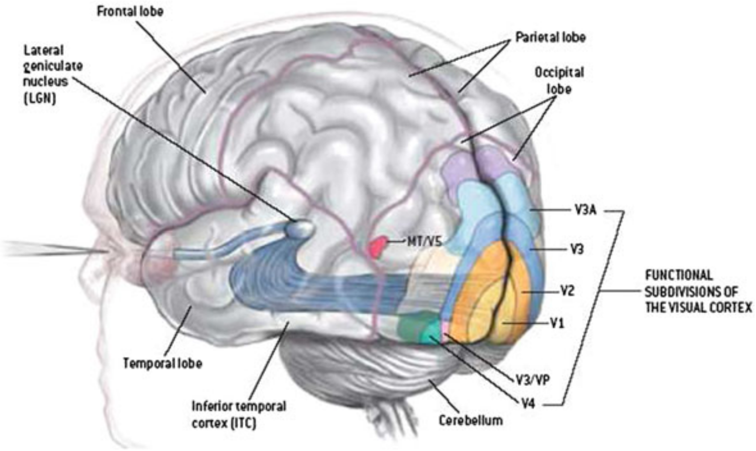

Fig. 2.3 Visual areas in the brain, adapted from Logothetis (1999)

evidence is clearly against a simple correspondence between the subcortical and the cortical pathways, and M and P signals mix largely inside V1 (Maunsell 1992; Ferrera et al. 1992).

The LGN performs a first processing of the visual data and forwards them almost entirely to the *primary visual cortex* (V1) in the occipital lobe (Lee 2003). The primary visual cortex and neighbor visual areas can be localized in Fig. 2.3.

Area V1, also called the *striate cortex*, is organized in a retinotopic manner, respecting the topological distribution of stimuli on the retina. In V1 basic visual features such as colors, bars or edges and their orientation are detected. Visual areas downstream from V1 are called *extrastriate*. The first extrastriate area, V2, receives most of V1 output and projects mainly to visual areas V3 and V4. Area V2 is retinotopic, has receptive fields that are larger than V1's and realizes a matching of V1 features in order to perform moderately complex visual tasks, such as detecting spatial frequencies and textures or separating foreground from background. Visual area V3 is still retinotopic and elaborates on the job of V2 to generate more complex invariant representations. V3 has large receptive fields and ability to detect more complex features regarding orientation, motion, depth and color of stimuli (Gegenfurtner et al. 1997; Adams and Zeki 2001). In V3 the data stream splits into the two pathways: dorsally towards the posterior parietal cortex (PPC) and ventrally to the inferior temporal (IT) cortex. Comparative studies between human and monkey (usually macaques) visual cortices reveal that their brains differ mostly in higher-order cortical regions, downstream from V3-V3A, and are more similar in lowest areas, such as V1 and V2 (Van Essen et al. 2001; Tootell et al. 2003; Tsao et al. 2003).

For what concerns stereoptic processing, binocular disparities (see box on disparities) are present in all visual areas, starting from V1 (Poggio et al. 1988; Cumming and DeAngelis 2001; Parker 2004). Areas V2 and V3 are increasingly capable of depth processing, in accordance with the size of their receptive fields (Backus et al.

2001; Rutschmann and Greenlee 2004). Both in humans and monkeys, area V3A is specialized for stereoptic depth, and computes also relative disparities between pairs of visual stimuli (Tootell et al. 1997; Backus et al. 2001; Tsao et al. 2003). Evidence regarding the role of disparity processing in visual areas is not conclusive though, as the distribution of different disparity tuning curves is rather smooth across areas (Adams and Zeki 2001).

Links between various disparity-selective cells allow to obtain more sophisticated response properties. For example, selectivity for absolute distance is obtained from disparities using additional information about eye position. Computation of disparity gradients is very likely performed in V3A and CIP using the outputs of many simple disparity selective cells (Adams and Zeki 2001; Tsutsui et al. 2005).

Visual area V5, more commonly known as the *middle temporal area* (MT), is very likely the most important brain region for the detection of moving visual stimuli. Both in humans and monkeys MT is selective for speed and direction of moving features (Orban et al. 2003), and its responsiveness to stereopsis signals suggests that it codes also for changes in object orientation (DeAngelis et al. 1998; Nguyenkim and DeAngelis 2003). Even though the contribution of MT is required for performing grasping actions toward moving targets (Schenk et al. 2005), there is no evidence for an involvement of MT in detailed 3D analysis of objects, and thus of its relevance for grasping actions toward static targets (Backus et al. 2001; Tsao et al. 2003).

Most projections in the visual cortex follow the described processing sequence, from V1 to higher order areas, but backprojections are widespread, and visual elaboration in the early visual areas is subject to global context influence, task requirements, and to higher order perception (Lee 2003). According to the modern view, the early visual cortex does not only perform the first, simple stages of visual processing, but is also involved in many higher levels of visual elaboration (Vanni et al. 2004). The visual cortex has been found to be more temporally compact than expected, and transmission times between areas spatially and hierarchically distant are very low (Bullier 2001). Primary areas are thus constantly involved in all stages of visual processing, and higher areas such as MT are in a position to modulate the response of V1 and V2 neurons and suit their response to the requirement of the visual task in a reactive way. Even the LGN seems to be integrated with higher areas, and a short-cut channel of M cells between LGN and MT might be the instrument used by the dorsal stream to quickly separate objects from background, and bias the processing in V1-V2 (Bullier 2001).

