

Perspective Review:

**Cortical Mechanisms for Transsaccadic Vision:
Extrinsic and Intrinsic Feature Updating**

Abbreviated Title: Cortical Mechanisms for Transsaccadic Vision

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Number of Figures: 8

Number of Supplementary Figures: 0

Number of Tables: 1

Number of Words (Abstract): 238

Number of Words (Introduction): 491

Number of Words (Discussion): 1577

Declarations of Interest: none.

Abstract

Transsaccadic vision is typically described as the ability to retain and integrate visual information across rapid eye movements (saccades) for the purpose of continuous perception. In this review, we break this down further into two fundamental processes: the cortical mechanisms that maintain extrinsic spatial properties (i.e., location, orientation) versus intrinsic identity cues (i.e., spatial frequency, shape) of objects across saccades. First, we summarize the computational problems associated with transsaccadic vision, emphasizing the need to retain and integrate both extrinsic and intrinsic feature information between fixations for predictive vision. Next, we briefly review psychophysical, neurophysiological, stimulation, and neuroimaging evidence that specific cortical mechanisms exist for these processes. Then, we focus on our recent experiments combining functional magnetic resonance imaging adaptation-inspired and functional connectivity approaches. These experiments suggest that parietal cortex (specifically, right supramarginal gyrus) contributes to spatial updating of object orientation, whereas dorsomedial occipital cortex (cuneus) supports updating of spatial frequency and object shape. Taken together with the previous literature, this supports the notion that an ‘extended parietal eye field’ is involved in the updating of extrinsic spatial cues, whereas dorsomedial occipital cortex is involved in updating intrinsic cues to object identity, both in communication with the broader functional networks for perception and action. Finally, we synthesize these results in a simple conceptual model for cortical updating and integration of object features and consider the implications for future studies of transsaccadic integration, the ‘binding problem’, and possible clinical applications.

Keywords

saccades, visual memory, integration, spatial updating, object features, fMRI adaptation, functional connectivity

Highlights

- The role of transsaccadic vision is discussed in terms of updating and integrating both extrinsic spatial features and intrinsic identity cues.
- Cortical mechanisms are reviewed for transsaccadic feature updating and memory, with emphasis on recent imaging and functional connectivity analysis.
- A conceptual model is proposed with separate mechanisms for transsaccadic updating of extrinsic vs. intrinsic object features.

- Future directions focus on conceptual progress and clinical applications.

Introduction

Humans make two to three saccades per second to align the fovea with objects of high interest in the visual field (Wade et al., 2003; Yarbus, 1967). By allowing the brain to focus on foveal information, rather than the entire visual field, this adaptation saves both cortical space and computational costs (Herwig, 2015). However, it also creates several computational challenges for the brain, with constant visual interruptions and repositioning of the retina relative to the world (Binda & Morrone, 2018a; Hamker et al., 2008; Ibbotson & Krekelberg, 2011; McFarland et al., 2015; Melcher & Colby, 2008; Teichert et al., 2010; Wurtz, 2008). The study of transsaccadic vision is sometimes regarded to be an esoteric topic, i.e., the intersection of the vision and saccade fields, but the reality is that sustained fixation is largely a laboratory phenomenon. Thus, transsaccadic vision *is* normal vision, so understanding its mechanisms is central to an understanding of vision itself.

To understand transsaccadic vision, one must first agree on its purpose. Many investigators have stated that the ultimate purpose of transsaccadic vision is to maintain a stable percept despite eye movements (Baltaretu et al., 2023; Bridgeman et al., 1994; Higgins & Rayner, 2015; Honda, 2006; Mathôt & Theeuwes, 2011; Melcher & Colby, 2008). While this is true from a subjective perspective, from an evolutionary viewpoint the primate visual system developed in a dynamic world full of moving animals and weather phenomena, now expanded to include people and vehicles, so stability in itself cannot be a biological imperative. From a more objective biological viewpoint, the visual system needs to identify *what* objects are, *where* they are, and do this rapidly enough to allow us to interact with the world in real time (Hayhoe, 2017; Hayhoe et al., 2025; Hayhoe & Ballard, 2005; Hayhoe et al., 2012; Land & Tatler, 2009). Done correctly, this ultimately will lead to the subjective perception of stability when our visual surroundings are stable (or not), appropriately reflecting the external reality that surrounds us.

