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Chapter Title

00835: Visuomotor control in the healthy and damaged brain

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Abstract

For a normally sighted person, nearly all aspects of everyday life involve visually-guided behaviour. Reaching out, grasping, and manipulating objects may seem like simple tasks, yet they require complex processing from a large network of brain regions. In the last two decades there has been an increased focus on the control of visually-guided action in Psychology and Neuroscience and a variety of innovative methods have been developed to investigate the neural basis of 'realistic' visuomotor behaviour in the human brain. In this chapter, we will provide an overview of what is currently known about the cortical areas implicated in the visuomotor control of hand movements (reaching, grasping), considering evidence from neuroscientific studies in humans and macaques and neuropsychological studies of people who have sustained brain damage.

Keywords

Vision; Motor; Eye movements; Reaching; Grasping; Tool use; Parietal cortex; fMRI; TMS; neurophysiology; neuropsychology; lesions; periphery; movement; action.

1. Why study visuomotor control?

Visuomotor control is a fundamental aspect of human behaviour that allows us to interact with the world around us. Reaching out, grasping, and manipulating objects may seem like simple tasks to us because we can perform them effortlessly with little, if any, conscious attention, yet they require complex processing from a large network of brain regions. To illustrate this complexity, think of how difficult it is for a child to learn how to grasp and use a knife (Fig.1A). In fact, human hand actions have so far outclassed the marvels of engineering, in that robotic systems cannot rival the human hand for versatility and elegance of movement (e.g., Leon et al., 2014).