2.3 The Action-Oriented Dorsal Stream

Visual region V3A can be considered as pertaining to the dorsal stream, which continues in the posterior parietal cortex, toward the top and sides of the brain. The *posterior parietal cortex* (PPC) is largely recognized as the main associative area of the brain dedicated to the coordination between sensory information and motor response (Sakata et al. 1997). The *intraparietal sulcus* (IPS) separates the superior and inferior lobes of the PPC. Several areas within and close to the IPS are dedicated to different visuomotor tasks (Sereno et al. 2014). Some of these areas are described in this chapter, but special focus is put on its most posterior and anterior sections, CIP and AIP respectively.

Many of the findings explained below concern monkey data, as single cell studies allowed to collect a great deal of evidence regarding the role of intraparietal areas in macaques. Only recently, although in an ever-growing fashion, brain imaging and TMS studies (see box) began to clarify the structure and tasks of the posterior parietal areas in humans.

Differences in control strategies depend also on structure, morphology and kinematics of body and limbs, and it is therefore very difficult to draw a full interspecies parallel (Christel and Billard 2002). The current evidence suggests that the human intraparietal cortex is more complex, and contains visuospatial processing areas that are not present, or much reduced, in monkeys (Grefkes and Fink 2005; Orban et al. 2006a). Neuroscientists argue that, under evolutionary pressure, parietal but not earlier regions adapted to endow humans with specific abilities (Striem-Amit et al. 2012), such as an improved motion-dependent 3D vision for tool manipulation (Vanduffel et al. 2002; Orban et al. 2006a).

Despite the differences, a rather clear parallel between monkey and human AIP is established (Grefkes et al. 2002; Choi et al. 2006; Orban and Caruana 2014). Also, many fundamental connections correspond across species, such as the *anterior intraparietal—ventral premotor* and the *medial intraparietal—superior colliculus* links (Rushworth et al. 2006). Hence, it is a common procedure to consider data of similar species in order to try and work out the mechanisms behind vision-based grasping in humans (Rizzolatti and Luppino 2001; Grefkes and Fink 2005). Important interspecies differences are nevertheless taken into account and discussed in the following sections.

2.3.1 Posterior Intraparietal Sulcus

The most posterior part of the IPS is the *caudal intraparietal sulcus* CIP, which is also referred to as cIPS, pIPS, PI or hCIP in the human case. Area CIP is mainly dedicated to local 3D shape and orientation processing. It receives projections from visual area V3 and V3A and is also active during visually guided grasping.

Neurons in CIP are strongly selective for the orientation of visual stimuli. Two exhaustive studies (Taira et al. 2000; Tsutsui et al. 2001) showed that selectivity toward disparity based orientation cues is predominant, but many neurons also respond (some exclusively) to perspective based orientation cues. Indeed, it seems that cue integration for obtaining better estimates of orientation is performed in this area (Welchman et al. 2005). This sort of processing by CIP neurons is the logical continuation of the simpler orientation responsiveness found in V3 and V3A. Similarly to V3A, CIP is not concerned with general purpose scene segmentation, but rather with processing the 3D layout of target local features (Tsao et al. 2003; Tsutsui et al. 2005). In CIP, orientation of features is represented in a viewer-centered way, so that the coding is especially suitable for visuomotor transformations for reaching-grasping purposes, rather than for feature integration with the purpose of composing complex scene interpretations (Sakata et al. 2005). This is consistent with the position of CIP in a central stage of the dorsal stream. As a further proof of this, CIP does not recognize the same object seen from two different viewpoints (James et al. 2002).

Neurons in CIP have been found to maintain a short-term memory of 3D surface orientation (Tsutsui et al. 2003). This suggests a possible role of CIP in visual tracking and feature matching processes. For example, they might maintain memory of surfaces during active vision, for tracking suitable grasping surfaces.

2.3.1.1 Surface Orientation Selective and Axis Orientation Selective Neurons

Two main neuronal populations have been distinguished in CIP: surface orientation selective and axis orientation selective neurons. *Surface orientation selective* (SOS) neurons were first studied, and their responsiveness described, by Shikata et al. (1996). They respond to a 2D shape in different orientations, but extract the signal of 3D surface orientation from a 2D contour viewed in a linear perspective: i.e., these neurons interpret the stimuli as the silhouette of a square plate slanted in depth (Sakata et al. 2005). Experiments executed changing the proportions of the visual features showed that the responsiveness is maximum for "square" shapes, in which the two major dimensions are similar, and elongation in either width or length inhibits the response. Regarding the third, minor dimension, it seems not affecting the response up to a certain thickness, but if this threshold is overcome a clear decrease in responsiveness can be noted.