From this biological viewpoint, the question is, how does the visual system serve its fundamental purpose in the face of constant eye movements? Just over 15 years ago,

Melcher and Colby (2008) published a landmark review that outlined several principles of transsaccadic perception based on the knowledge we had at that time. A few years later, our current lab proposed more specific cortical mechanisms based on the transcranial magnetic stimulation (TMS) data available at that time (Prime et al., 2011). However, considerable advances have been achieved since then. Here, we update this topic by reviewing the computational challenges associated with transsaccadic vision and the psychophysical, neurophysiological and neuroimaging evidence for specific mechanisms, with a focus on our recent transsaccadic adaptation studies (Baltaretu et al., 2020, 2021, 2023; Dunkley et al., 2016; Tomou et al., 2025). This evidence leads us to argue that there are separate cortical mechanisms for transsaccadic updating, approximately corresponding to the ‘what’ and ‘where’ functions described above.

The Computational Problem(s) of Transsaccadic Vision.

Transsaccadic vision poses several specific computational problems for the brain. In the following text and Figure 1 we break these down into four problems and their solutions.

Visual Smear / Suppression. Saccades cause retinal motion relative to the world, which could result in blurred vision and/or confusion between self-generated and external motion (Campbell & Wurtz, 1978; Castet & Masson, 2000; Idrees et al., 2020; Ilg & Hoffmann, 1993; Judge et al., 1980; Shioiri & Cavanagh, 1989). In theory, efference copies (the internal sense of eye motion from the motor system) could cancel this motion to offer continuous visual perception during saccades (Helmholtz, 2013; Sherrington, 1918; Sommer & Wurtz, 2008; Subramanian et al., 2019; Sun & Goldberg, 2016; von Holst & Mittelstaedt, 1950). However, this is biologically limited by the ability of the visual system to process high speeds of motion and generate perfectly calibrated efference copies in space and time (Castet & Masson, 2000; Shioiri & Cavanagh, 1989). As a result, perisaccadic vision (vision during saccade execution) is blurred and thus suppressed through both passive and active mechanisms, leaving most people effectively blind during saccades (Bremmer et al., 2009; Castet & Masson, 2000; Diamond et al., 2000; Higgins & Rayner, 2015; Kleiser et al., 2004; Matin, 1974; W. Richards, 1969; Schweitzer et al., 2025; Shioiri & Cavanagh, 1989; Thilo et al., 2004; Wurtz, 2008; Zimmermann, 2020; though, see also Idrees et al., 2020). This gives rise to a second problem:

