

A focus on the multiple interfaces between action and perception and their neural correlates.

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ABSTRACT

Successful behaviour relies on the appropriate interplay between action and perception. The well-established dorsal and ventral stream theories depicted two distinct functional pathways for the processes of action and perception, respectively. In physiological conditions, the two pathways closely cooperate in order to produce successful adaptive behaviour.

As the coupling between perception and action exists, this requires an interface that is responsible for a common reading of the two functions. Several studies have proposed different types of perception and action interfaces, suggesting their role in the creation of the shared interaction channel. In the present review, we describe three possible perception and action interfaces: i) the motor code, including common coding approaches, ii) attention, and iii) object affordance; we highlight their potential neural correlates. From this overview, a recurrent neural substrate that underlies all these interface functions appears to be crucial: the parieto-frontal circuit. This network is involved in the mirror mechanism which underlies the perception and action interfaces identified as common coding and motor code theories. The same network is also involved in the spotlight of attention and in the encoding of potential action towards objects; these are manifested in the perception and action interfaces for common attention and object affordance, respectively. Within this framework, most studies were dedicated to the description of the role of the inferior parietal lobule; growing evidence, however, suggests that the superior parietal lobule also plays a crucial role in the interplay between action and perception. The present review proposes a novel model that is inclusive of the superior parietal regions and their relative contribution to the different action and perception interfaces.

1. Introduction

Despite the close functional relationship between action and perception, they have been treated as separate entities for a long time. Several kinds of experimental evidence suggest that visual information related to perception and action is processed by two distinct functionally- and neuro-anatomically-defined pathways. In visual processing the classic distinction has been made between object “what” versus spatial “where” information (Ungerleider and Mishkin, 1982). Goodale and Milner (1992) reframed this “two visual systems theory” by redefining the roles of the two visual systems, highlighting the distinction based on the goals of awareness/recognition (“what”) versus visuomotor control (“how”). The two visual systems theory posits that visual processing

subserving action is carried out by the dorsal stream, stemming from visual occipital area V1 and projecting through visual association areas, the middle temporal cortex, and the middle superior temporal cortex to the posterior parietal cortex (PPC). The visual processing subserving perception of the spatial environment is carried out by the ventral stream, starting from V1 to visual association areas to the inferior temporal cortex. Functionally, the dorsal stream relies on fast, unbiased, egocentric processing of the spatial environment (Adam et al., 2016; Ferber et al., 2005), whereas the ventral stream is slower, subserves the formation of spatial representations in memory, and may use non-egocentric reference frames (Adam et al., 2016; Buneo and Andersen, 2006). However, Milner and Goodale proposed a revision of their perception/action model suggesting that programmed and coordinated

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behaviours, such as the act of prehension, require the ventral and dorsal streams to work together through reciprocal cross-connections between areas in the two streams (Milner and Goodale, 2006), and extensive anatomical evidence corroborates this hypothesis (Borra et al., 2008; Felleman and Van Essen, 1991; Gamberini et al., 2009). More recently, Goodale and Milner (2018) reinforced the vision that dorsal and ventral streams must work together in the generation of adaptive behaviours notwithstanding the original evidence that Patient D.F. who had visual form agnosia (ventral stream damage) was able to perform pointing and grasping actions compared with visual stimuli discrimination tasks (Goodale et al., 1991; Milner et al., 1991). In fact, the proposed revision of the perception and action model above is complemented by experimental findings regarding the access of the motor system in perception for an integrated perception-action coupling (Hommel et al., 2001; Schütz-Bosbach and Prinz, 2007; Viviani, 2002); it is also validated by and the evidence that the dorsal pathway contributes uniquely to the perception of several visuospatial properties that are not redundant with the representation in the ventral cortex (Freud et al., 2016, 2020). It is therefore interesting to mention which visuospatial attributes are processed by the dorsal visual stream. The first visual attribute is the processing of depth information which was documented in many studies in both human and non-human primates (Orban, 2011; Orban et al., 2006). These studies showed dorsal stream responses to depth information induced by monocular (Georgieva et al., 2008; Nelissen et al., 2009; Vanduffel et al., 2002) and binocular cues (Georgieva et al., 2009; Janssen et al., 2000; Yoshioka et al., 2021), and responses to the global 3D structure of the objects (Freud et al., 2015, 2017b). The second is the orientation of a stimulus, in fact damages to the parietal cortex results in impairments in the ability to process orientation and mirror-orientation of stimuli (Martinaud et al., 2014, 2016). Also Imaging studies in healthy participants also revealed that the dorsal pathway, and not the ventral one, is sensitive to the orientation of objects and to mirror transformation of the scenes (Dilks et al., 2011; Valyear et al., 2006). The third visual attribute is represented by the perception of object motion: that is a relevant cue when perceiving objects in 3D, naturalistic environments. Regions of the dorsal pathway are activated by 3D information and by motion cues (Erikhman et al., 2018). The fourth attribute is the shape perception of shape, which was classically attributed to the ventral pathway. In fact, early neuroimaging studies revealed shape-selectivity in the lateral and posterior fusiform cortices within the ventral occipitotemporal pathway (Grill-Spector et al., 1998; Malach et al., 1995), but later studies showed shape selectivity in the parietal cortex associated with attentional mechanisms (Chao and Martin, 2000; Mruczek et al., 2013). More recently, shape selectivity was found in multiple regions of the dorsal pathway for non-tool objects (Bracci and Op de Beeck, 2016; Freud et al., 2017a), for novel objects with no semantic associations (Freud et al., 2015; Konen and Kastner, 2008), and even for 2D line drawings of objects or basic shapes (Konen and Kastner, 2008; Sereno and Maunsell, 1998). The shape representation in the dorsal pathway is not uniform across the parietal cortex (Kravitz et al., 2011), but it follows a representational gradient, with greater shape sensitivity in more posterior regions compared with the anterior regions that are more tuned to visuomotor processing (Freud et al., 2017a). Furthermore, the dorsal shape representations are more adaptive than the ventral representations, and they reflect task demands. For example, fMRI activations due to object categories observed in the dorsal region decreased when participants executed a task that was unrelated to the objects, whereas the ventral regions showed activations that were unrelated to the task (Vaziri-Pashkam and Xu, 2017, 2019; Xu, 2018). Another example related to the task-dependent object representation comes from Bracci et al., (2017), where they found that the human parietal cortex (the dorsal pathway) does not preferentially represent particular object properties, but, together with the frontal regions, represents task-relevant object properties. Conversely, Ayzenberg and Behrmann (2022) suggested that the ventral pathway does not represent the global shape of objects, but represents objects as a set of local image

features. Despite this evidence, the causal involvement of the ventral pathway in object recognition is not questionable. In fact, humans are able to recognize familiar objects from small image patches (Holzinger et al., 2019; Ullman et al., 2016). However, these results suggest a broader network for shape perception that includes the dorsal pathway. While it is clear that perceptual processes occur in both dorsal and ventral pathways, there is still the open question of which interface allows the interaction between action and perception and the corresponding neural substrates. One of the most influential theoretical views refers to the motor codes applied in the common coding approach (Prinz, 1997), in which perceived events and planned actions share a common representational domain. Within this view, the actions are coded in terms of their perceptual consequences. In themselves, these cognitive codes are neither perceptual nor motor in nature (Musseler, 1999), but are connected to motor and perceptual codes.