The second class of CIP neurons, *axis orientation selective* (AOS) neurons, represent the 3D orientation of the longitudinal axes of elongated objects. According to Sakata et al. (1998), their response increases with decreasing thickness (the two minor dimensions) and with increasing length (the major dimension), showing complementarity with SOS neurons. It is not clear from the provided data if the reduced responsiveness with thicker objects is only due to the relative proportion between the object dimensions or also by some comparison with the hand size. This issue will be discussed in Sect. 6.1.

Some AOS neurons are shape selective, and distinguish for example between cylinders and square columns of similar length and thickness. This suggests that disparity gradients are used in CIP to detect also the curvature of objects (Katsuyama et al. 2005; Naganuma et al. 2005; Sakata et al. 2005). Shape-selective AOS neurons in CIP are thus likely to maintain a prototype of 3D shape representation, as all curved surfaces can be characterized by a shape index and a curvedness index (de Vries et al. 1994).

2.3.1.2 Human CIP

The correspondence between monkey CIP and areas of the human intraparietal sulcus is still problematic, especially if compared with the rather well accepted interspecies matching of early visual and anterior intraparietal areas. Neuroimaging research showed nevertheless that a posterior region of the IPS activates for stimuli similar to those processed by CIP in monkeys, although human CIP seems to be located more medially in the human intraparietal sulcus than in monkeys, as stressed by Grefkes and Fink (2005). An area located in the posterior part of IPS and clearly involved in complex orientation discrimination and coding of 3D object features have been observed by Tsao et al. (2003). The authors call it *caudal parietal disparity region* (CPDR), and suggest that it might be part of the human correspondent of CIP. A similar responsiveness to stereopsis defined stimuli has been registered in other studies (Shikata et al. 2003; Brouwer et al. 2005). Activation in the posterior part of the human IPS has been found using fMRI during orientation discrimination tasks, for both monocular and binocular stimuli (Shikata et al. 2001; Naganuma et al. 2005). Although a clear correspondence is yet to be achieved, the data collected by Shikata et al. (2001, 2003) and other studies clearly indicate that, similarly to its role in macaques, the function of human CIP is that of coding 3D features of target objects for providing AIP with the information necessary for visually-guided hand movements.

2.3.1.3 CIP as a First Meeting Place for the Two Streams

Some findings (see e.g. the work of Tsutsui et al. 2003) suggest that the role of CIP might be more complex than just extracting object visual data and forwarding it to AIP. Memory related activity of CIP neurons indicates that this area might be involved in higher-order 3D visual perception. For example, visual areas V1/V4 do not have such sustained activity, whilst higher ventral stream area LOC has. There are also cues regarding direct connections between CIP and ventral stream areas. Firstly, CIP probably receives input from V4 (Baizer et al. 1991), and this would be the first connection between ventral and dorsal pathways after the splitting (see also Zanon et al. 2010). Moreover, some LOC neurons are selective for orientation and curvature of surfaces, but LOC receives most input from area V4, which is not sensitive to curved surfaces (Orban et al. 2006b). A link between CIP and LOC is the most likely explanation for such findings (Tsutsui et al. 2003). The first link, in the ventral → dorsal direction, could represent a ventral contribution to the process of pose and shape estimation in CIP. In fact, shape recognition allows to follow basic assumptions about objects' geometry and exploit common knowledge about the world in order to estimate size and pose of objects (e.g. to know that an object has square faces permits to use perspective in order to estimate its orientation). The dorsal → ventral link might instead accelerate object identification providing LOC with precise geometric information of local object features. Overall, 3D shape processing seems to possess a contextual nature, and on-line information is probably integrated with abstract representations in order to obtain the most likely interpretations of the visual data (Todd 2004).

Summarizing, CIP has a very precise 3D orientation response, probably obtained through the integration of disparity based, stereoptic cues (prevalent) and monocular, perspective cues. Overall, a population of mixed CIP neurons, including different types of SOS and AOS neurons, is able to provide full information about 3D proportion and orientation of a target shape. This information is forwarded to AIP, where 3D orientation and shape can be coded as a unique, combined feature, and possible *affordances* (see box below) can be generated.

The original definition of *affordance* was introduced to indicate any possible action that an agent can perform in the environment (Gibson 1979). An affordance is related to an object, or to a set of objects, and to the agent abilities. A grasping affordance exists only if a graspable object is present in the environment and if the agent is actually able to grasp it. In this book the term affordance is used with a restricted meaning, to refer to a grasping possibility offered by an object to the human or the robot hand.

2.3.2 Anterior Intraparietal Sulcus

The most frontal part of the IPS is the *anterior intraparietal sulcus*, AIP, sometimes called aIPS or, for humans, hAIP. Both for monkeys and humans, AIP is largely recognized as the area of the brain dedicated to the visuomotor transformations necessary to map visual stimuli onto hand configurations suitable for grasping target objects.

Several electrophysiological studies on macaques monkeys showed that AIP activates at the visualization of a possible target object, and remains active during preshaping and manipulation (Taira et al. 1990; Sakata et al. 1995; Murata et al. 2000). On the contrary, AIP is not explicitly involved in spatial analysis that is not related to action: e.g., it is not active during perceptual size discrimination, for 2D pictures, or for non-graspable objects.