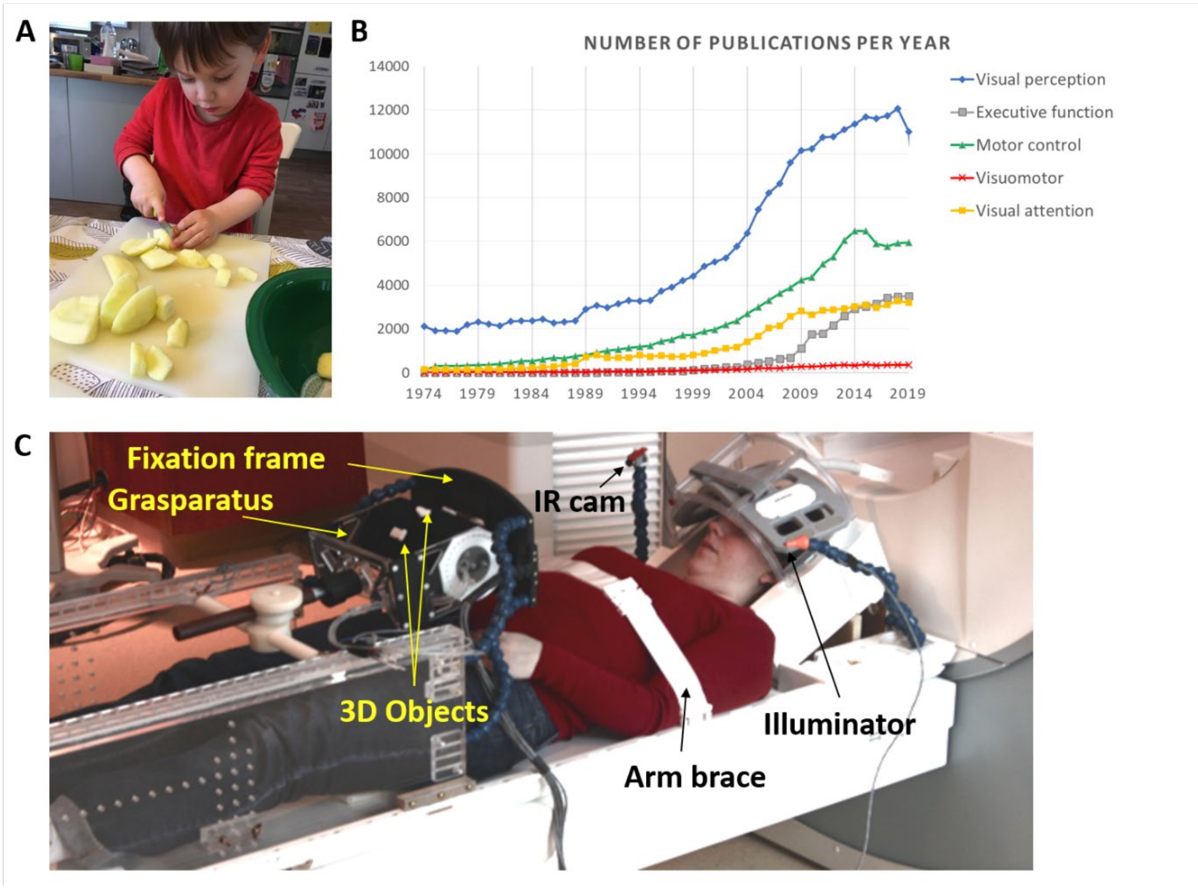

Figure 1. (A) Example of an everyday visually-guided action: child using a knife to slice apples. **(B)** Number of papers per year (since 1947) indexed in PubMed which mention the words '*visuomotor', 'motor control', 'visual attention', 'visual perception', 'executive function',* (data retrieved on 13/02/2021 from PubMed). The term 'executive function' was included for visual comparison against the other terms. The number of studies which refer to *'visuomotor'* is markedly much smaller than for the other search words. The number of studies mentioning 'motor control' has doubled in last two decades, but is still only half the number that mention *"visual perception"*. **(C)** Side view of *real* action fMRI set-up used by Rossit et al. (2013). The participant's head is tilted to permit direct view of the 3D objects and fixation (without the use of mirrors like in traditional fMRI studies). The objects are attached to the "Grasparatus II" (Culham et al., 2003b), which is placed behind the fixation frame. An illuminator LED is directed towards the central object and a camera sensitive to visible and infrared light records hand movements.

For a normally sighted person, nearly all aspects of everyday life involve visually-guided behaviour, but surprisingly most psychology/neuroscience textbooks separate visual and motor systems, and many devote little, if any, space to this topic. As illustrated in Fig.1B, the study of visuomotor control has also received significant less attention than other areas of study. The methodology of most neuroscientific studies that investigate the link between the visual brain and behaviour, especially inside the MRI scanner, have focused on manual key presses made in response to two-dimensional pictures, even when researching the neural basis of tool use (e.g., Lewis, 2006). Such reductionist methodologies fail to capture the richness of 'real-world' human brain-behaviour relationships (e.g., Krakauer et al., 2017). However, over the past two decades, there has been an increased focus on the control of real-world visuomotor behaviours, such as reaching and grasping, and innovative methods have been developed to study the neural bases of these abilities in humans (e.g., Culham et al., 2003a; Gallivan and Culham, 2015; Knights et al., 2020; Fig.1B-C).

In this chapter, we will provide an overview of what is currently known about the cortical areas involved in the visuomotor control of hand movements (reaching, grasping) considering evidence mostly from fMRI studies of brain activation in healthy people (Section 2) and neuropsychological studies of people who have sustained damage to visuomotor brain regions (Section 3).

2. Visuomotor control in the brain

2.1. Dual stream models of visual processing

Although our experience of the visual world may seem unitary, neuroscientists have characterised visual processing as highly modular with many separable, though interacting, components. A large-scale anatomical distinction has been drawn between the dorsal and ventral visual processing streams that diverge from early visual areas in occipital cortex. The dorsal stream extends from V1 to the posterior parietal cortex (PPC) and the ventral stream from V1 to the inferior temporal cortex. A functional interpretation of this anatomical division was proposed by Ungerleider and Mishkin (1982), based on their observations of the contrasting behavioural effects of lesions of the temporal and parietal cortex in macaque monkeys. Ungerleider and Mishkin argued that the ventral "what" stream is tuned to intrinsic features of objects within the scene (e.g., size, shape, texture, colour) and mediates object recognition, while the dorsal “where” pathway is tuned to the spatial layouts of the visual scene and mediates the localisation of objects.

In 1992, Goodale and Milner proposed an alternative perspective, often known as the perception-action model, or the “what” and “how” model. They suggested that both visual streams process information about spatial layout and the intrinsic features of objects, but that the processing within each stream is specialized for different behavioural purposes (Goodale and Milner, 1992; Milner and Goodale, 1995, 2006, 2008). The ventral “what” stream transforms visual inputs into conscious perceptual representations and plays a critical role in the recognition of visual objects and patterns (vision-for-perception). The dorsal “how” pathway integrates the incoming visual information with body-based information (e.g., hand position), to generate appropriate representations for immediate action (vision-for-action). This pattern of specialization is supported by multiple sources of evidence, although some authors have argued that the functional interactions between the two visual streams are too extensive to warrant a strict segregation (e.g., Schenk and McIntosh, 2010), and others have proposed additional pathways emerging within the PPC (e.g., Rizzolatti and Matelli, 2003; Kravitz et al., 2011; Binkofski and Buxbaum, 2013). In the next section, we will focus on the specialization of the dorsal visual stream for the visual guidance of actions.

2.2. Brain regions involved in visuomotor control

According to Milner and Goodale (1992), the dorsal vision-for-action stream culminates in the PPC, a large cortical region that receives and integrates multimodal sensory information to create a praxic goal-directed representation of the world around us. The PPC is positioned between the occipital lobe and the somatosensory cortex (in the postcentral gyrus), thus being ideally situated to integrate visual information from the external world with somatosensory information about body posture and movement. Laterally, the PPC is divided by the intraparietal sulcus (Fig.2) into inferior and superior parietal lobules. On the medial aspect of the parietal lobe, and anterior to the parieto-occipital sulcus, lies the precuneus (see Fig.2). Beyond these major anatomical subdivisions, several functional subregions of the PPC have been identified specialized for different types of visuomotor behaviour: eye movements, reaching, grasping and tool use.