Schneider and Deubel (2002) and Rizzolatti and Craighero (1998) considered attention as the interface between action and perception. According to their view, the planning of an action leads to increased attention to action-congruent features. Mirror neuron data (Gallese et al., 1996) places this interface in the premotor cortex. The affordance view, on the other hand, considers that the affordances of objects automatically activate associated motor processes to interact with them (Gibson, 1979; Tucker and Ellis, 1998; Witt and Proffitt, 2008). The present review summarizes the most relevant components considered as the interface between action and perception, such as motor codes together with common coding, attention, and object affordance, and their corresponding neural correlates. Moreover, particular focus is given to the functional properties of area V6A located in the superior parietal cortex (SPL) of the macaque and human brain. The majority of studies have focused on the role of the anterior parietal cortex (AIP) located in the inferior parietal lobule (IPL), a crucial area for the interplay between action and perception (Goodale and Milner, 2018). However, as area V6A is reciprocally connected with area AIP (Borra et al., 2008; Gamberini et al., 2009, 2021; Passarelli et al., 2011), and given its relevant role in reach-to-grasp actions, a function requiring the interplay of the dorsal and ventral stream as originally suggested by Milner and Goodale in 2006, we propose a novel model of action and perception, highlighting the degree of contribution of the SPL in the different identified interfaces. This framework becomes more inclusive and broadens the view on other brain regions of the dorsal stream that are dynamically involved in action and perception coupling; this coupling changes according to task requirements. Fig. 1 shows a diagram of the perception and action system, considered as both distinct and integrated.

1.1. Motor codes for perception and common coding for perception and action

The recruitment of the motor system or of the motor competences represents the core of the motor theories of perception. The first theory was Lieberman's motor theory of speech perception (Lieberman et al., 1967), originating from the observation that people perceive spoken words by identifying the vocal tract gestures with which they are pronounced rather than the sound patterns generated by that speech. Although strongly debated, Lieberman's motor theory of speech perception inspired other research fields that found the involvement of motor codes in perception such as the theory of common coding of action and perception (Hommel, 2019; Hommel et al., 2001; Prinz, 1997). Since the most important development of the motor code approach is represented by the common coding theory for action and perception, from this point on, only this latter theory will be described. It starts from the idea that action and perception occupy a common representational domain (Hommel, 2019; Hommel et al., 2001; Prinz, 1997). As reported in the Introduction, the common domain or the common code reflects the perceptual events that the actions produce. The first description of the common coding approach comes from Prinz (1997), and is reported

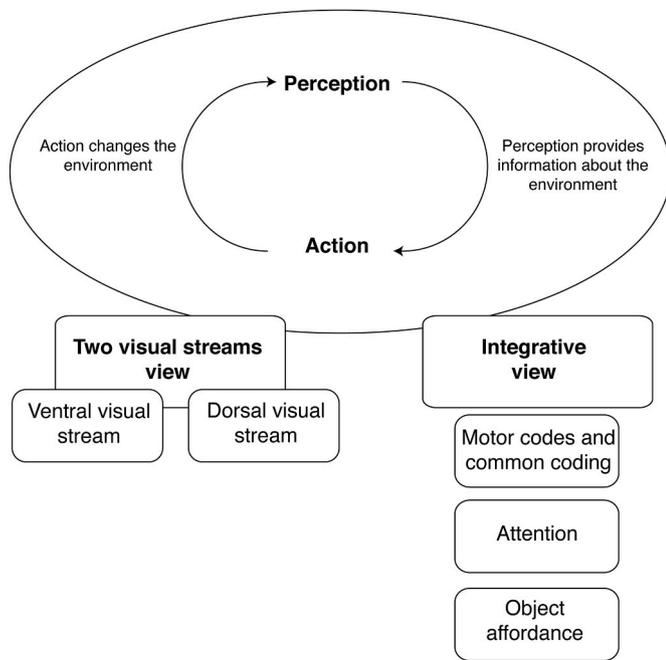


Fig. 1. General schematic diagram of the two views that describe the action and perception channels as distinct (left) or integrated (right).

in Fig. 2. The lower part of Fig. 2 (continuous lines) shows the two main components of perception and action control. The afferent part is reported on the left and is bottom-up, indicating the events in the environment that lead to patterns of stimulation in sensory organs and generate sensory codes in the brain. The efferent part is reported on the right with the activity occurring in a top-down manner. These signals start with motor codes in the brain that represent patterns of excitation in the peripheral effector organs and are able to activate them. Once they receive the input, the muscles contract or relax and the organism acts in a certain way (Prinz, 1997). At this point, there is sensory stimulation on one side and muscle activation on the other: two codes that are not able to interact with each other directly. The communication between the two is made possible only by some transformation or

translation, and is represented by the joint area between event code and action code at the top of Fig. 2. A typical illustration of this can be found in a reaction time experiment in which the participant has to press one of two keys with either their left or right hand in response to one of two lights (e.g., red or green). In this example, the sensory codes represent the two colours and the motor codes represent the two hands. This requires a translation of the codes for colours into codes for the muscles controlling the two hands. Over the last three decades, the translation process has been described as a series of internal operations underlying the mapping of the response to stimuli (Massaro, 1990; Sanders, 1980; Welford, 1968).

Another example that explains common coding for action and perception is that of two people sitting opposite each other at a table. The table has a cup and a jar of coffee on it. If one person picks up the jar and pours coffee into the cup while the other person watches the action, both people have a very similar representation of the action according to the common coding theory. This example indicates that perception and action use a common representational domain and this suggests that observing an action that one is capable of performing may activate the corresponding action representations (van der Wel et al., 2013).

1.1.1. Neural correlates of the motor codes and common coding for perception and action

The common coding theory for perception and action is a functional theory that does not make particular predictions about the corresponding neural correlates. The recruitment of the motor system in the perception of objects on which some type of action is to be executed is the study of movement intention; this represents a crucial issue in the study of the PPC in the monkey model (Andersen and Buneo, 2002). In 1985, Goldberg and Bruce reported that the neurons recorded in the PPC showed enhanced visual activity whenever the animal attended to a stimulus, both when it responded with a saccade and when it did not (Goldberg and Bruce, 1985). Conversely, in the FEF area, the enhanced neural activity was visible only when the animal responded to the stimulus with an eye movement. The results of Goldberg and Bruce (1985) suggested that the PPC is involved in the attentional processes in a way that is not strictly correlated with the eye movement (as in the case of FEF), but with the selection of significant stimuli (i.e., relevant for action). Snyder et al. (1997) conducted an experiment designed to separate the effect of spatial attention from the intention. In this study,

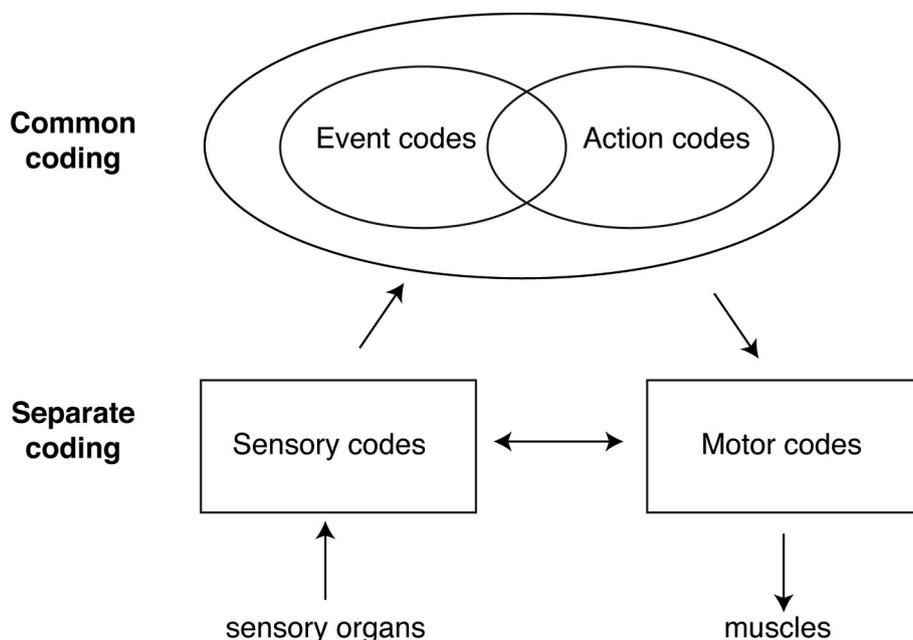


Fig. 2. The common coding approach. Bottom, separate coding of sensory and motor codes and their translation. Top, Common coding of event and action codes.

the animals attended to a flashed target and planned a reaching movement or a saccade to it. They recorded the neural activity from the IPL (the lateral intraparietal area (LIP)) and from the SPL (the parietal reach region (PRR)). They found that, during eye movement planning, the IPL was more activated than the SPL, and the reverse occurred during the planning of the reaching movement. They concluded that the prominent role of the PPC was in the planning of movements of specific effectors (Snyder et al., 1997; Andersen and Buneo, 2002).