Different AIP neurons are tuned to different objects, to different views of the same object, and to different grips. Although some AIP neurons are specific to one spatial aspect only, similarly to CIP's, axis orientation and shape are often represented as a combined 3D feature in AIP, an probably constitute the full coding of a graspable feature (Sakata et al. 2005). Moreover, some neurons in area AIP discriminate not only between simple solid shapes, but also between complex objects composed of two or more components. According to Sakata et al. (1999), these neurons may be sensitive to very small details critical for the selection of a grip pattern.

In Murata et al. (2000) a detailed description of experiments performed with several different conditions is provided. Neurons in AIP are found to be selectively activated according to shape (one or more of a set including ring, plate, cube, cylinder, cone and sphere), size and orientation of stimuli. Different activation patterns were observed during fixation and visually-guided grasping tasks. Again, selectivity for shape/size/orientation is often merged in a combined selectivity that can be identified as a grasp configuration.

2.3.2.1 Classification of AIP Neurons

Although AIP keeps active from object observation to the end of movement execution, some AIP neurons are selective for one of the following grasping sub-phases: set, preshape, enclose, hold, release (Ro et al. 2000; Debowy et al. 2001). This subdivision is much clearer though in the premotor cortex.

A better documented classification of AIP neurons in subpopulations can be done according to their preferential response in different acting conditions (Sakata et al. 1995; Murata et al. 2000). Three main types of AIP neurons were first classified, *visual* (V), *visuomotor* (VM) and *motor* (M), and the first two classes have been further subdivided into two, *object* (O) and *non-object* (NO), for a total of five neuronal classes:

object type visual-dominant neurons, O-V, respond equally to simple visual presentation (fixation) of graspable 3D objects and during visually-guided grasping actions; these neurons show no activity during grasping in the dark or when direct view of the ongoing action is unavailable;

non-object type visual-dominant neurons, NO-V, respond during visually-guided grasping only, and their activation starts just before hand-object contact; they show no activation during fixation and grasping in the dark;

object type visuomotor neurons, O-VM, are selective during fixation and during grasping actions both in the light and in the dark, but show a clear preference for visually-guided actions compared to fixation and grasping in the dark;

non-object type visuomotor neurons, NO-VM, are selective for grasping actions both in the light and in the dark, with a clear preference for visually-guided actions compared to grasping in the dark; they show no activation during fixation;

motor-dominant neurons, M, are equally responsive during grasping in the light and in the dark, showing no preferential activation between the two cases; they show no activation during fixation.

On a temporal scale, object type neurons, both O-V and O-VM start their activation at the sight of the target object, and seem thus to be in charge of planning the action, transforming the spatial visual information coming from CIP into a more purely grasp-related form. At the action onset and until the contact, visuomotor neurons, both O-VM and NO-VM, reach the top of their activity, revealing a crucial role in the execution of the hand preshaping movement. Neurons NO-V and M also increase their activity during action execution, NO-V neurons only if vision is available, M neurons also in the dark. All five types of neurons remain active during the hold phase until object release, but all of them show a gradually decreasing activation. In the dark, only VM and M neurons stay active, and for the first the responsiveness is reduced compared to the light condition. Hence, neurons in AIP are not only dedicated to plan and begin grasping actions, but also to monitor them during their evolution.

Regarding neural coding, it seems that object type neurons (O-V and O-VM) describe a shape-based representation of objects, whilst motor neurons (M) code for the hand configuration suitable for grasping. Non-object type neurons (NO-V and NO-VM) maintain a someway intermediate representation. Summarizing, it appears that the classification object/non-object/motor accounts for the transformations required to pass from a visual to a motor representation of the target object. The traditional visual/visuomotor/motor classification is more likely related to temporal aspects of action execution.

2.3.2.2 Human AIP

In humans, AIP is located at the junction between anterior IPS and inferior PCS (postcentral sulcus). Again, it is considered the most important area involved in the planning and monitoring of grasping actions. The coincidence with monkey AIP is rather uncontroversial, as many fMRI studies have been consistently showing grasping-related activation in the anterior part of the IPS for more than a decade (Binkofski et al. 1998; Culham et al. 2003; Cavina-Pratesi et al. 2007a). For detailed reviews of such studies, refer to Castiello and Begliomini (2008) and Tunik et al. (2007).

The most relevant difference between species is likely the absence of tactile response in macaque AIP (Murata et al. 2000), contrasted to the clear responsiveness during haptic exploration and purposive manipulation for human AIP (Jäncke et al. 2001; Grefkes and Fink 2005). In fact, AIP is increasingly activated during multimodal processing, suggesting that it might play a specific role in cross-modal transformations of object representation between visual and tactile modalities during grasping (Grefkes et al. 2002). Indeed, the current view of AIP as an associative "visual" area is probably biased by the amount of research on vision, and AIP might finally reveal itself to be as much tactile as visual (Roland et al. 1998).

In humans, AIP is preferentially activated during grasping with precision grips in comparison with full-hand power grips, suggesting a fundamental role in the fine calibration of finger positioning, as required in precision grip tasks (Ehrsson et al. 2000; Begliomini et al. 2007; Cavina-Pratesi et al. 2007b). AIP is probably involved also in controlling action execution by monitoring the difference between an efference copy of the motor command and visual and tactile sensory experience (Rice et al. 2006b). Various studies assign a more dynamic role to AIP beyond grasp planning. For example, transcranial magnetic stimulation of AIP ends in a clear disruption of online grasp control (Glover et al. 2005; Tunik et al. 2005), suggesting that the job of AIP is critical in the online monitoring/adjustment of hand movements.