The PPC integrates and transforms sensory information into movement-relevant coordinates that can support the planning of actions. The representation of a viewed object is initially coded with respect to the eye and then integrated with sensory information about the position of the head and body. These coordinate transformations allow a target object's position to be represented with respect to a specific effector, such as the hand, enabling the computation of appropriate movement vectors to bring the hand to the object. This visuomotor information is then fed forward to premotor cortex in the frontal lobe, to be integrated with information about action goals and contexts coming from prefrontal cortex. Following this integration, motor commands for action execution are issued from the primary motor cortex (Fig.2), modulated by the cerebellum and basal ganglia.

Eye movements are the most studied visuomotor function (for a recent review see Coiner et al., 2019) with fMRI studies repeatedly finding that the parietal eye field (a functional region located medially to the intraparietal sulcus in the superior parietal lobule, also named the lateral intraparietal area), is strongly activated for saccadic eye movements. The parietal eye field contains a topographic representation of the external world in retinotopic coordinates for both eye movements and peripheral attention (Sereno et al., 2001). Smooth pursuit eye movements activate a ventral frontoparietal network (including the parietal eye field and precuneus) also involved in the shifts of visual attention that precede saccadic eye movements (Corbetta et al., 2008; Corbetta and Shulman, 2002). Visually-guided hand actions have been less investigated in fMRI due to numerous technical challenges, such as limited space inside the scanner and disruptions of the magnetic field caused by arm and head movements (Culham et al., 2003a). However, the pioneering work by Culham and colleagues in developing specialized set-ups and imaging protocols has enabled studying human brain regions involved in *real* reach and grasp movements executed towards directly-viewed objects (i.e., without the use of mirrors; e.g., Culham et al., 2003a,b; Fig 1C).

Visuomotor control is thought to be modular, including dissociable functional components such as computing the location of the object relative to the hand (reaching/transport component) and shaping the posture of the hand and fingers according to the object's size, shape and orientation (grip/grasp component), in preparation for object contact (Arbib, 1981; Jeannerod; 1981). A well-established model, illustrated in Fig.2, proposes two separate parieto-frontal visuomotor circuits termed the dorso-medial and dorso-lateral systems, projecting to the frontal lobe from medial and lateral PPC subregions respectively (Rizzolatti and Matelli 2003). The dorsomedial circuit connects the PPC with the dorsal premotor cortex (Caminiti et al., 1991), whereas the dorsolateral system connects the anterior intraparietal sulcus with the ventral premotor cortex (Rizzolatti et al., 1988; Murata et al., 1997). The dorsomedial system is postulated to control the reaching component, and the dorsolateral system controls the grasping component, both sending outputs to the primary motor cortex for action execution (Caminiti et al., 1998; Culham and Valyear, 2006; Davare et al., 2011; Jeannerod et al., 1995; Vesia and Crawford, 2012).

Functionally, the dorsomedial system, which includes the superior parieto-occipital cortex, the medial part of the intraparietal sulcus and dorsal premotor cortex (Fig.2), has been implicated in programming arm transport during reaching (Davare et al., 2011; Vesia et al., 2010), the selection of wrist posture (Fattori et al., 2009; Monaco et al., 2011) and online corrections to correct for programming errors or sudden changes in object position (Grol et al., 2007; Rizzolatti and Matelli, 2003). The dorsolateral system, which includes a circuit from the caudal intraparietal sulcus to the anterior intraparietal sulcus and the ventral premotor cortex (Fig.2), has been implicated in programming hand shaping during grasping (Cavina-Pratesi et al., 2010a; Vesia et al., 2013), actions that require precise placement of the fingers (Grol et al., 2007) and action understanding (Rizzolatti and Matelli, 2003). However, this division between the dorsomedial and dorsolateral systems is not always supported, and an alternative view suggests that the dorsomedial system subserves both the reach and grasp components (e.g., Galletti et al., 2003; Grafton, 2010; Fattori et al., 2010; Gallivan et al., 2011; Monaco et al., 2011, 2014; Turella and Lingnau, 2014). Despite this controversy, neuroimaging studies have repeatedly identified three functional subregions within the PPC that are of particular relevance for visually-guided hand actions: the anterior intraparietal sulcus, the superior parieto-occipital cortex and the precuneus.