However, increasing neurophysiological evidence consistent with the common coding theory is rapidly accumulating. The finding of mirrorneurons in the premotor and parietal cortex of the macaque monkey has represented a possible neural correlate of the common code theory (Rizzolatti and Craighero, 2004). In fact, mirror neurons discharge when an object-directed action is performed but also when an action is perceived (Rizzolatti and Craighero, 2004; van der Wel et al.,

2013). A variety of studies investigated the role of mirror neurons in parieto-frontal circuits in monkeys (Bonini et al., 2010; Caggiano et al., 2009; Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti and Sinigaglia, 2010) and humans (Iacoboni et al., 2005; Mukamel et al., 2010). In particular, the mirror neuron system can be referred to as two principal hubs: the frontal lobe and the IPL. This type of neuron was first discovered in area F5 of the ventral premotor cortex of macaques (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1997), where neurons that are responsive to the presentation of an object as the monkey grasps it are also present (Murata et al., 1997; Raos et al., 2006). Area F5 is active during both the observation and execution of specific goal-directed actions involving the hand and the mouth (Ferri et al., 2015) due to the coexistence of motor and mirror neurons. Mirror properties were also discovered in the IPL of the macaque brain (Rozzi et al., 2008). Mirror neurons in the parietal area PF/PFG of the IPL also

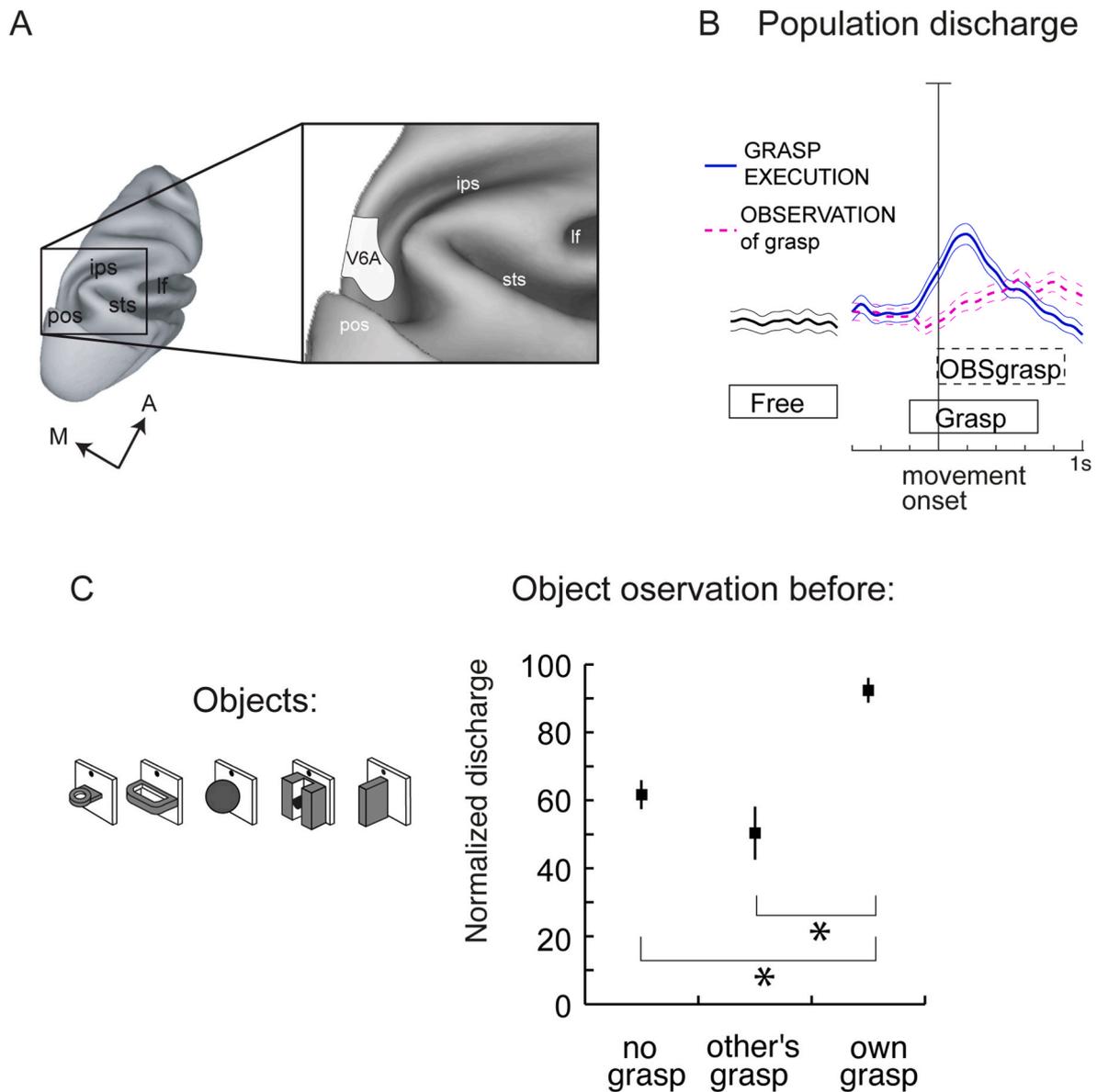


Fig. 3. V6A location in the macaque brain and functional properties. **A**, Dorsolateral view of the macaque right hemisphere: area V6A is shown in white in the enlargement square. Pos, parieto-occipital sulcus; ips, intraparietal sulcus; sts, superior temporal sulcus; lf, lateral fissure; A, anterior; M, medial. **B**, Population discharges (N = 23), expressed as averaged spike density functions. Continuous blue lines indicate the average neural activity recorded during grasping execution and Dashed magenta lines indicate the activity during the observation of the experimenter's grasping. **C**, *Left*, Image of the five objects shown to the monkeys. *Right*, Average activity of putative mirror neurons during object observation in passive observation (no grasp), before other's grasp (other's grasp), and before own grasp (own grasp). Asterisks indicate significant differences (post hoc test, Bonferroni corrected, $p < 0.05$). Error bars are the standard errors. The neural discharges in reaction to object vision are deeply modified according to the action context to which the same object belongs. Figure modified from Breveglieri et al. (2019).