There are also insights that AIP may execute more "cognitive" tasks and be connected to ventral stream regions. First of all, AIP and nearby areas respond to action recognition when grasping is involved (Fogassi et al. 2005; Shmuelof and Zohary 2005), indicating a more perceptual role than traditionally thought (Culham and Valyear 2006). Also, a region close to the intraparietal sulcus has been found active during object recognition from non-canonical viewpoints (Sugio et al. 1999). The authors suggest that recognition in those cases may be supported by information regarding functional properties of the object, extracted in the CIP-AIP circuit.

Other studies mention direct connections from the inferior temporal cortex to AIP (Fogassi and Luppino 2005; Borra et al. 2007) and other areas of the IPL, suggesting that AIP could use some ventral information in order to plan and execute appropriate grasping actions. Thus, after CIP, also AIP is probably connected, maybe even bidirectionally, to ventral areas, confirming the view that the collaboration between the streams is more strict than previously thought.

2.3.3 Ventral Premotor Cortex (PMv) and Other Motor Areas

The motor cortex occupies the posterior half of the frontal cortex. It is composed of anterior and posterior motor areas, the former connected to the prefrontal cortex, the latter to the posterior parietal cortex. Posterior motor areas can be further subdivided in the *primary motor cortex* M1 (also called F1), and premotor areas F2-F5. Area M1, upon reception of signals coming from the premotor cortex, activates and controls movements of specific body parts. The primary motor cortex is closely linked to corresponding areas in the primary somatosensory cortex S1, which in the case of grasping provides the tactile feedback necessary to adapt the grip to the inertial forces and the object structure (Rizzolatti and Luppino 2001).

A modern view of the organization, function and connectivity of the motor cortex has been proposed by Rizzolatti et al. (1998). The main concept is that the motor cortex is formed by a mosaic of separate areas containing independent body movement representations, which are used in motor control according to the requirements specified by corresponding areas of the posterior parietal cortex (Luppino and Rizzolatti 2000). Thus, parieto-premotor connections form a series of circuits devoted to specific sensorimotor transformations. Rizzolatti et al. (1998) define these circuits as the basic functional units of the motor system, which transform sensory information into action. According to the authors, although their hypothesis is mostly derived from monkey data, brain-imaging and anatomical evidence suggest that the same principles underlie the organization of the human motor cortex as well.

Two such circuits that have been clearly identified in monkeys connect ventral premotor areas F4 and F5 with intraparietal areas VIP and AIP respectively. The former circuit performs the sensorimotor transformations necessary for arm, neck and face movements, the latter permits the execution of hand and mouth movements, and is directly responsible for grasping actions (Luppino et al. 1999). Although their tasks are clearly related, these two circuits are described as anatomically segregated, suggesting a parallel processing between reaching and grasping actions, which are integrated only in the initial planning and the final execution phase, not in the intermediate sensorimotor transformation steps. In humans, kinematic and lesion studies support a parallel and concurrent parieto-premotor processing for reaching and grasping movements (Jeannerod 1997).

The literature description of F5 is consistent with its direct link with AIP. About half of F5 neurons can be considered visuomotor, as their activation begins during object fixation. Although their responsiveness is very similar to the visuomotor neurons of AIP (Murata et al. 1997, 2000), motor specificity of F5 neurons does not depend on the object shape but on the grip used to grasp the object (Raos et al. 2006). Additionally, neurons in F5 can code for full actions, such as grasping or pulling, and for action segments, such as preshaping or holding. Moreover, many F5 neurons are selective for one of precision grip (predominant), finger prehension or whole hand prehension (Rizzolatti et al. 1988). According to Rizzolatti and Luppino (2001), neurons in F5 code for spatial characteristics and temporal segments of grasping movements, hence constituting a vocabulary of motor prototypes to select and compose in the final action.

One of the most popularly known neuroscientific discoveries of the last decades concerns F5. This region is in fact the place where *mirror neurons* were observed for the first time (Di Pellegrino et al. 1992; Rizzolatti et al. 1996). Mirror neurons fire when the subject is performing a certain action, as normal premotor neurons of the same area, but also when the subject observes someone else performing the same action. They have been related to the ability of social interactions through understanding/prediction of other people's movements (Rizzolatti and Arbib 1998), to learning by imitation, and to the explanation of social behavior impairments as in autism (Williams et al. 2001).

The *ventral premotor cortex* (PMv) is still poorly characterized in humans. In fact, fMRI research failed to show consistent activation in the putative human equivalent of F5 during grasping movements (Castiello and Begliomini 2008). Nevertheless, PMv is still believed to play a key role in the preparation and execution of grasping actions. TMS studies showed its importance for grasping, and its task sharing with the *dorsal premotor cortex* (PMd) (Davare et al. 2006). Although the homology with macaque F5 remains controversial, there is a distinct evidence for a dissociation between PMv and PMd roles in controlling precision grasping in humans. Similarly to F5, PMv seems to perform the visuomotor transformations necessary to shape the hand to a target grip (Chao and Martin 2000), whilst PMd may control the correct timing of the action (Davare et al. 2006).