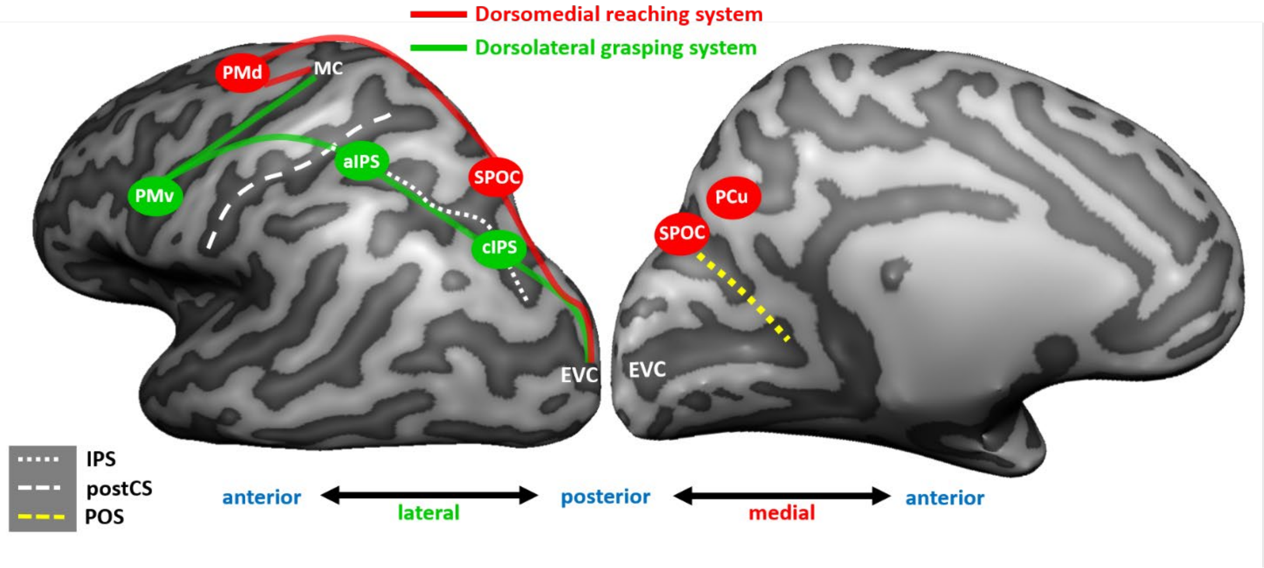

Figure 2. Major functional human brain regions involved in visuomotor control shown in lateral and medial views of a left hemisphere cortical surface reconstruction of a reference brain (COLIN27 Talairach) available from the neuroElf package (http://neuroelf.net). The dorsolateral grasping system (green) and dorsomedial reaching system (red) are shown along with their connections. Major sulci are also highlighted for guidance. Acronyms: EVC, Early Visual Cortex; cIPS, caudal Intraparietal Sulcus; aIPS, anterior Intraparietal Sulcus; PMd, Dorsal Premotor Cortex; PMv, Ventral Premotor Cortex; MC, Motor Cortex; SPOC, Superior Parieto-Occipital Cortex; PCu, Precuneus; IPS, Intraparietal Sulcus; postCS, post-Central Sulcus; POS, Parieto-Occipital Sulcus.

The anterior intraparietal sulcus is a functional PPC region located in the lateral surface of the PPC at the junction between the anterior portion of the intraparietal sulcus and the post-central sulcus (e.g., Rossit et al., 2013; Fig.2). The anterior intraparietal sulcus is thought to be important for pre-shaping fingers for object grasping (Binkofski et al., 1998; Culham et al., 2003b, 2006; Frey et al., 2005), albeit the region is also activated by reaching alone (Culham et al., 2006; Filimon et al., 2009). Several lesion studies in humans and macaques have argued that the anterior intraparietal sulcus is causally involved in grasping (for review see Andersen et al., 2014). More than two decades ago, neurological patients with lesions in the anterior intraparietal sulcus were reported not to scale their grip appropriately for objects of different sizes, whereas the grip-scaling of patients without such lesions was similar to that of healthy controls (Binkofski et al., 1998, Jeannerod et al., 1994; Cavina-Pratesi et al., 2010b; see Section 3). Similarly, Gallese et al. (1994) found that inactivation of monkey AIP (an area thought to be homologous to the human anterior intraparietal sulcus) resulted in abnormal grip formation, particularly when a precision (finger-thumb) grip was required. Transcranial magnetic stimulation (TMS) studies in healthy participants confirm that disruption to the anterior intraparietal sulcus causes grasping impairments (Rice et al., 2006, 2007; Davare et a., 2007; Cohen et al., 2009; Vesia et al., 2013; Tonin et al., 2017) and deficits in rapid online corrections of grip aperture (Tunik et al., 2005; Glover et al., 2005; Rice et al., 2006; Le et al., 2014).