discharge during both observation and execution of complex actions such as grasping an object to place it at a target location or to eat it. Additionally, the firing activity is modulated by the final goal of the action (Bonini et al., 2010). The IPL receives visual information from the eyes and somatosensory information from the mouth, hands, and arms (Rozzi et al., 2008). This suggests that the visuo-motor organization of the IPL may build the neural basis of the ability to understand the intention of others' actions (Fogassi and Luppino, 2005). A recent study investigated the effect of grasp execution and observation of others' grasping on the activity of neurons in an area of the SPL belonging to the reach-to-grasp network, the medial parietal area V6A (see Fig. 3A) (Breveglieri et al., 2019). This area contains a large number of neurons that code for the execution of one's own grasping but do not respond to the observation of the same action performed by others. This means that most V6A cells easily discriminate one's own actions from the actions of others. A small subset of V6A neurons (20%) discharge during both grasp execution and the observation of another's grasping, apparently complying with the original definition of mirror neurons (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1997). It must however be highlighted that the incidence of mirror neurons in V6A is much lower than in the IPL or in ventral premotor cortex. Fig. 3B reports the population activity for executed and observed grasps. Unlike the classic mirror neurons that were originally described (Gallese et al., 1996), V6A neurons showed little or no correspondence in the discharge between the executed and observed actions, both at a single-cell level and at the population level. Interestingly, in V6A, the neural representation of an object changed according to whether grasping was allowed/performed or whether the object was the target of another agent's grasping. Fig. 3C shows the different encoding of the object at the neural population level when the object is seen outside or within the action context: V6A neurons appear to primarily code the relevance of the target object in the grasping context rather than another agent's observed action (Breveglieri et al., 2019). From Fig. 3C it is evident that the V6A activity was stronger when the monkey observed the object before its own grasp and weaker when the same object was observed with no grasping required (no grasp) or before the other's grasp, suggesting that action planning increases the visual response evoked by object observation (Breveglieri et al., 2019). This is a clear demonstration, at a neuronal level, that object encoding, at least in the SPL, may depend on subsequent actions on the objects. In other words, it is a demonstration that in the SPL there is one interface between action and perception. The different encoding of mirror neurons of object shapes in different ways according to the action context is, in our opinion, a clear example of the interplay between the two visual systems, in which the inferior and superior parietal lobes demonstrate a different contribution.

1.2. Attention

Another candidate for an interface between perception and action is related to attentional mechanisms. A large body of evidence deriving from different experimental paradigms supports attention processes playing a prominent role in visual perception (Pashler, 1997; Schneider and Deubel, 2002), since a limited amount of information present in the retina can be processed up to the level of conscious availability. For example, studies on the change blindness paradigm (Rensink, 2000; Simons and Levin, 1997) have shown that a small number of objects from a natural scene can be monitored in order to detect changes. Given this limitation of conscious visual perception, selection processes are required.

A second function of attention, called "selection for action", refers to the action domain (Allport, 1987). The basic idea is that natural environments contain many potential targets for motor actions. But motor actions (i.e., grasping or pointing) are typically directed towards only one target at a time. Therefore, a selection process is required to provide information regarding the spatial features of the intended target object (its location, size, shape, etc.), about the motor system, and to

discriminate information from other objects for motor control (Allport, 1987).

The "Visual Attention model" (VAM) (Schneider, 1995) combines the selection for perception and the selection for spatial motor action in a common attention mechanism which selects one object at a time for high priority processing (Schneider and Deubel, 2002; Schneider, 1995). This attentionally mediated coupling of selection for perception and spatial motor action predicts, at a behavioural level, that, during the programming phase, the preparation of a spatial motor action binds the perceptual processing system to the movement target and its location. In other terms, the perceptual representation of the external world during movement preparation should be the most appropriate for the movement target, and the intention to attend to a certain object for perceptual analysis should lead to the implementation of motor programs towards this object.

An alternative theory is that selective attention does not result from a control system that is separate from sensorimotor circuits, but derives from the activation of the same circuits that, in other conditions, determine perception and motor activity (Rizzolatti and Craighero, 1998). This is the so-called "premotor theory" of attention formulated by Rizzolatti and Craighero (1998) based on neurophysiological data, and by Rizzolatti et al. (1987) based on psychological findings. According to this theory, spatial attention derives from an endogenous or exogenous activation of cortical pragmatic maps, that is, of those maps that transform spatial information into movements. When one of these maps becomes active there are two consequences: i) an increase in the readiness to respond, at a motor level, to some spatial sectors; ii) a facilitation in processing stimuli coming from that spatial sector towards which the motor program, controlled by the pragmatic map, was prepared (Rizzolatti and Craighero, 1998). The crucial assumption is that in humans and higher mammals, there is a phase in which motor programs are planned and not executed. This phase, which occurs in response to an exogenous stimulus or endogenously, is what can be defined as spatial attention.

1.2.1. Neural correlates of the common attention for perception and action

In primates, selection signals for visual spatial attention originate in high-order areas of the prefrontal cortex (PFC) (Bichot et al., 2015; Ma et al., 2012; Rossi et al., 2007; Tremblay et al., 2015) where task demands and multiple sources of information are integrated in non-retinocentric frames of reference. These selection signals are translated into retinocentric signals, perhaps in the lateral intraparietal area (Andersen et al., 2004; Bisley, 2011; Buschman and Kastner, 2015), and conveyed to the frontal eye field (FEF), a gaze control area of the PFC. The FEF encodes spatial information into retinocentric coordinates (Joiner et al., 2017; Moore and Zirnsak, 2017) and communicates topographically with retinocentric visual areas in the posterior cortex.

A relevant aspect of the central role of attention at the interface between action and perception is the observation that the coordinates used by motor areas to guide an arm/hand movement to objects located at different spatial locations, regardless of eye direction and body position, in light or darkness conditions, are those of the spotlight of attention (Von Helmholtz, 1867). As the attention is directed to the locations of planned movements (Deubel and Schneider, 1996; Kowler and Blaser, 1995; Rizzolatti et al., 1987), the coordinates of spotlight of attention could indicate the goal of movement to the motor areas in all the environmental conditions described above (Galletti et al., 2022). This hypothesis is strongly supported by the deficits observed in patients affected by optic ataxia syndrome. Optic ataxia is an impairment of visually guided reaching movements which is not attributable to primary visual, proprioceptive, or motor deficits (Perenin and Vighetto, 1988). The patients showing this visuomotor deficit present damage that is also likely to include the human homolog of area V6A (Fattori et al., 2017; Karnath and Perenin, 2005). These patients can reach and grasp foveated targets in an accurate way, but when they are asked to reach and grasp a non-foveated object they misreach the target. In these

patients, the so-called “magnetic misreaching” has been observed, a condition in which they reach towards the gazed position rather than towards the object presented in peripheral vision (Carey et al., 1997; Jackson et al., 2005). Together with the well-established visuomotor

deficits in OA, some results revealed visuo-perceptual deficits exhibited as a deficit in orienting in the attentional field (Pisella et al., 1993). A study by Striemer et al. (2007) clearly demonstrated that OA patients have marked deficits in orienting attention. Specifically, the results