2.3.4 Other Dorsal Stream Areas

Consistently with the view of Sakata et al. (1997); Rizzolatti et al. (1998) and other studies (e.g. Buneo and Andersen (2006)), premotor-parietal circuits perform both direct and inverse coordinate transformation between vision and effector systems, to allow programming and monitoring of complex motor actions. The circuit linking AIP with F5 is not the only one necessary for the execution of accurate grasping actions, as proximal limb movements, eye and head coordination, and various posture movements are all required in order to allow the hand to perform a correct shaping sequence. Some other well-recognized areas of the posterior parietal cortex are briefly described below (for more detailed descriptions please refer to Culham et al. (2006) and Grefkes and Fink (2005)).

LIP is the *lateral intraparietal area*, also called *parietal eye field*, PEF and, for humans, hLIP or hPEF. Evidence for the role of this region in humans, and inter-species analogies are well recognized, although most studies indicate a more medial location of human LIP compared to monkey LIP. Area LIP aids in the execution of saccadic eye movements and transformation between retinotopic and head-centered coordinates (Grefkes et al. 2004; Scherberger and Anderson 2004; Sereno et al. 2014). Neurons in LIP have been found to be modulated by both proprioceptive and retinal stimuli, suggesting that LIP contributes to distance estimation combining vergence and disparity through a gain modulation effect (Naganuma et al. 2005; Genovesio and Ferraina 2004).

VIP is the *ventral intraparietal area*, involved in head movements coordination and near-head space analysis. Area VIP receives strong input from the motion selective area MT and responds to optic flow, detecting movements in head-center coordinates during self-motion (Bremmer et al. 2001). It is also likely that VIP contributes to multimodal integration in the dorsal stream, as it is activated by visual, tactile and auditory stimuli, showing congruent receptive fields across modalities (Bremmer et al. 2002; Lewis and Essen 2000). Although many of its properties have been observed in human cortical areas, consistent data are not yet available for defining a clear human correspondent of monkey VIP.

PRR is the *parietal reach region*, the area of the PPC dedicated to perform the reference-frame transformations and the sensorimotor coordinations necessary for pointing and reaching movements (Grefkes et al. 2004). Most probably, PRR performs also a monitoring of ongoing actions and adjust them according to an efference copy of the motor signal (Kalaska et al. 2003; Gréa et al. 2002). In monkeys this area is quite well circumscribed, it includes MIP—the *medial intraparietal sulcus*—and visual area V6A. On the other hand, pointing and reaching movements in humans seem to involve several disjunct areas of the superior parietal lobe, such as: V6A (Pitzalis et al. 2013), MIP/mIPS (medial intraparietal sulcus, Reichenbach et al. (2014)), PCu (precuneus) and POJ (parieto-occipital junction); the exact purpose of the movement (reaching vs. pointing) and the position of the target (central vs. peripheral vision) are among the factors that differentiate the cortical activation (Grefkes et al. 2004; Davare et al. 2012).

2.4 Object Recognition and Stream Integration

Compared to early visual areas, neurons in higher order areas such as V4 and the LOC have larger receptive fields, and can integrate information across long distances in the visual field (Grill-Spector et al. 1998; Bullier 2001). Object areas along the ventral stream can thus represent visual stimuli with increasingly complex and invariant representations.

2.4.1 The Lateral Occipital Complex

The *lateral occipital complex* (LOC) is the region of the human brain in which viewpoint invariant object representation for immediate visual recognition is performed (Grill-Spector et al. 2001). The LOC receives high level visual input from V4 and integrates visual elements that share similar attributes of orientation, color, or depth into objects and extract them from the background (Grill-Spector 2003). Object representation in LOC is highly invariant with respect to the stimulus type, showing equally good performances with either 3D or silhouette images, different color maps, lightning and so on. This suggests a higher level, conceptual representation of objects, independent of the actual stimulus that allowed recognition (Kourtzi and Kanwisher 2000).

The LOC is constituted by two different areas, anterior and posterior, which seem to maintain slightly different object representations (Malach et al. 2002). The anterior or ventral part is called *ventral temporo-occipital* area (vTO/VOT, Grill-Spector 2003), but also *posterior fusiform* (pFs, Kourtzi et al. 2003), and responds more invariantly to position and size, suggesting a volumetric 3D object representation (Moore and Engel 2001). The posterior area, the *lateral occipital cortex*, LO, is instead more invariant to the orientation of 2D shapes and to illumination changes. Similar subdivisions have been found in the monkey *inferior temporal* cortex IT (Janssen et al. 2000; Gattass et al. 2005). The *occipito-temporal transition* TEO, which shows a highly invariant response to object identity, is the most likely correspondent of human LOC (Webster et al. 1994; Denys et al. 2004). Although these findings need to be completed and clarified, they suggest a possible mechanisms for object identification and recognition which involves both structural and image-based processing (Tarr and Bülthoff 1998). Object recognition would be achieved integrating, through feature correlation and saliency maps, a partially viewpoint-dependent 3D information (from vTO) with a silhouette classification performed by LO (Kourtzi and Huberle 2005). This solution would solve the long-standing issue on the nature of object recognition, confirming the validity of both the multiple view object representation model (Bülthoff et al. 1995) and the viewpoint invariance hypothesis (James et al. 2002).

