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Lateral Intraparietal Region (LIP)

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Synonyms

Lateral intraparietal area

LIP: A Dorsal Stream Region

An influential idea in cognitive neuroscience is that primates have at least two cortical visual processing streams that differ in both anatomy and function (e.g., Milner and Goodale 1995). Information on the patterns of light that hits the eyes is sent to the primary visual cortex in the occipital lobe at the back of the brain. Some of this information is then further processed in the ventral stream, going ventrally from the primary visual cortex to the temporal lobe. The ventral stream is important for object identification and has thus been dubbed the "what" stream. The dorsal stream, also originating in the primary visual cortex but ending in the parietal lobe, plays a role in representing spatial information and has therefore often been called the "where" stream, but has more recently been called the "how" stream because of its importance in action guidance (Fig. 1).

Spatial distortions from parietal damage have long been known. Holmes (1919), about a hundred years ago, described the symptoms of patients who suffered from gunshot wounds to the posterior and upper parts of the parietal lobe. These patients seemed unable to construct spatial representations from visual information; their eyes would randomly drift instead of purposefully scanning the scene, they would reach for an object in the completely wrong direction, and they would even directly walk into walls as if they had no idea of their position in space.

Initially it was thought that an all-purpose spatial representation resided in the posterior parietal lobe. However, primates are capable of complex interactions with their environment. Complex action capabilities might require not just a single representation of space, but many specialized ways of representing where things are and how to potentially react to them. A monkey swinging from branch to branch presumably needs to have a neural system capable of calculating the direction and distance of the next branch relative to where she is looking, relative to where her hand is with which she intends to grasp the branch, and so on. Since the visual information is originally only available in a retinotopic frame of reference, where nearby neurons tend to respond to light falling on locations close to each other on the retina of the eye, these new spatial representations require the transformation of the original retinotopic space into so-called egocentric coordinate frames, where spatial locations of important

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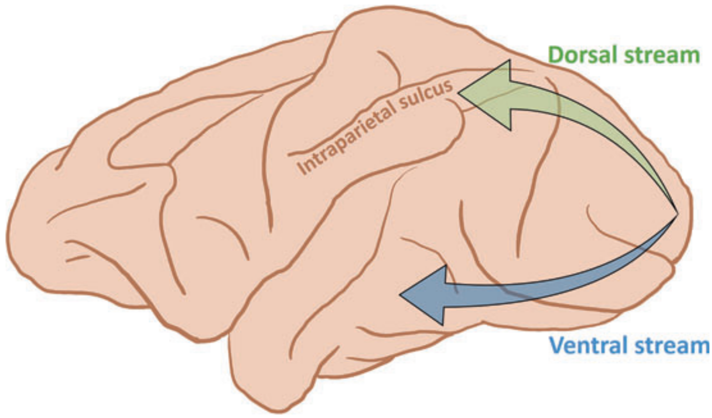


Lateral Intraparietal Region (LIP), Fig. 1 The primate visual system processes visual information along two processing streams. Both streams originate in the primary visual cortex. The ventral stream reaches the temporal cortex, while the dorsal stream goes toward the parietal cortex. The lateral intraparietal region (*LIP*), a brain region near the endpoint of the dorsal stream, lies on the lateral bank of the intraparietal sulcus

things in the world are coded with reference to a part of the animal's own body, such as the eyes, head, hand, trunk, or mouth (Milner and Goodale 1995).

The main function of the parietal cortex in primates is often thought to be to carry out such transformations from sensory signals to a format more directly useful for motor output or action guidance (Cohen and Andersen 2002; Milner and Goodale 1995; Rizzolatti et al. 1997). Within the intraparietal sulcus, several regions can be found, each of which might mainly encode locations in a reference frame centered on a particular part of the body, such as the head or eye (Cohen and Andersen 2002; Colby and Goldberg 1999). An eye-centered reference frame is obviously of use when deciding where to look next, and the lateral intraparietal region (LIP), a region high up in the dorsal visual stream, has been implicated in such eye movement guidance; several other roles of this region have also been proposed, including "higher" cognitive functions such as visual attention.

Anatomy

As the name implies, the lateral intraparietal region lies on the lateral bank of the intraparietal sulcus (Andersen et al. 1985). The region has been heavily studied in the macaque monkey, but homologous regions are thought to exist in the human brain; human intraparietal regions IPS1 and IPS2 are likely candidates as these regions show various functional similarities with area LIP in monkeys (Silver and Kastner 2009).