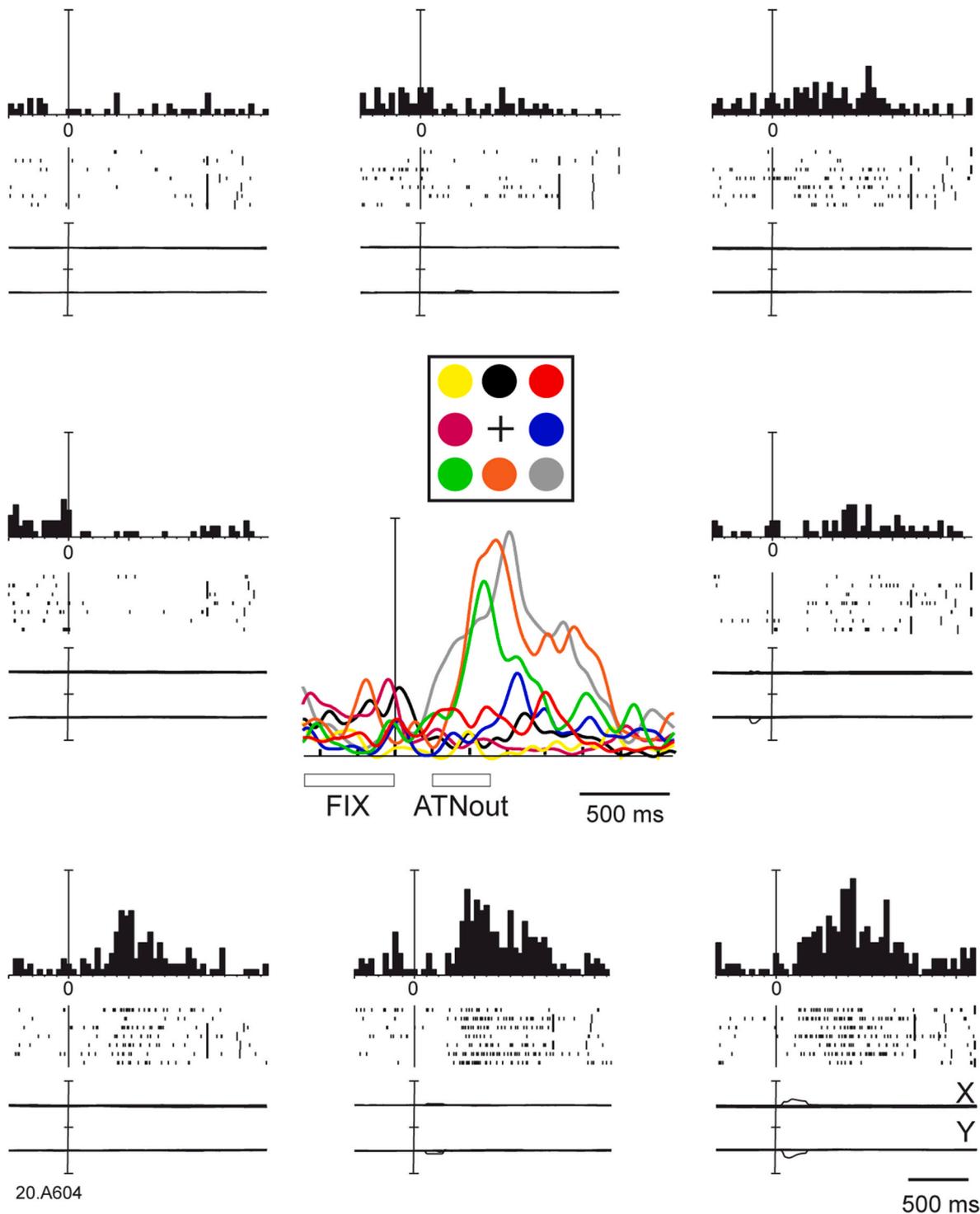


Fig. 4. Example of V6A neuron modulated by the covert shift of spatial attention. In the dark, the animal gazed at a stationary target at the centre of the screen (cross symbol) and was required to covertly attend to one of the 8 peripheral regions in random sequence (coloured dots). While fixating, the animal had to detect a target (5 ms red flash) in one of the 8 positions and respond to it by releasing the button without breaking fixation. Each diagram contains the peri-event time histogram, raster plots, and eye position signals, and is positioned in the same relative position as the cue on the panel. In the central part, the spike density functions of the neural activity for each of the 8 cue positions are superimposed and aligned with the cue onset. The mean duration of epochs FIX and shift of attention (ATNout) are indicated below the SFDs. Neural activity and eye traces are aligned with the cue onset. Scale bar in peri-event time histograms, 70 spikes/s. Bin width, 40 ms. Eye traces: scalebar, 60°. The neuron was spatially modulated by covert shifts of spatial attention, with stronger activation when attention was shifted towards the bottom part of the visual space. Figure modified from Galletti et al. (2010).

indicated that they were slower to respond to targets in their ataxic field regardless of cue type (valid, invalid, or no cue). The authors suggested that this effect could be due to a decrease in the salience of contralesional stimuli. This means that when a cue or a target appears in the ataxic field, attention may not be allocated with the same extent as for the ipsilesional stimuli (Striener et al., 2007). Based on these observations, the peripheral mislocalisation and magnetic misreaching in optic ataxia may be explained by an impairment in decoupling the spotlight of attention from the direction of gaze (Galletti et al., 2022; Pisella et al., 2021; Rossetti and Pisella, 2018).

Together with the evidence from OA patients, other studies in humans by Rushworth and co-workers (2001a, 2001b, 1997) investigated the role of the PPC in the covert orienting of attention and motor attention. Motor attention is defined as the process of covert attention associated with the covert preparation of limb movements as opposed to eye movements (Rushworth et al., 1997). When collecting evidence in patients with lesions in the left and right PPC and in healthy participants through transcranial magnetic stimulation (TMS) and PET protocols (Rushworth et al., 1997, 2001a, 2001b), Rushworth and co-workers demonstrated that the left PPC is crucially involved in disengaging the focus of motor attention from one movement to another when the pre-cue, indicating the target to covertly attend, is different to the target of the motor response (Rushworth et al., 1997). A bridge between the involvement of the human and monkey PPC in the attentional processes is elegantly demonstrated, using fMRI protocols, by Astafiev et al.

(2003) who reported that responses in the SPL which partly corresponds to area V6A in the macaque were related to spatial attention activity regardless of effector information (Astafiev et al., 2003; Calton et al., 2002). The left IPL was recruited for pointing preparation but not for spatial attention as this region is more motor-related than the SPL (Astafiev et al., 2003). Furthermore, the study by Astafiev et al. (2003) suggested that humans and macaques share a more similar functional organisation in the PPC (i.e., IPS or SPL) than in the frontal cortex. This similarity is consistent with a common evolutionary plan coupled with a relatively uniform scaling of area sizes (Astafiev et al., 2003).

The neural encoding of shifts of spatial attention that is useful to orchestrate arm movements has been documented in another SPL macaque area, V6A, adjacent to area PRR (Fattori et al., 2017). At a single-cell level, V6A shows activity modulated by the covert shift of attention (Galletti et al., 2010, 2022) during a task in which the animal was required to change the direction of spatial attention without changing the direction of gaze. Fig. 4 shows an example of a V6A neuron that strongly discharged when the animal's covert attention was shifted towards the bottom part of the visual space. Recently, in humans, several neuroimaging studies demonstrated the involvement of the human SPL, in which the putative human area V6A (hV6A) is located, in covert shifts of attention (Caspari et al., 2017; Kelley et al., 2008; Molenberghs et al., 2007; Vandenberghe et al., 2001; Yantis et al., 2002). All these studies showed a strong activation during a covert shift of attention of different areas, also involving the region of the human