Interestingly, the anterior intraparietal sulcus is strongly activated by the mere presentation of pictures of graspable objects and, even more strongly, by pictures of tools (e.g., Chao and Martin, 2000; Buxbaum and Saffran, 2002; Boronat et al., 2005; Hermsdörfer et al., 2007; Peeters et al., 2009; Mruczek et al., 2013; Macdonald and Culham, 2015). The intraparietal sulcus region selective to pictures of tools (IPS-Tool) overlaps with an area that selectively responds to pictures of hands (IPS-hand) compared to pictures of bodies without hands (Bracci et al., 2016; 2018; Peelen et al., 2013). As we have argued elsewhere (Knights et al., 2020), stimulus features often thought to drive the organisation of category-selective visual areas, like form (Coggan et al., 2016), animacy (Konkle and Caramazza, 2013) or manipulability (Mahon et al., 2007), poorly explain this shared topography, because hands and tools differ on all of these dimensions. Instead, their overlap may reflect a joint representation of high-level action information related to skilful object manipulation (Bracci et al., 2012; 2016; Striem-Amit et al., 2017), perhaps coding the function of hand configurations relevant for complex hand-object interaction such as tool use (Perini et al., 2014; Bracci et al., 2018).

More sophisticated fMRI methods that allow real 3D tool manipulation in the scanner (e.g., Gallivan, et al., 2009; Valyear et al., 2012; Brandi et al., 2014; Styrkowiec et al., 2019; Knights et al,, 2020) and multivariate fMRI analysis routines (for a recent review see Gallivan and Culham, 2015) have further advanced our understanding of the role of the PPC in tool use. For example, such studies have revealed that certain areas within the PPC represent tool identity, the types of manipulation associated with tools (Brandi et al., 2014; Rossit et al., 2018) and are selective for familiar, but not arbitrary, actions performed with tools (Valyear et al., 2012). In our group, we have recently found that grasp-typicality representations (i.e., whether a tool is being grasped appropriately for use) are evoked from IPS-hand (Knights et al., 2020). We suggest that this region is optimized for processing hands and their movements and may represent complex manual responses in humans, such as tool manipulation.

Two further functional PPC subregions involved in visuomotor control are the superior parieto-occipital cortex (located in the medial surface of the PPC at the superior end of the parieto-occipital sulcus; e.g., Rossit et al., 2013) and the precuneus**.** Both areas have been repeatedly shown to play a role in visuomotor control of reaching and grasping movements, especially when directed to stimuli in peripheral vision (e.g., Connolly et al., 2003; Prado et al., 2005; Clavagnier et al., 2007; Filimon et al., 2009; Cavina-Pratesi et al., 2010a; Rossit et al., 2013; Vesia et al., 2017; but see Martin et al., 2015). Pitzalis et al. (2006) demonstrated that the human visual area V6 (in the close vicinity of the superior parieto-occipital cortex) shows a large representation of the lower visual field and, unlike other visual areas, does not have a preference for foveated stimuli (for a review of human V6 subdivisions see Pitzalis et al., 2015). In a similar vein, the superior parieto-occipital cortex over-represents near (versus far) gaze positions, perhaps for the processing of objects within graspable distance (Quinlan and Culham, 2007). Both the superior parieto-occipital cortex and precuneus also preferentially code 3D objects in near (within-reach) rather than far (out of reach) space (Gallivan et al., 2009) and are more active during real hand actions towards objects viewed in the lower than the upper peripheral visual field (Rossit et al., 2013). The superior parieto-occipital cortex and precuneus may thus be specialized for processing visual information within the space where hand actions most frequently occur (Rossit et al., 2013; Previc, 1990; Danckert and Goodale, 2003). Similarly, monkey neurophysiology has shown that neurons in the medial parietal cortex of area V6A, a visual area in the macaque thought to correspond to human superior parieto-occipital cortex, are also particularly sensitive to arm movements (for a recent review see Gamberini et al., 2020). Specifically, just like the human superior parieto-occipital cortex, macaque V6A neurons respond to both reaching and grasping (Fattori et al., 2017) particularly when directed to non-foveated peripheral objects (Marzocchi et al., 2008; Fattori et al., 2005, 2010). V6A neurons also over-represent the lower visual field (Gamberini et al., 2011) and are modulated by gaze position (Hadjidimitrakis et al. 2011, 2012; Breveglieri et al. 2012).