LIP has sometimes been further subdivided into a ventral (LIPv) and a dorsal zone (LIPd) based on differences in architecture, connectivity, and function (e.g., Chen et al. 2016; Lewis and Van Essen 2000; Webster et al. 1994). For example, LIPv has strong reciprocal connections to brain regions involved in visual motion processing, including area MT, while LIPd might be relatively more connected to particular regions of the ventral stream (Lewis and Van Essen 2000; Webster et al. 1994). Anatomical differences as well as potential different functional roles could indicate that LIPv and LIPd are two separable brain regions.

Visual Orienting

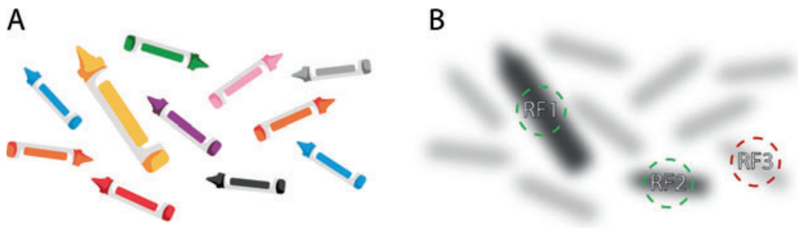
Orienting was originally considered to be a nonspecific reflex that involved turning the eyes, head, and ears (for animals whose ears prick up) to the direction of stimulation (Sokolov 1963). Orienting in primates might mainly rely on shifts in eye position, although orienting can more broadly be thought of as engaging with an outside source through coordinated overt bodily movements and covert attentional deployment for the purpose of information gathering. LIP is generally thought to play an important role in visual orienting, in particular visuospatial attention and saccadic eye movements (jerky eye movements that rapidly change the location of gaze), although the precise function of this brain region is still widely debated (see Bisley and Goldberg 2003, 2010; Colby and Goldberg 1999; Gottlieb et al. 1998).

LIP is well situated to guide orienting based on visual information. It has structural connections with several visual areas such as V2, V3, V4, and MT (Lewis and Van Essen 2000). It is also connected to areas implicated in oculomotor behavior such as the superior colliculus (SC; Ferraina et al. 2002; Field et al. 2008), the frontal eye fields (FEF; Lewis and Van Essen 2000; Ferraina et al. 2002), and the cerebellar oculomotor domains (Prevosto et al. 2010). LIP appears to mainly represent space in an eye-centered coordinate frame, useful for calculating where important things worth attending to and looking at are relative to the center of gaze (Cohen and Andersen 2002).

An LIP neuron might show light-sensitive, memory-related, and/or saccade-related activity, responding vigorously when a visual stimulus is shown in a particular location relative to the center of gaze, when no stimulus is currently shown in a particular location, but this location has to be memorized, or before, during, or after a monkey makes a saccadic eye movement to a particular location (Barash et al. 1991). A preferred spatial location of an LIP neuron can be referred to as the neuron's receptive field (more emphasis on visually evoked responses) or response field (less emphasis on visually evoked responses) or just simply the neuron's RF. Neurons in LIP can however transiently shift their spatial representations immediately preceding an intended saccadic eye movement, where a neuron might briefly code for a location not relative to the current center of gaze, but relative to the immediate future center of gaze were the saccadic eye movement is to be executed, a process known as remapping (Duhamel et al. 1992). LIP might thus be said to have the available machinery to represent space not just relative to current eye position, but also relative to the center of a "virtual eye." This predictive remapping might help with the integration of visual information across eye movements and contribute to the apparent stability of the visual world even when the eyes jump around a visual scene.

Although LIP neurons tend to be light-sensitive, in the sense that their activity generally increases when a visual stimulus appears in their RF, there is some indication that visually related activity might not primarily represent the visual properties of a viewed object. Instead, it might mainly indicate the priority assigned to a location and/or the object occupying that location; the activity of neurons within LIP as a whole could thus serve as a priority map (Balan and Gottlieb 2006; Bisley and Goldberg 2010), where visual stimuli in different locations are assigned different weights based on their salience, current task demands, as well as other factors such as long-term experience (Fig. 2). High priority might thus be assigned to an object in a particular location if it is visually striking (such as when viewing something bright among dark things or dark among bright things) or behaviorally relevant (such as when an object's visual features match those of a searched-for target). If LIP mainly serves the role of a priority map, LIP activity might neither primarily represent visual attention nor the intention to move the eyes, a subject of some debate. Instead, it could provide information on where important things might be found, information which can then be utilized to orient the eyes and attention to the most active location of this priority map (e.g., Bisley and Goldberg 2010).