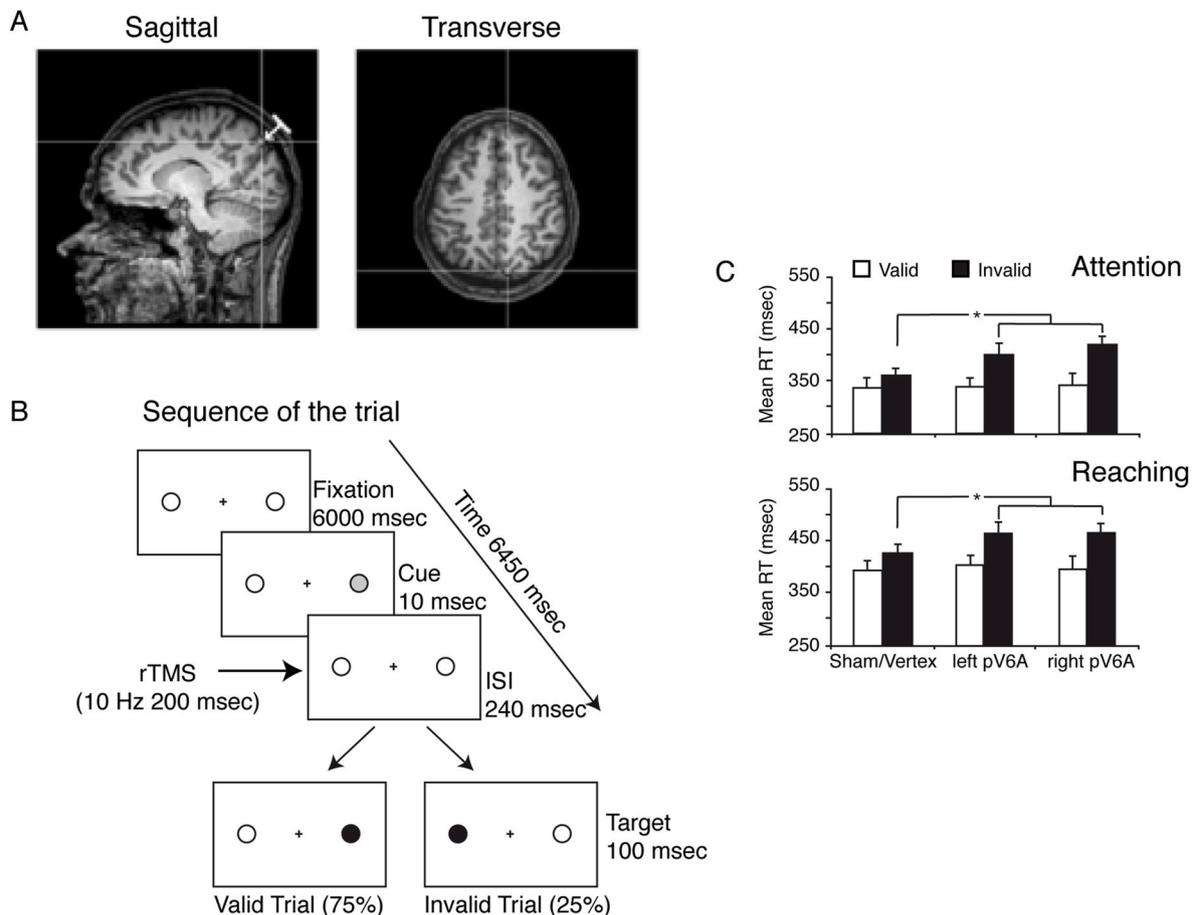


Fig. 5. Effect of the rTMS over the putative human V6A. **A**, The neuroanatomical region stimulated with rTMS (white arrow) is indicated by intersection lines in a sagittal (left) and a transverse (right) section of the T1-weighted MRI. Average Talairach coordinates (Talairach and Tournoux, 1988) in Fig. 1 of Ciavarro et al. (2013). **B**, Trial sequence of the valid and invalid trials of the detection and reaching tasks. **C**, rTMS effects on attentional orienting and reorienting during a detection task (Attention, top histogram) and a reaching task (bottom histogram) task. Mean RTs (\pm SEM) to valid and invalid trials as a function of stimulation condition show that a similar effect of validity was observed in both the attention and the reaching task. The longer reaction times in invalid trials when V6A is targeted by TMS indicate its involvement in responses that need a shift of attention from the cued location. Figure modified from Ciavarro et al. (2013).

SPL described as dorsal area V6A (Pitzalis et al., 2013, 2015; Tosoni et al., 2015). Additional support comes from the transcranial magnetic stimulation (TMS) study of Ciavarro et al. (2013) on healthy human participants. The study consisted in the application of online repetitive TMS over hV6A during an attention task requiring covert shifts of attention, and during a reaching task requiring planning of reaching movements towards peripheral cued targets in space (see Fig. 5). The results demonstrated the causal role of hV6A in attentional “reorienting” and not in maintaining attention at a spatial location (“orienting”) which involves the more lateral parietal regions (Corbetta and Shulman, 2002; Serences and Yantis, 2007). All these studies support the view that V6A is involved in decoupling the spotlight of attention from the direction of gaze, by signalling the location of the action target. The crucial involvement of the SPL and, specifically, of area V6A in attentional processing subserving visual space perception and action, is elegantly described in a recent review by Galletti et al. (2022), and suggests a strong contribution of the SPL in the attention interface.

1.3. Object affordance

Object affordance, a key concept in cognitive science, plays a crucial role in shaping perception and action coupling in our interactions with the environment. Within a general framework, it includes the idea which can be described as: “how we understand the world is defined by what we can do with it”. According to Gibson’s affordance theory, introduced in 1979, affordances are not inherent properties of objects but rather relational properties between the objects and the individuals perceiving them (Gibson, 1979). More specifically, affordances are not determined solely by the physical properties of objects but also depend on the abilities, intentions, and goals of the perceiver. To illustrate the concept of object affordances, consider the example of a cup compared to a staircase. A cup affords holding liquids and being grasped by its handle. Similarly, a staircase affords ascending or descending, offering a structured and spatially defined means of vertical movement. These examples demonstrate how affordances are not determined solely by the physical properties and design of the objects but also by the user’s capabilities and intentions, enabling adaptive and context-specific actions.

Psychophysical research has provided compelling evidence supporting the existence and influence of object affordances on perception and action. A broad spectrum of experimental paradigms and techniques have been employed to investigate the perceptual and cognitive processes associated with object affordances.

A body of research has consistently supported the idea of automatic potentiation of action components by seen objects and their affordances. Tucker and Ellis conducted a series of research investigations using the stimulus-response compatibility paradigm, demonstrating the phenomenon of object affordance on reaction times (Ellis and Tucker, 2000; Tucker and Ellis, 1998, 2001, 2004). In their early study, participants were presented with black and white images of common graspable objects displayed in different orientations, such as upright, inverted, left, and right. The task required participants to press a button with either their left or right hand based on the orientation of the object. The results revealed a stimulus-response compatibility effect, with faster reaction times observed when the hand used to press the button corresponded with the hand affordance indicated by the object orientation. For instance, left-hand responses were faster when the object was oriented for a left-hand reach-to-grasp, while right-hand responses were faster when the object was oriented for a right-hand reach-to-grasp (Tucker and Ellis, 1998). Additionally, in a related study, Tucker and Ellis (2001) further delved into the influence of object category and proximity on individuals’ responses. In a series of experiments, participants were presented with a set of forty common real objects, categorized as either natural or manufactured and positioned at 15 cm and 2000 cm. Participants were instructed to hold a response device and provide speedy responses based on the object’s category by executing either a precision or a power grip response. The results indicated that participants’

response times were influenced by the stimulus-response compatibility effect. This effect was found to be transient and dependent on the visibility of the object, regardless of its spatial location, whether it was within or outside the peripersonal space (Tucker and Ellis, 2001). The absence of genuine reach-to-grasp actions in the experimental paradigm may have limited the ability to fully capture the intricate interplay between object affordances and their contextual spatial location. Indeed, subsequent research has provided evidence supporting the notion that affordances are subject to a spatial constraint, whereby the perception of potential actions is influenced by the spatial proximity and accessibility of objects (Costantini et al., 2010). This implies a fundamental relationship between the spatial environment in which an object is located and the affordances offered by the object. Here, the peripersonal space concept, proposed by Rizzolatti and colleagues (1997), further supports this idea (Rizzolatti et al., 1997). Peripersonal space refers to the region surrounding an individual’s body that is within arm’s reach and is actively involved in motor actions and interactions with objects (Rizzolatti et al., 1997). Objects located within this spatial domain are perceived to have a stronger influence on the affordances they provide, as they are more accessible and easier to interact with for the perceiver (Linkenauger, 2015; Witt and Riley, 2014).