Nevertheless, neither V6A nor the superior parieto-occipital cortex are involved solely in visuomotor control. Both regions also play a role in attentional functions necessary to select salient information in the environment. Evidence from monkey neurophysiology has shown that V6A neurons, sensitive to peripheral arm movements, and modulated by gaze position, respond to covert shifts of attention (Galletti et al., 2010). These covert shifts enable attention to be directed to peripheral locations without moving the eyes (i.e., in conditions of fixed gaze), thus allowing V6A neurons to select reaching goals and to maintain and/or update the spatial coordinates of objects during hand movement (Galletti et al., 2010). In a similar vein, Ciavarro and colleagues (2013) report that 'virtual lesions' to the anterior superior parieto-occipital cortex in healthy participants caused increased reaction times during both attentional and reaching tasks to targets preceded by an invalid cue (i.e., in a different location than the target), but not to validly cued targets (i.e., cue appeared in the same location as target). The authors suggest that attentional reorienting signals in the superior parieto-occipital cortex are used to rapidly update ongoing actions to behaviourally relevant objects presented at unattended locations. Taken together, these results suggest that the role of the superior parieto-occipital cortex in visuomotor control depends on whether gaze is fixed or not and that this region may also participate in attentional functions such as encoding signals for shifting attention between peripheral locations and peripheral reach goals (e.g., Yantis et al., 2002; Vesia et al., 2010; Ciavarro et al., 2013, Clavagnier et al., 2007).

While functional brain imaging can reveal which brain areas are activated during visuomotor behaviours, stronger causal inferences about the critical roles of these areas are supported by studying the functional consequences of disruption to the PPC, which we consider in the next section.

3. Optic ataxia: a disruption of visuomotor mechanisms

Early evidence that the PPC is involved in the visual guidance of reaching came from clinical observations of brain-damaged patients. The Hungarian neurologist, Rezsö Bálint, wrote a case study of a man with severe disturbances of attention and action, whose subsequent autopsy showed to have bilateral lesions of the PPC (Bálint, 1909, portions translated to English by Harvey, 1995). This case study provided a detailed description of a complex clinical pattern, now known as Bálint's syndrome. Bálint's careful observations isolated one component of this patient's condition as inaccurate reaching with his right hand towards visual targets. This could not be ascribed to a general visual problem, because he could reach accurately to the same targets with his left hand, nor to a general motor problem, because the right hand could reach without error to non-visual targets such as body parts. Bálint named this misreaching symptom 'Optic Ataxia' because it seemed to be a visual (optic) form of motor incoordination (ataxia): a specific *visuomotor* impairment.

Other neurologists in the same era, studying the consequences of gunshot wounds to posterior brain regions of soldiers, also noted disturbances of reaching movements, eye movements, and visuospatial awareness (Inouye, 1909, translated to English by Glickstein and Fahle, 2000; Smith and Holmes, 1916). Holmes (1918) observed that misreaching was more severe for visual targets in peripheral vision, and sometimes worse in one visual field than the other. Many of these soldiers probably had optic ataxia, but the co-occurrence of disordered eye movements and attention made the misreaching difficult to characterise separately. Indeed, Holmes saw misreaching as just one expression of a general 'visual disorientation', a failure to localise objects by sight, rather than a specific visuomotor problem.

A resurgence of interest in optic ataxia came, towards the end of the twentieth century, from the study of relatively 'pure' cases following unilateral brain lesions, less severely affected by concurrent deficits of eye movements and attention. In 1988, Perenin and Vighetto published a study of ten patients with prominent misreaching after unilateral parietal lesions (3 right hemisphere, 7 left hemisphere). The study included neuropsychological and neurological examinations, and video-analyses of visually-guided reaching and grasping. The patient gazed straight ahead at the camera and reached with either hand to grasp a large pencil, or post the hand through a slot, presented at a variety of visual locations. The patients were impaired in reaching for the pencil, and in orienting the hand to match the slot, but the errors were modulated by where the target was presented, and which hand was used. Misreaching usually showed a 'field effect', being more severe for the contralesional visual field (i.e., the left field for a lesion in the right hemisphere, and vice-versa), and often showed a 'hand effect', being more severe for the contralesional hand. Most patients showed both patterns to some degree, so that coordination was usually worst for the contralesional hand in the contralesional field (Fig. 3A; see also Rondot et al., 1977).