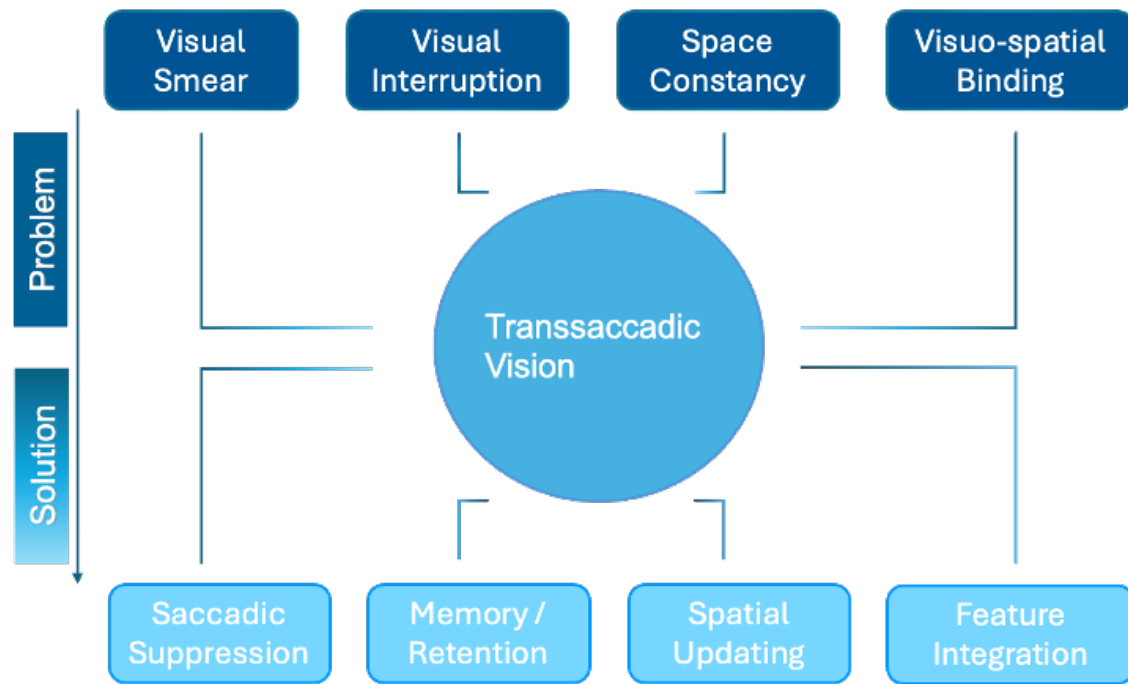


Fig. 1. Computational problems associated with transsaccadic vision. Highlighted are the four main problems (upper boxes; dark blue) associated with transsaccadic vision (i.e., perception across saccades), along with the corresponding solutions (lower boxes; light blue). See main text for references.

Visual Interruption / Transsaccadic Memory. Saccades frequently interrupt vision for 30-100 ms (Bahill et al., 1975; Enderle, 2005). Then, an additional ~100-200 ms is required to transmit and process visual information in the cortex (Amano et al., 2006; Hegdé, 2008; Lamme & Roelfsema, 2000; Matin, 1974; Matin et al., 1993; Ross et al., 2001; Wutz et al., 2016; Yoshor et al., 2007). If the brain simply discarded all the information from previous fixations (O'Regan & Noë, 2001), this would render humans effectively blind half the time – a dangerous situation for any species. Fortunately, it appears that at least some important information is retained (i.e., remembered) and available for predictive processing at the new gaze position (Blackmore et al., 1995; Burr et al., 1994; Kong et al., 2021; Prime et al., 2007, 2010, 2011; Tanaka et al., 2014), at least until visual information can be processed (see next section for details).

Space Constancy / Spatial Updating. This leads to a third challenge for transsaccadic vision: because saccades discretely re-orient the retina relative to the world, any new

visual information entering the retina will not be in spatial register with the original visual information (Crespi et al., 2011; Geng et al., 2008; Graef et al., 2001; Jonikaitis & Belopolsky, 2014; Luabeya et al., 2024; Shafer-Skelton et al., 2017). This requires some additional mechanism to *spatially update* information across fixations (Deubel et al., 2010; Hamker et al., 2011; Klier & Angelaki, 2008; Mohsenzadeh et al., 2016; White & Snyder, 2007). In subsequent sections of this review, we will consider several potential mechanisms that have been proposed to solve this problem.

Binding Problem / Feature Integration. This final computational problem is central to transsaccadic vision, but poorly understood. As noted above, it is not enough to know *where* things are; it is also necessary to know *what* they are. More specifically, we need to know the spatial location, orientation and motion of objects, and we need to use object-specific stimuli to infer the identity of their source. And further, all this information (both stored and new) must be properly integrated across saccades to optimize predictive vision. This is particularly important in tasks that require integration of foveal vision across many saccades, such as scene perception and recognizing large complex objects (Blackmore et al., 1995; Castelhana & Henderson, 2005; Choi et al., 2025; Dowd & Golomb, 2020; Hayhoe et al., 1991; Hegdé, 2008; Kovacs & Harris, 2019; Oostwoud Wijdenes et al., 2015; Reuther et al., 2020; Shafer-Skelton et al., 2017; Williams & Castelhana, 2019).