Thus, the assumption that ventral stream object representations should be highly viewpoint invariant would not collide with findings suggesting that in active object exploration for recognition subjects search for "preferred" views (James et al. 2001). Similarly, the integrated model would partially explain why 3D orientation response in V4—compatible with both viewpoint dependent and viewpoint invariant models (Hinkle and Connor 2002)—is stimulus-dependent (Hegdé and Essen 2005). On the other hand, object recognition is very likely a gradual process rather than a binary one. Bar et al. (2001) and Grill-Spector et al. (2000) observed that activation in the anterior LOC is modulated by the actual level of recognition, and not by the nature of the stimulus. In any case, geometric data are integrated with additional information, regarding for example color and texture of objects, to speed up and make object recognition more reliable (Humphrey et al. 1994).

Regarding possible connections of ventral stream areas with the intraparietal sulcus, a direct link has been found in the macaque brain between the most 3D responsive ventral inferior temporal area (the lower bank of the superior temporal sulcus) with CIP (Janssen et al. 2000). This link could indicate both a ventral contribution to pose estimation and a dorsal help in object recognition, as explained in Sect. 2.3.1.3.

2.4.2 Other Brain Areas Involved in Grasping

Several areas of the brain not belonging to the two streams are involved in the preparation and/or execution of vision-based grasping actions. A brief description of some very important ones is provided below.

Somatosensory cortex. Located in the anterior part of the parietal cortex, just behind the central sulcus, it is composed of the *primary somatosensory cortex* SI, the equivalent of V1 for the sense of touch, and the secondary somatosensory cortex SII. The former is active in correspondence to any tactile stimulation on the body, the second performs an elaboration of the sensory input in order to detect more complex patterns such as roughness, hardness, compliance estimation in hand haptic exploration (Reed et al. 2004; Newman et al. 2005). Activation of somatosensory areas during grasping is consistently observed (see e.g. Ehrsson et al. 2000; Gardner et al. 2002; Begliomini et al. 2007) and, for what concerns the spatial aspects of grasping and manipulation, higher level processing of tactile information is very likely performed by AIP and nearby areas (Roland et al. 1998).

Prefrontal cortex. The basic role of the prefrontal cortex, PFC, is the organization and orchestration of thoughts and actions in accordance with internal goals and attentional mechanisms (Lebedev et al. 2004). In the specific case of grasping, the PFC is believed to mediate action selection with information on the specific task to perform (Passingham and Toni 2001; Johnson-Frey et al. 2005).

Basal ganglia. Although much is still unrevealed regarding the exact function of this ancient part of the brain, the basal ganglia are probably involved in mediating between rival perceptions and/or competing motor actions. Both area AIP and the ventral premotor cortex receive inputs from the basal ganglia, but from non-overlapping regions, suggesting that they use different selection/evaluation signals that can be used in deciding among candidate target features or hand configurations in grasping (Clower et al. 2005).

Cerebellum. The function of the cerebellum is still under debate. Nevertheless, its involvement in the coordination of action execution and in adaptive sensorimotor control is well recognized (Ramnani et al. 2001; Barlow 2002). In particular, it has been argued that the cerebellum is where internal forward models, largely used in sensorimotor control, are located (Kawato et al. 2003). The cerebellum has an important common feature with the posterior parietal cortex, as both play a role in sensorimotor prediction, more during action execution for the cerebellum, more planning-related for the parietal cortex (Blakemore and Sirigu 2003). Moreover, a considerable component of cerebellar output is devoted to influencing the functional operations of posterior parietal cortex, and neurons of the cerebellum that project to AIP overlap the output channel to the PMv, indicating the existence of a three-way circuit AIP-PMv-Cerebellum (Clower et al. 2005; Tunik et al. 2005).

2.4.3 The Visual Streams in Action

The underlying idea of the original two streams theory (Goodale and Milner 1992; Milner and Goodale 1995) is that visual information has direct control over action in the dorsal stream, without any intervening mental representations. According to this view, neural activity in the dorsal stream does not reflect the representation of objects or events, but rather the direct transformation of visual information into the required coordinates for action. As stated by Jeannerod et al. (1995): “object attributes are processed differently according to the task in which a subject is involved. To serve object-oriented action, these attributes are subjected to a pragmatic mode of processing, the function of which is to extract parameters that are relevant to action, and to generate the corresponding motor commands”.

A basic assumption of the processing dualism is that the ventral stream makes use of a contextual coding system for size, distance and orientation of objects, while the dorsal stream needs “real-world” metrics to properly interact with the environment. The patterns of activity of LOC, AIP and other areas of the two streams strongly support this hypothesis, confirming the contrast between the *conceptual* and the *pragmatic* ways of processing of the two streams.