Numerous scenarios, including reaching and grasping actions, have demonstrated the relationship between affordances, spatial location, action, and perception. Empirical evidence suggests that when individuals use an extending tool to reach targets located beyond arm’s length, they perceive the targets as being closer than when they reach them without the tool (Costello et al., 2015; Witt et al., 2005; Witt and Proffitt, 2008). This perceptual effect is contingent upon the specific intention to use an extending tool of sufficient length that enables reaching of the targets, as judgments of proximity are not influenced when the tool is too short (Davoli et al., 2012; Osieurak et al., 2012) or when the targets remain in an unreachable spatial location (Witt et al., 2005). Analogous effects have been observed when employing grasping paradigms. Manipulation of the apparent size of the hand elicits opposing modulations in object size perception (Linkenauger et al., 2010, 2011). Similarly, during the trajectory of the hand, manipulation of the object’s size exerts a significant influence on the object’s perceptual representation (Cesaneck and Domini, 2018; Sanz Diez et al., 2022). These effects are contingent upon the object’s inherent graspability: when confronted with objects surpassing a critical size threshold, the perceptual after effects become negligible. The multifaceted interconnection among affordances, spatial location, action, and perception extends beyond laboratory settings and permeates everyday sports activities, in which accumulated experience amplifies the synergistic integration of these factors (Gray, 2013; Lee et al., 2012; Witt and Dorsch, 2009; Witt and Proffitt, 2008; Witt and Sugovic, 2010).

Although further research is needed, current psychophysical studies have clearly deepened our understanding of the complex relationship between human perception and action, highlighting the dynamic interplay between object affordances, their spatial location, and our motor intentions.

1.3.1. Neural correlates of the common object affordances for perception and action

The activation of cortical regions associated with motor functions is observed when interacting with objects and associated affordances. This idea comes from the neural activation induced by objects, which partially overlaps with regions involved in the object-action interaction. At a neural level, the central focus lies in comprehending the mechanisms through which individuals perceive affordances. Neuroscientific investigations have provided additional insight into the neural substrates and correlates underlying the perception-action coupling in object affordances. Neuroimaging studies that utilise functional magnetic resonance imaging (fMRI) have identified specific brain regions and connectivity networks involved in the processing and integration of object affordances.

Affordances are facilitated by the dorso-dorsal system, primarily encompassing the bilateral superior parietal cortex and the intraparietal sulcus (Osiurak et al., 2017; Vingerhoets, 2014). The bilateral superior parietal cortex has been consistently implicated in affordance perception and reach-to-grasp movements. Specifically, this region is involved in the integration of visual and proprioceptive information and plays a crucial role in transforming perceived affordances into action plans (Gaveau et al., 2014; Jeannerod et al., 1995; Pisella et al., 2000; Vingerhoets, 2014). Numerous studies have made significant contributions towards elucidating the role of the parietal cortex in the perception of object affordances and the execution of hand actions. These studies have employed experimental paradigms that involve either actual, pantomimed, or imagined manipulation of objects (Vingerhoets, 2014). Significant activations in the left intraparietal sulcus and left posterior dorsolateral frontal area were observed by Moll et al. (2000) when adults engaged in pantomiming or imagining the use of everyday life objects (Moll et al., 2000). Likewise, when pantomiming the use of objects, a notable activation in the dominant left hemisphere was observed, encompassing regions such as the SPL, supramarginal gyrus, premotor area, and supplementary motor area (SMA) (Choi et al., 2001). These findings are consistent with those from Imazu and coworkers (2007), who reported a significant activation in the left inferior parietal lobule when healthy right-handed individuals either pantomimed an action or imagined manipulating an object (Imazu et al., 2007). Other studies have provided evidence of the contribution of the superior parieto-occipital cortex during the perception of objects that afford specific actions, as opposed to objects lacking such affordances (Cavina-Pratesi et al., 2010a; Filimon et al., 2009; Gallivan et al., 2009, 2013; Quinlan and Culham, 2007). Indeed, all these findings align with those studies examining cerebral activation related to observed or imagined prehension movements. These studies have consistently reported activation in areas such as the intraparietal sulcus, as well as the inferior and superior parietal lobules (Binkofski et al., 1998; Buccino et al., 2001; Decety et al., 1994; Grafton et al., 1996; Grèzes et al., 2003; Grèzes and Decety, 2002; Vingerhoets et al., 2009, 2010). Additional evidence from

the SPL comes from monkey studies that show the involvement of this part of the brain in the encoding of object affordance. Breveglieri and collaborators (2015) directly demonstrated that V6A neurons were modulated by object affordance using a task in which the object's visual features were maintained nearly constant while the object affordances were changed due to the two objects evoking different types of grips (Breveglieri et al., 2015). An exemplar neural behaviour related to object affordance is reported in Fig. 6 in which a V6A neuron discharged during the vision of a handle regardless of its thickness, whereas the plate, evoking another type of grip, did not elicit any response, despite the visual similarity. Conversely, the thin and thick versions of the two objects, despite having a very different appearance, evoked the same discharge, indicating a similar encoding. In this study, it was proposed that contextual information on graspable objects may be used by area V6A of the SPL to guide the object interaction in cooperation with area AIP in the IPL. This information exchange is then aimed at selecting or generating appropriate grasping movements (Breveglieri et al., 2015; Fattori et al., 2017).

With the aim of depicting the contribution of IPL and APL as interfaces that link perception to action, it is worth mentioning a study in which V6A neural activity was tested in a paradigm similar to that used to study area AIP (Murata et al., 2000). Similarities and differences were found in the two areas of interest. In both areas object selectivity and the incidence of the different categories of neurons were similar (visuomotor neurons, neurons discharging differently in light and dark conditions during grasping; motor neurons, that is neurons discharging similarly in light and dark; and visual neurons, those discharging only in light and not in dark conditions). However, important differences between the two areas emerged. In fact, in the majority of AIP neurons both visual and motor components influenced the selectivity for grips, whereas in area V6A the motor component was the one that particularly guided the cell's selectivity (Breveglieri et al., 2018; Murata et al., 2000). Other experiments showed that a large amount of AIP neurons (90%) were sensitive to visual stimuli such as fragments of shapes (Romero et al., 2014), whereas only a minority of V6A cells were sensitive to simple

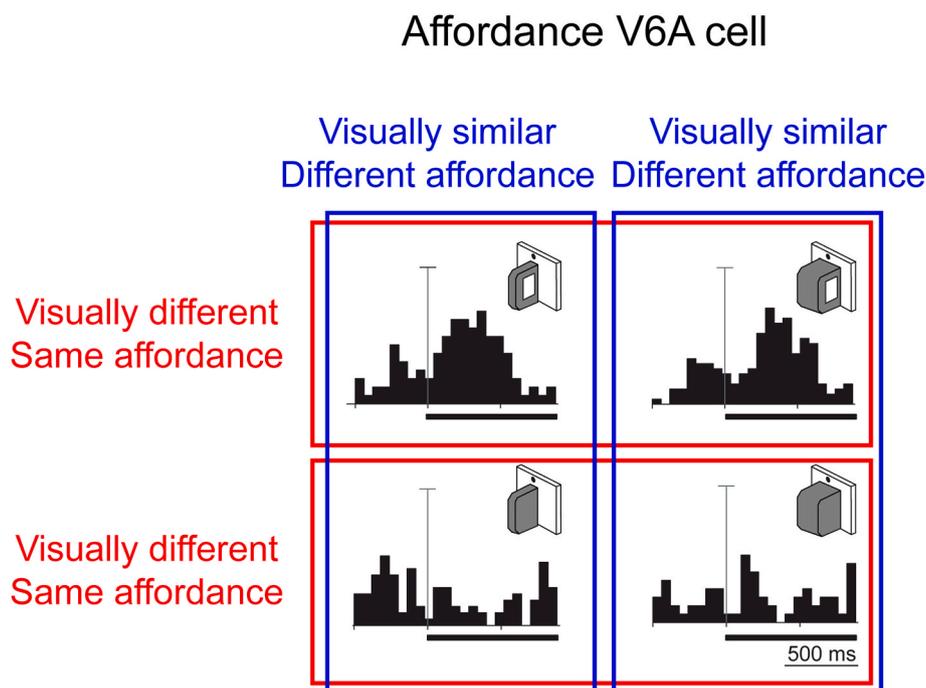


Fig. 6. Example of V6A neuron encoding object affordance. The neuron was tested for the same or different affordance and for the same or different visual properties of the objects. Neural activity is represented as peristimulus time histograms aligned (vertical line) with the onset of object illumination. The horizontal thick black line represents the time interval of object illumination. Vertical scale bars on histograms: 45 spikes/s. Different affordances (columns) evoke different activations, whereas different visual properties elicit similar responses. Modified from Breveglieri et al. (2015).