In the following sections of this review, we will focus mainly on the latter three aspects of transsaccadic vision (memory, updating and integration), specifically, as it relates to the ‘where’ and ‘what’ aspects of vision.

Psychophysical Evidence for Transsaccadic Memory and Integration.

Memory Capacity. In the past, opinions about the capacity of transsaccadic memory have varied wildly from essentially nothing (Bridgeman et al., 1975; Bridgeman & Mayer, 1983; Bridgeman & Stark, 1979; O’Regan & Noë, 2001) to highly detailed information (Castelhana & Henderson, 2005; Henderson & Hollingworth, 2003; Parker & Tas, 2025). The current consensus is that transsaccadic memory (maintenance of visuospatial information across eye movements) is attention-dependent and has a limited capacity similar to visual working memory, and likely shares many of the same mechanisms (Awh

et al., 2006; Cronin & Irwin, 2018; Deubel et al., 2002; Hollingworth et al., 2008; Irwin & Gordon, 1998; Prime et al., 2007; Stewart & Schütz, 2018; Tanaka et al., 2014; Theeuwes et al., 2009, 2011), subject to certain nuances discussed below. In practice, this amounts to 3-4 visual objects (Irwin, 1992, 1993; Irwin & Gordon, 1998; Kong et al., 2021; Prime et al., 2007); although, ‘limited resource models’ suggesting the mechanism is not discrete (Bays & Husain, 2008). Moreover, transsaccadic vision involves the retention and integration of *multiple* ‘what’ and ‘where’ object features. In the following, we expand this notion to two feature categories: *extrinsic spatial properties* and *intrinsic identity cues*.

Extrinsic Spatial Properties. We refer to object location, orientation (of the entire object), and motion as ‘extrinsic’ spatial properties, because they are generally imposed upon objects by external forces, as opposed to arising from the object. The visual system has the capacity to preserve the spatial properties of at least some task-related objects across saccades (Hayhoe, Aivar, et al., 2003; Hayhoe et al., 1992; Hayhoe, Shrivastava, et al., 2003; Land et al., 1999; Land & Hayhoe, 2001). This notion dates back to von Helmholtz (1866; trans. Helmholtz, 2013) and has been confirmed by countless studies (Bays & Husain, 2007; Binda & Morrone, 2018; Burr & Morrone, 2011; Deubel et al., 2002; Irwin & Gordon, 1998; Hallett & Lightstone, 1976; Higgins & Rayner, 2015; Melcher & Colby, 2008; Prime et al., 2011). For example, Prime et al. (2006) showed that participants can compare lines glimpsed from different gaze fixations to compute their intersection point (Fig. 2A), requiring updating and integration of both line location and orientation.

How is this done at the computational level, in the brain? It has been shown that some visual information remains linked to its original retinal location after saccades (Afraz & Cavanagh, 2009; Chiu & Golomb, 2025; Choi et al., 2025; Golomb & Kanwisher, 2012b; Harrison & Bex, 2014; Knapen et al., 2009; Mathôt & Theeuwes, 2013; Shafer-Skelton et al., 2017; Shafer-Skelton & Golomb, 2018), but this does not explain the type of spatial updating and integration described above. One possibility is that this information is transformed, using eye and head position signals, into higher-level egocentric frames fixed to the head or body (Graef et al., 2001; Karn et al., 1997; Yang et al., 2024). While there is evidence that this occurs in other systems for multisensory integration, spatial cognition, and motor control (Avillac et al., 2005; Caruso et al., 2021; Duhamel et al.,

1997; Mullette-Gillman et al., 2005; Pouget et al., 2002; Smith & Crawford, 2005), there is relatively little physiological evidence that this mechanism is dominant in the visual system. A popular alternative is that limited amounts of spatial information can be updated (see neural mechanisms below) (Andersen et al., 1985; Cavanaugh et al., 2016; Colby et al., 1995; Duhamel et al., 1992; Gancarz & Grossberg, 1999; Henriques et al., 1998; Lee & Tehovnik, 1995; Mays & Sparks, 1980b; Sparks, 1989). Network modeling studies have shown that visual information can then be transformed into motor frames without the need for intermediate spatial frames (Blohm et al., 2009; Smith & Crawford, 2001, 2005).