On the other hand, there is a growing experimental evidence for multiple interaction between the streams (Zanon et al. 2010; Verhoef et al. 2011; Perry et al. 2014; Wokke et al. 2014). The original theory has to be constantly updated and suited to new findings (Goodale and Haffenden 2003; Goodale and Westwood 2004; Goodale 2008; Cloutman 2013). For what concerns grasping, there is probably a ventral stream contribution to the grip selection process, through semantic knowledge and memories of past events (Goodale and Milner 2004). Human research demonstrated that choosing a grip depends not only on its visual properties, but also on the meaning we attach to it (Creem and Proffitt 2001; Tankus and Fried 2012) (ventral stream data) and the expected task consequent to the grip (Ansuini et al. 2006; Ikkai et al. 2011) (prefrontal cortex data).

As mentioned in Sect. 2.1.1, visual agnosia patient DF shows normal grasping abilities, as her dorsal stream correctly computes grasping parameters. Nevertheless, her grips on tools are functionally inappropriate, as she does not identify the target object due to her damaged ventral stream, at least until haptic exploration allows her to properly recognize the object (Goodale and Milner 2004). It looks as the decision on exactly "where" to grasp the object can be taken independently from the ventral stream, but with no selection of the object feature or part more suitable for the interaction with the hand, as any semantic meaning of the action is extraneous to the dorsal stream. Moreover, DF cannot scale her grip aperture properly when she has to grasp an object that was removed from view only two seconds earlier (Goodale et al. 1994). According to the authors, this is likely due to the need of accessing object memories stored in, or accessible through, the ventral stream. Patients with optic ataxia exhibit the opposite pattern, as their grasping performances improve if a delay is introduced between target presentation and movement onset, suggesting that memory-mediated action are likely to use different mechanisms in which the dorsal pathway is less critical (Milner et al. 1999, 2001). Psychophysical experiments on delayed grasping in different conditions with normal subjects support the idea that memory-guided grasping relies on the processing of stored information shared with the perception-based ventral system (Singhal et al. 2007).

2.5 The *Third* Stream of Visual Processing

As explained above, AIP is the cortical region in which visual information is used to code an appropriate grasping configuration for a target object, and the detailed parameters of the selected action are determined by processing in the dorsal stream. Nevertheless, action selection is very likely aided by visual processing in the ventral stream. For example, a full object description might be necessary for specifying grip and load forces through estimation or recall of the object weight. Such representation could be used also to avoid grasping objects that can not be grasped, because they are heavy, uncomfortable to handle or even dangerous (Goodale and Humphrey 1998; Westwood et al. 2002).

Considering possible different acting conditions, although some basic grasping movements may be made without the influence of the context or any top-down visual knowledge (Goodale and Milner 2004), in most cases parietal grasp selection is probably driven top-down by semantic information, especially for tools and well known objects (Creem and Proffitt 2001; Frey et al. 2005). In support of this view, Sugio et al. (2003a) showed that different brain areas activate depending on the familiarity with the object, confirming that AIP elaboration is less critical if the object is well known, suggesting that in these cases the ventral stream does most of the job and the action is mainly memory-driven. Other findings (Himmelbach and Karnath 2005) suggest that, although there may be a dramatic shift between the dorsal and ventral systems instantly after the target has disappeared, there also seems to be a progressive change depending on the time delay between target presentation and movement onset.

The above described interaction mechanisms between the streams might be explained by the existence of a so called "third pathway" (Rizzolatti and Matelli 2003; Hoeren et al. 2013). In fact, it has been proposed that the areas of the posterior parietal cortex constituting the classical dorsal pathway should be subdivided into two different sub-systems separated by the intraparietal sulcus (Fogassi and Luppino 2005; Jeannerod and Jacob 2005; Kravitz et al. 2011; Binkofski and Buxbaum 2013). Areas of the *superior parietal lobe* above the IPS, would perform the sensorimotor transformations traditionally assigned to the dorsal stream, related to the online analysis of visual data aimed at generating suitable motor reactions. The second system would contain the *inferior parietal lobe*, below the IPS, including AIP, LIP and regions that seem to be especially human and not matched by structures in other primate's brains (Rushworth et al. 2006). These areas would be dedicated to higher level visuomotor representations, such as those related to the mirror system, which seems to include this part of the PPC (Rizzolatti and Craighero 2004). Indications for a cognitive role of the IPL (and especially AIP) beyond the traditional pragmatic processing have been put forth by several studies (Gallese et al. 1999; Chao and Martin 2000; Derbyshire et al. 2005; Culham and Valyear 2006; Hamilton and Grafton 2006; Durand et al. 2007; Tunik et al. 2007; Schintu et al. 2014). According to this view, a grasp for AIP is a sensorimotor transformation from visual information about the object to motor commands for grasping the object, but also a meaningful action that puts in relation the agent with a feature of the environment. The new, ventro-dorsal stream of the inferior parietal lobe would constitute an ideal convergence focus for the integration of conceptual ventral information with traditional online dorsal data (Rozzi et al. 2006; Gallese 2007). More research is though needed to assess and develop this hypothesis.

This chapter introduced the main neuroscience concepts which will be used and referred to throughout the book. Additional details regarding functions and connectivity of brain areas useful for modeling purposes will be provided in the next chapters.

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