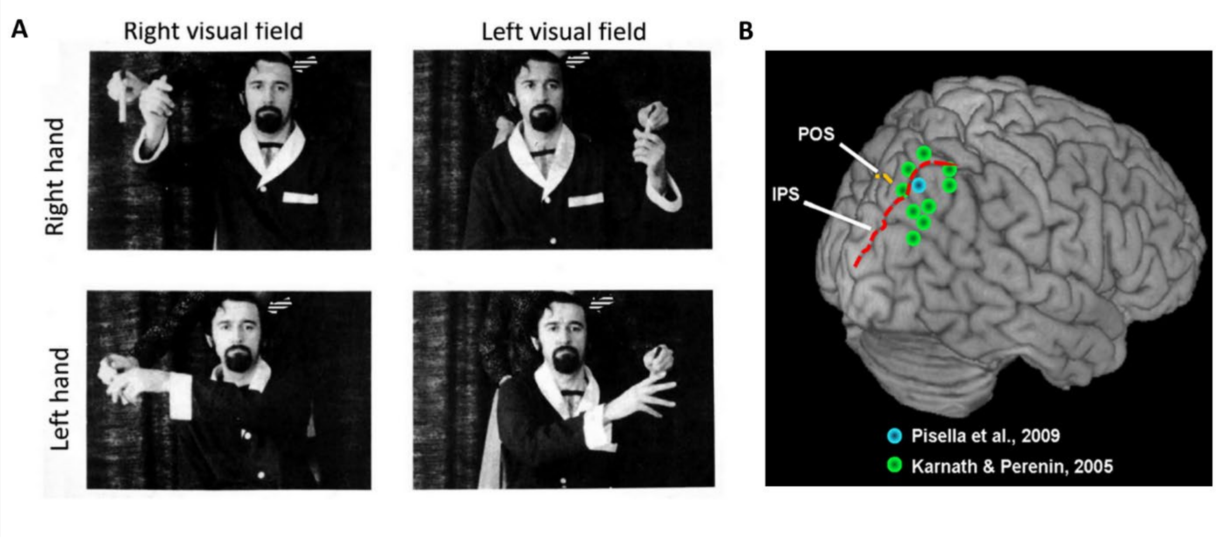

Figure 3. (A) Misreaching errors exhibited by patient with right optic ataxia when the pen is presented in his contralesional (right) visual field (field effect) and when he is required to grasp it with the contralesional (right) hand (hand effect). The arrow indicates that the responsible brain lesion is the left hemisphere. Reproduced with permission from Pisella et al. (2021). **(B)** 3D rendering of the right-hemisphere of the human brain (using MRICROn software: https://www.nitrc.org/projects/mricron). The locations depicted in the figure represent the lesion locations most frequently associated with optic ataxia in Karnath and Perenin's analysis (2005; in green) and Pisella et al. (2009; in blue). For guidance the following sulci are also delineated: IPS, Intraparietal Sulcus; POS, Parietal-Occipital Sulcus. Reproduced with permission from Harvey and Rossit (2012).

In contrast, accuracy was almost always close-to-normal when the targets were presented centrally, or if the patients were first required to turn their head and eyes to the target. Errors were still sometimes made with the contralesional hand, but these were usually minor and could be corrected before completion of the movement. This ‘non-foveal’ pattern of optic ataxia, with a preservation of performance in central vision, is very typical after the acute stages of brain injury, or prior to advanced stages of degeneration. Non-foveal optic ataxia may cause minimal disruptions in daily life, because we can usually direct our gaze to look at the things we reach for, though problems are more likely if an action-relevant object is in peripheral vision, for instance when guiding the foot onto a flight of stairs. A special assessment, along the lines of Perenin and Vighetto’s procedure, is required to expose the symptom clinically (e.g., Borchers et al., 2013). Inaccurate reaching to peripheral vision, with accurate reaching to central vision, is indicative of optic ataxia (Rossetti et al., 2019).

In 2005, Karnath and Perenin analysed structural brain imaging data (CT or MRI) from 16 patients diagnosed with optic ataxia following unilateral lesions. Karnath and Perenin used a lesion-subtraction analysis (see Rorden and Karnath, 2004) to investigate whether specific areas of brain damage distinguished this group from 36 unilateral stroke patients without optic ataxia. The lesions most frequently associated with optic ataxia were in the lateral and medial parieto-occipital junction in both hemispheres. As can be seen in Fig. 3B, laterally the centre of lesion overlap affected the junction between the inferior parietal lobule, superior parietal lobule, and the superior occipital cortex. The lesion overlap also extended medially to the precuneus, close to the parieto-occipital sulcus. Similar results were later reported by Pisella et al. (2009; see Fig. 3B), whose lesion overlap of patients with optic ataxia was centred in parieto-occipital regions. A subsequent experiment using online TMS to disrupt these brain areas in healthy participants (without brain lesions) found increased variability of reaching movements when the medial part of the intraparietal sulcus was targeted, and spatially inaccurate reaches when the superior parieto-occipital cortex was targeted, further supporting the critical involvement of these regions in visually-guided reaching (Vesia et al., 2010).

Notably, the misreaching errors induced by TMS deactivation of the superior parieto-occipital cortex showed a spatial bias towards the point of fixation, which corresponds to the prevailing pattern of spatial bias in optic ataxia. Blangero et al. (2010; see also: Ratcliff and Davies-Jones, 1972) charted the patterns of reaching errors in seven patients with unilateral optic ataxia, finding a consistent bias towards fixation when reaching for targets in the contralesional field, with the size of the reaching error increasing exponentially with target eccentricity (Vindras et al., 2016). This pattern is consistent with the hypothesis that reaching to the point of gaze is the default arrangement for hand-eye coupling, and that coordinate transformations allowing for any other arrangement are dependent upon parieto-occipital visuomotor modules with a rich representation of the peripheral visual field (Rossit et al., 2013). One prediction would be that, if the damage were sufficiently severe, then patients would always reach to the point of fixation, whatever the target position. This pattern, known as ‘magnetic misreaching’, can indeed be observed in some cases of bilateral parieto-occipital stroke, or degeneration (Buxbaum and Coslett, 1997; Carey et al., 1997; Jackson et al., 2004).