Visual landmarks (i.e., allocentric cues) are also known to augment this transformation process (Byrne et al., 2010; Byrne & Crawford, 2010; Golomb et al., 2010; Lisi et al., 2015). Landmarks appear to be most important when they are close to the target (Deubel, 2004), embedded in context (Germeys et al., 2004), when target reliability is low (Byrne & Crawford, 2010; Hayhoe et al., 1992; Karn et al., 1997), and for longer-term stability (Boon et al., 2018; Chen et al., 2014). Note that these mechanisms are not mutually exclusive: transsaccadic integration is thought to integrate target, saccade, and landmark information in an optimal fashion (Byrne et al., 2010; Niemeier et al., 2003, 2007).

Intrinsic Object Features. In addition to preserving spatial locations and orientations across saccades, the brain must retain identity information. One simple purpose of this is to ensure that the correct object has been targeted (Poth & Schneider, 2016). However, when identification requires multiple foveal fixations to determine an object's identity, this means updating specific object features like spatial frequency, shape, color, and texture (Fig. 2B). We refer to these as 'intrinsic' features, because they arise (in part) from physical properties of the object itself. While not everything may fit neatly into this intrinsic-extrinsic distinction (e.g., shape from shadow depends on both the object and external lighting), the distinction is generally useful.

An uptick in progress has been made to better understand the processing of intrinsic features (Goktepe & Schütz, 2023; He et al., 2017; Hübner & Schütz, 2021a, 2021b; McConkie & Currie, 1996; Moussaoui et al., 2025; Parker & Tas, 2025; Schütz & Souto, 2015; Sharvashidze et al., 2024; Tas & Parker, 2023; Wagner & Schütz, 2023; Wittenberg et al., 2008; Wolf et al., 2019), despite being less understood compared to spatial

updating. Features, such as color, have been shown to draw saccades toward postsaccadic targets that match those of presaccadic cues (Hollingworth et al., 2013), suggesting an interaction between saccades and color perception (Bompas & O'Regan, 2006; Spering et al., 2008). Changes in surface features and spatial frequency across