Visual attention and eye movements are highly related, so that when something catches attention, it generally also catches the eye. It might therefore make sense to use a single common priority map both for attentional and oculomotor guidance. However, overt (eye movements) and covert (visual attention) visual orienting can be separated, such as when you refrain from rudely staring at a weird-looking person that you nonetheless watch from the corner of your eye. The two



Lateral Intraparietal Region (LIP), Fig. 2 Prioritizing visual information. Panel (**a**): In this hypothetical example, the task is to find the *black* crayon among several other crayons. Panel (**b**): A schematic depiction of a hypothetical priority map, where darker colors signify greater priority. As *black* is a behaviorally relevant feature in the visual search task shown in panel A, anything *black* in the original scene is assigned a high priority value. However, one crayon is noticeably different from all of the rest due to its larger size. As this object is visually salient even though it is not the searched-for object, it could also be assigned a relatively high priority; all things equal, something that stands out from the rest of the environment is worth exploring. If this object would fall within the RF of a particular LIP neuron (*RF1*), one might expect this neuron to increase its activity, signifying high priority; the same is to be expected from a second LIP neuron whose RF lies in the location of the searched-for target color (*RF2*). However, a third LIP neuron – whose RF encompasses an inconspicuous object not directly relevant to the current task – might not become particularly active, signifying the low priority assigned to the object in this location (*RF3*). An object within a location assigned the highest priority, as represented by the activity of a population of LIP neurons, might then be selected to become the focus of attention as well as the target of an animal's saccadic eye movement. The original crayon images were designed by Vexels.com and are used in the current images with the consent of Vexels.com

subdivisions of LIP, LIPd and LIPv, have been proposed to play different roles in attentional and oculomotor guidance, with LIPd activity being primarily related to the planning of saccadic eye movements to particular locations (overt visual orienting), while LIPv might take part in overt as well as covert visual orienting (Liu et al. 2010). It has however also been proposed that LIPd is more dedicated to visual processing, while LIPv is more important for saccadic eye movements (Chen et al. 2016). The functional differences of LIPd and LIPv are still not well understood.

Other Functions

Several studies on LIP muddy the waters when it comes to the precise function of this brain region, as LIP activity appears to be affected by several nonspatial factors that either modulate spatial representations of LIP neurons or are even independent of them (Gottlieb and Snyder 2010). For example, LIP neurons have been reported to be involved in numerical processing, as the activity of several LIP neurons systematically changes with the number of visual elements (Roitman et al. 2007). The activity of LIP neurons can also be affected by learned category membership, such as when a monkey is taught to treat several motion directions as members of two distinct motion categories with an arbitrary category boundary (Freedman and Assad 2009). Some LIP neurons can respond selectively to the shape of visually presented objects (Sereno and Maunsell 1998; Sigurdardottir and Sheinberg 2015). They can become selective for color arbitrarily associated with a particular behavior (e.g., red means look left; green means look right), and this color selectivity can be separated from a neuron's preferences for saccadic eye movement direction (Toth and Assad 2002). There has also been a body of work looking at the role of LIP in decision-making (Gold and Shadlen 2007). Several other nonspatial factors also appear to affect LIP responses (for further discussion, see Gottlieb and Snyder 2010).

However, it is somewhat unclear to which extent LIP is actively involved in nonspatial tasks and to which extent nonspatial signals in LIP mainly support the region's role in visual orienting (Gottlieb and Snyder 2010). For example, it has been suggested that shape selectivity in LIP might support overt and covert visual orienting, where the shape of an object biases the eyes and attention in a particular direction either due to learning or because of inherent biases (Sigurdardottir and Sheinberg 2015). Surgically removing area LIP also does not prohibit the relearning of a task that requires monkeys to arbitrarily associate colors with actions, suggesting that at least some such arbitrary associations are not dependent on this region (Rushworth et al. 1997). Similarly, Katz et al. (2016) recently showed that while decision-related signals in LIP were strong, they apparently did not play a causal role in decision-making as inactivation of this region did not impair decision-making performance. Instead, silencing LIP neurons affected spatial selection and oculomotor behavior, consistent with this region's primary role in visual orienting.

Conclusion

LIP is a high-level brain region somewhat far removed from purely sensory- and purely motor-related areas. It is therefore perhaps not surprising that LIP neurons show complex activity related to various aspects of sensation, cognition, and action. However, while LIP might well partake in other functions, this region's importance for the guidance of overt and covert visual orienting is especially well established. LIP might serve the role of a priority map, where various bottom-up and top-down signals directly influence weights given to objects in different spatial locations, thus biasing where one looks and pays attention.

Cross-References

► Attention
► Decision-Making
► Dorsal Pathway
► Non-Human Primates
► Orienting
► Parietal Lobe
► Primates
► Saccadic Eye Movement

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