visual stimuli (Galletti et al., 1999; Gamberini et al., 2011). Given these findings, area AIP is more visually driven than V6A, which is more affected by somatosensory/motor inputs (i.e., the hand shape used for grasping). This difference is consistent with their different patterns of cortical inputs, with AIP connected with the ventral visual stream and the dorsolateral frontoparietal network (Borra et al., 2008), and area V6A connected with the extrastriate cortex, but not receiving inputs from the ventral visual stream (Gamberini et al., 2009; Passarelli et al., 2011). In conclusion, these differences reflect a different functional role of the two areas, with AIP being more involved in fine manipulation and V6A in fast and coarser grasping, but integrating attentional and affordance/contextual information (Breveglieri et al., 2018; Fattori et al., 2017). Even if area V6A does not receive direct inputs from the ventral visual stream, it is directly connected with area AIP (Borra et al., 2008; Gamberini et al., 2009; Matelli et al., 1998; Shipp et al., 1998). Both areas can cooperate in action and perception coupling which, in this case, is translated into an act of prehension; this has also been found in works on brain imaging in humans (Di Bono et al., 2015; Fabbri et al., 2016).

Additional evidence points to the involvement of the premotor cortex and the SMA in the processing of object affordances. The premotor cortex, responsible for motor planning and preparation, exhibits increased activity when individuals perceive objects that afford specific actions (Choi et al., 2001; Jacobs et al., 2010), and even when they merely name object manipulations (Grafton et al., 1997). Similarly, the SMA, responsible for action selection and initiation, shows activation in reach-to-grasp actions (Cavina-Pratesi et al., 2010b), suggesting its potential involvement in the coordination of motor responses associated with object affordances.

Further investigations have expanded beyond conventional imaging methodologies to explore the neural underpinnings of object affordances utilising innovative techniques such as TMS. TMS studies have demonstrated that the disruption of the activity of specific areas impairs the perception and execution of object-specific actions (Andres et al., 2013; Davare et al., 2006; Rice et al., 2006; Tunik et al., 2008). These findings provide causal evidence for the crucial role of these brain regions in processing object affordances.

The perception of object affordances involves a complex network of brain regions responsible for the integration of sensorimotor functions, as well as action planning, and initiation. This network enables the transformation of perceived affordances into precise and contextually appropriate motor responses. While our current understanding of object affordances has been significantly enhanced by neuropsychological and neuroimaging research, there are still ongoing debates regarding their specific roles in theory, action control, and cognition. These debates address fundamental questions related to attentional dependence, dynamic perception in different contexts, and the interplay between affordance processing and spatial representation (Humphreys et al., 2013; Kourtis et al., 2018; Kourtis and Vingerhoets, 2015; Kumar et al., 2021; Osieurak et al., 2017). The further exploration of these topics promises to provide valuable insight into the dynamic nature of perception-action relationships and the modulation of object affordance processing. Future research endeavours will focus on integrating contextual information and investigating the complex interrelationships between perception, action, and the environment. A relevant example of the future developments regarding this topic comes from recent studies that extended the concept of “object affordance” to “social affordance” in which the intraparietal area AIP plays a crucial role. This concept stems from the evidence that motor plans in an observer’s brain can be automatically recruited not only by observed objects but also by observed actions (Albertini et al., 2020; Bonini et al., 2014; Caggiano et al., 2009; Lanzilotto et al., 2016; Livi et al., 2019; Maranesi et al., 2017). Contextual information strongly influences what action is most appropriate as a response to an observed one (Lanzilotto et al., 2019). Specifically, information regarding static and dynamic properties of objects reach the AIP from regions of the ventral and the dorsal visual

stream, respectively. The integration of this information allows for the generation of the visuomotor representation of others’ actions that, as suggested for objects (Cisek, 2007; Jeannerod et al., 1995), can guide the selection and planning of the observer’s potential motor action in response to other agents, depending on the current context (Orban et al., 2021). By delving deeper into the study of object and social affordances, we will continue to advance our understanding of the intricate mechanisms underlying perception and action in the context of our surrounding world; both the IPL and SPL appear to crucially contribute to object affordance, by taking into account different aspects.

2. Conclusions and future perspectives

One of the relevant problems tackled in the present review revolves around the interface between perception and action. The original view defined these two functions as processed by two different neural substrates but, at the same time, intrinsically correlated with each other. The accumulating evidence shows that both the ventral and dorsal pathways contain neural substrates that process object perception, but without redundancy. However, if the presence of perception in the dorsal stream which is traditionally considered an “action domain” is not in doubt, the communication between these two functions must be possible due to the presence of a common domain. How does this occur? This possibility is made feasible by the existence of an interface between perception and action which creates a common flow of information and allows for their reciprocal interaction. Here, we examined all possible interfaces between perception and action and performed an overview of the most relevant neural correlates subserving them.

In all descriptions concerning the neural substrates underlying the several action perception interfaces (i.e., common coding, attention, and affordances), the posterior parietal cortices play a prominent role in the combination of perception and action. In fact, even if the interfaces change, the involvement of the inferior and the superior parietal lobes remains constant. More specifically, the IPL together with the premotor areas is active during action observation (Rizzolatti and Sinigaglia, 2010), suggesting that a motor-based perception aimed at understanding others’ actions spans this brain stream. Given this evidence, the mirror mechanism represents the neural bases of the motor codes and common coding interfaces discussed above.

The posterior parietal cortices are also involved in the attentional interface between perception and action. Several areas appear to be modulated by the spotlight of attention when it is directed to the locations of planned movements (Deubel and Schneider, 1996; Galletti et al., 2022; Kowler and Blaser, 1995; Rizzolatti et al., 1987). In particular, the SPL area V6A, which is connected with the dorsal premotor area and part of the parieto-frontal circuit, is strongly activated when the spotlight of attention is used to guide goal-directed movement because it combines bottom-up stimuli (visual information) with top-down motor signals (action plans). On these grounds, the SPL could be the putative candidate to host the neural substrate of the common attention interface for perception and action.

Finally, different studies have demonstrated the involvement of the posterior parietal cortices in the encoding of object affordance as discussed above. This part of the brain contains all that is necessary to integrate what the environment offers to the observer in order to interact with objects (Gibson, 1979). Indeed, the concept of object affordance suggests a strong connection between visual perception and motor behaviours with a strong contribution of both the IPL and SPL. Given this evidence, the SPL and IPL could be fully considered to be the neural correlates of the perception and action interface for object affordance.

Future perspectives could aim to exploit theoretical knowledge concerning the mechanisms underlying action and perception coupling (i.e., common coding, attention, affordance) in order to translate them to AI application domains in the field of assistive devices. The use of the action-based perceptual information could be helpful in improving all those artificial intelligent systems that require the reading of

appropriate action intentions, at the same time taking object representation, contextual information, and task requirements into consideration. From the studies summarised in this review, we surmise that the interplay between the inferior and parietal lobule is crucial to orchestrate all this information and generate the most appropriate action representation that can be used by the new generation of artificial “perceptual-motor systems”.

Credit author statement

Bosco Annalisa: Conceptualization, Writing- Original draft preparation, Writing- Reviewing and Editing, Validation. **Sanz Diez Pablo:** Writing- Reviewing and Editing; **Filippini Matteo:** Writing- Reviewing and Editing. **De Vitis Marina:** Writing- Reviewing and Editing. **Fattori Patrizia:** Supervision, Writing- Reviewing and Editing, Funding acquisition.

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Data availability

Data will be made available on request.

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