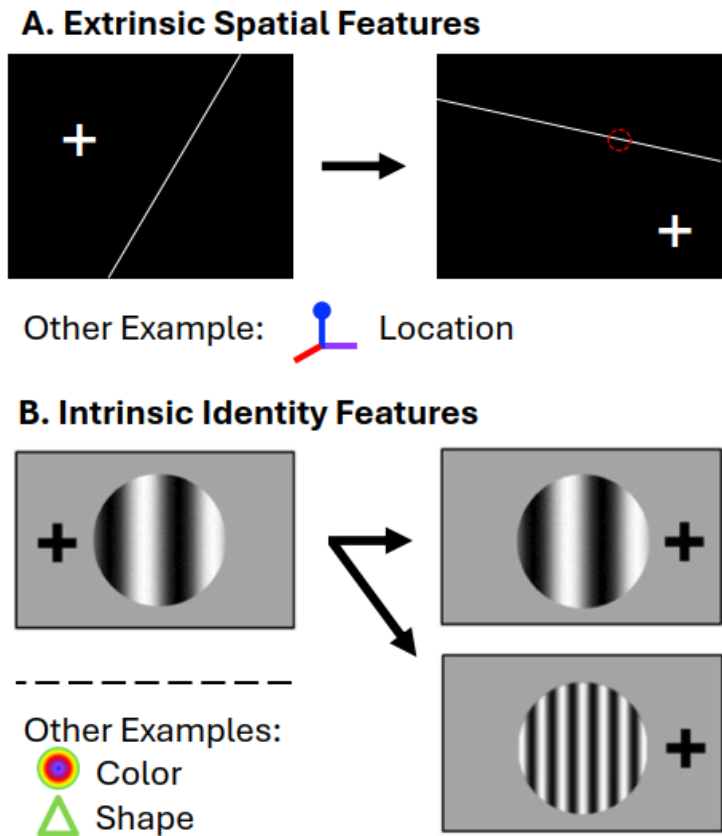


Fig. 2. Transsaccadic visual paradigms, contrasting extrinsic (A) vs. intrinsic (B) feature updating. A) A modified, pared down depiction of a paradigm (Prime et al., 2006) that was used to test the updating of line orientations (extrinsic object feature) across a saccade in order to indicate where they intersect (red circle). B) This simplified paradigm (Baltaretu et al., 2021) tested the updating of an object's spatial frequency (intrinsic object feature) across a saccade and required a same / different judgment. Other examples include location and motion for extrinsic features, and color and shape for intrinsic features.

saccades have also been shown to influence object identification (Richard et al., 2008; Tas et al., 2012; Herwig & Schneider, 2014). Finally, when triangular and circular objects were interchanged across saccades, percepts were drawn toward the shape of the postsaccadic target (Herwig et al., 2015; Hübner & Schütz, 2021a; Melcher, 2005). It is

thought that transsaccadic perception of such object features helps to maintain perceptual continuity (Demeyer et al., 2010; Köller et al., 2020; Tas et al., 2012), though this is only possible if the brain maintains identity information across saccades. If such a distinction is useful in studying perceptual effects on behaviour for extrinsic and intrinsic object feature updating across saccades, is this also observed in the brain?

Primate Neurophysiology.

Primate neurophysiology studies have mainly focused on the spatial updating / remapping of location information across saccades. Sparks and Mays first showed that the superior colliculus updates the saccade vector plan when interrupted by an intervening saccade (Freedman & Sparks, 1997; Mays & Sparks, 1980a; Sparks, 1986; Sparks & Mays, 1983). Duhamel et al. (1992) later showed that neurons in the lateral intraparietal cortex (LIP) show predictive 'remapping', i.e., a pre-saccadic extension of their eye-centered response fields to include the future location of a flashed visual stimulus (Gottlieb & Goldberg, 1999; Gottlieb et al., 1998; Heiser & Colby, 2006; Kusunoki et al., 2000). From a functional perspective, this is equivalent to predictive updating of the memory trace, driven by an efference copy of the saccade plan (Colby et al., 1995; Gottlieb et al., 1998; Kusunoki et al., 2000; Mohsenzadeh et al., 2016; Sommer & Wurtz, 2008; Sun & Goldberg, 2016).

These results have been extended to various visual and visuomotor areas of the brain, ranging from occipital to frontal cortex (Batista et al., 1999; Hartmann et al., 2017; Merriam et al., 2003; Nakamura & Colby, 2002; Neupane et al., 2016; Umeno & Goldberg, 2001; Walker et al., 1995). Other studies have confirmed that the corpus callosum is required when saccades necessitate remapping of information across visual fields / cerebral hemispheres (Albano & Wurtz, 1982; Berman et al., 2005, 2007; Colby et al., 2005).

One more recent study suggested that the predictive signals might not be as spatially specific as originally assumed (Zirnsak & Moore, 2014). This appears to be different for different cells (Hartmann et al., 2017; Neupane et al., 2016), and might depend on the task-relevance of the stimulus. Response field activation for task-relevant stimuli (e.g., those required for action) disperses during saccades (Colby et al., 1995; Gottlieb et al., 1998; Kusunoki et al., 2000; Mohsenzadeh et al., 2016; Sommer & Wurtz, 2008; Sun &

Goldberg, 2016), but remains spatially selective. This is perhaps most clear during smooth pursuit, where visual memory is continuously updated retinotopically in a precise fashion (Dash et al., 2015, 2016; Fukushima et al., 2013; Krauzlis, 2004).