Clinical observations and experimental research have also established other aspects of visuomotor impairment in optic ataxia. Perenin and Vighetto (1988) noted that as well as reach-to-grasp movements being misdirected, orienting of the wrist and pre-shaping of the hand are also commonly impaired. That is, optic ataxic patients often extend a flat hand, with little or no shaping of the grasp before object contact (Jeannerod, 1986; Jeannerod et al., 1994). Patients with optic ataxia are also slow to update an ongoing reach if the target is suddenly moved, suggesting an impairment of online correction mechanisms (e.g., Gréa et al., 2002; McIntosh et al., 2011; Pisella et al., 2000), and they may fail to adjust the path of their reach to take account of potential obstacles (Schindler et al., 2004). Moreover, although optic ataxia is defined by misreaching, placement of the feet can also be inaccurate, suggesting that the impaired visuomotor transformations are not tightly specific to arm movements (Evans et al., 2013).

It is not yet clear whether these additional features of optic ataxia are separable symptoms or just further manifestations of the core visuomotor problem. For instance, a failure to pre-shape the grasp might be due to a separable impairment of a module controlling grip shaping, or it could be that the patient extends a flat hand in order to ‘cast a wide net’ as a secondary compensation for the spatial inaccuracy of the reach. Cavina-Pratesi et al. (2010) designed an ingenious experiment to test between these possibilities in a patient with optic ataxia. They found that grip scaling was considerably more impaired when the patient reached to grasp a distant object, than when he had to form the grasp to enclose a nearby object, suggesting that the grip-shaping deficit was a secondary consequence of an inaccurate reach. This does not mean that separable grip-scaling deficits could not arise, but there is no positive evidence for this at present.

Many other questions about the character and causes of optic ataxia require further investigation. For instance, it is likely that optic ataxic field and hand effects have distinct functional bases, the former depending upon impaired coding of visual target position, and the latter on impaired coding of effector position from proprioceptive information (Blangero et al., 2007). Research into this and other issues has been hampered by the fact that it is rare to find patients with optic ataxia that is not complicated by impairments of attention or perception. Indeed, in recent years, it has been suggested that some degree of attentional impairment may always accompany optic ataxia, and should perhaps be understood as part of the same functional deficit (Aguilar-Ro et al, 2021; McIntosh et al., 2011; Pisella et al., 2007, 2021). This is consistent with recent evidence that the superior parieto-occipital cortex and V6A are involved in shifting attention between peripheral locations and peripheral reach goals (e.g., Yantis et al., 2002; Vesia et al., 2010; Ciavarro et al., 2013; see Section 2). Overall, studies of patients with optic ataxia provide convincing evidence for a critical role of the PPC in visually-guided action, but may be less well-suited to mapping the finer functional details. Naturally-occurring brain lesions are often large, and do not respect anatomical or functional boundaries; so more controlled methods such as TMS will also be essential to understanding which brain regions are causally involved in which aspects of visuomotor behaviour in humans.

4. Summary

Visually-guided actions, such as reaching to grasp a mug, involve complex visuomotor processing, perhaps especially when these actions are directed towards peripheral locations. Brain imaging and stimulation studies with healthy humans, macaque neurophysiology, and studies of human neurological patients converge in showing that regions within the posterior parietal cortex (the anterior intraparietal sulcus, precuneus and superior parieto-occipital cortex) are specialised for such visuomotor functions. Notably, the superior parieto-occipital cortex also seems to be involved in attentional processing, and future studies will elaborate further on the functional links between attention and visuomotor processing in the PPC.

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List of relevant webpages

- In this captivating TED talk, Prof. Daniel Wolpert discusses how the brain evolved, not to think or feel, but to control movement: https://www.ted.com/talks/daniel_wolpert_the_real_reason_for_brains?language=en
- *fMRI for Newbies* is a webpage developed by Prof. Jody Culham that features great resources regarding brain anatomy and fMRI techniques covered in this chapter: http://www.fmri4newbies.com/
- Prof. Melvyn Goodale talk '*Visual Routes to Knowledge and Action: (almost) 25 Years of Two Visual Systems*': https://www.youtube.com/watch?v=Te4xmwI1Y_k
- In this video a neurologist (Prof. Bob Rafal) tests a patient with optic ataxia: https://www.youtube.com/watch?v=BkOb9FR5Lgk

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