Less is known about the transsaccadic neurophysiology of updating other visual features. Most spatial updating studies did not consider features beyond location (Duhamel et al., 1992; Gottlieb & Goldberg, 1999; Hartmann et al., 2017; Kusunoki et al., 2000; Neupane et al., 2016; Umeno & Goldberg, 2001; Walker et al., 1995). Two notable exceptions are that LIP shows modest transsaccadic updating of shape-related information (Subramanian & Colby, 2014) and the superior colliculus appears to retain and update orientation information across saccades (Chen & Hafed, 2018; Fracasso et al., 2023), but it is widely believed that these updating processes contribute to transsaccadic feature updating (Khayat et al., 2004; Melcher & Colby, 2008; Prime et al., 2008, 2011; X. Wang et al., 2024).

Finally, numerous studies have explored the role of the visual ventral stream and hippocampus in the configurational relationships underlying object perception and spatial cognition respectively (for reviews, see: Ayzenberg & Behrmann, 2022; Bi et al., 2016; Burgess, 2008; Grill-Spector, 2003; Hartley et al., 2014; Martin & Barense, 2023; Murray et al., 2007; Palmeri & Gauthier, 2004). Recent neurophysiological experiments in monkeys suggest that landmark information (possibly from this source) converges with egocentric saccade target information in frontal cortex to stabilize saccade target coding (Bharmauria et al., 2025).

TMS Studies.

Online transcranial magnetic stimulation (TMS) provides a safe way to disrupt local cortical processing in humans during transsaccadic behaviors (Table 1). For example, Morris et al. (2007) showed that online TMS pulses over parietal cortex during saccades can disrupt the updating of location information. Perisaccadic single-pulse TMS over right inferior parietal cortex reduced the memory capacity of stimulus orientation from the usual 3-4 objects to just one, consistent with a loss of spatial information (Prime et al., 2008). This was interpreted as a loss of the saccadic updating signals, but there was still a weaker effect during fixation that might suggest a broader role (see 'cortical feature

updating' below). Stimulation over the frontal eye fields (FEF) had bilateral saccade-specific effects (Prime et al., 2010), consistent with a more specific loss of efferent updating signals (Duhamel et al., 1992; Goldberg & Bruce, 1990; Sommer & Wurtz, 2008).

Table 1. Summary of TMS studies on transsaccadic updating.

TMS Site	Transsaccadic Vision Affected	Reference
Right Parietal Cortex (IPS)	Disruption of Spatial Updating	Morris et al. 2007
Right Inferior Parietal Cortex (PEF)	Reduced Orientation Memory Capacity	Prime et al. 2008
Left & Right FEF	Reduced Orientation Memory Capacity	Prime et al. 2010
Left & Right Early Visual Cortex (V1/V2)	Disrupt Updating into Affected Field	Malik et al. 2015
Left dlPFC	Peri-saccadic Disinhibition	Tanaka et al. 2014
Right dlPFC	Post-Saccadic Disinhibition	Tanaka et al. 2014

In similar TMS experiments, unilateral stimulation over early visual cortex (EVC) disrupted transsaccadic updating of visual orientation, but only when the saccade brought the remembered stimulus *into* the visual field corresponding to the TMS-stimulated cortical hemisphere (Malik et al., 2015). TMS stimulation over dorsolateral prefrontal cortex (dlPFC) produced more complex effects, including either increased or decreased performance, depending on the timing of the pulse relative to saccade onset and the hemisphere stimulated (Tanaka et al., 2014). This is consistent with the distinction between spatially-specific mechanisms in early visual cortex versus more complex top-down control and working memory related processes in prefrontal cortex (Barbey et al., 2013; Funahashi, 2014; Grimault et al., 2009; Johnson et al., 2007; Levy & Goldman-Rakic, 1999; Pierrot-Deseilligny et al., 2003; Rossi et al., 2009; Tanaka et al., 2014).

Based on the latter experiments, it was proposed that transsaccadic feature integration might involve feedforward, lateral, and recurrent connections, involving feedback of

fference copies and top-down signals to the more orderly occipital retinotopic maps (Prime et al., 2007, 2008, 2010, 2011). This was consistent with models of transsaccadic vision (Hamker, 2003, 2005) and imaging studies (Harrison & Tong, 2009).

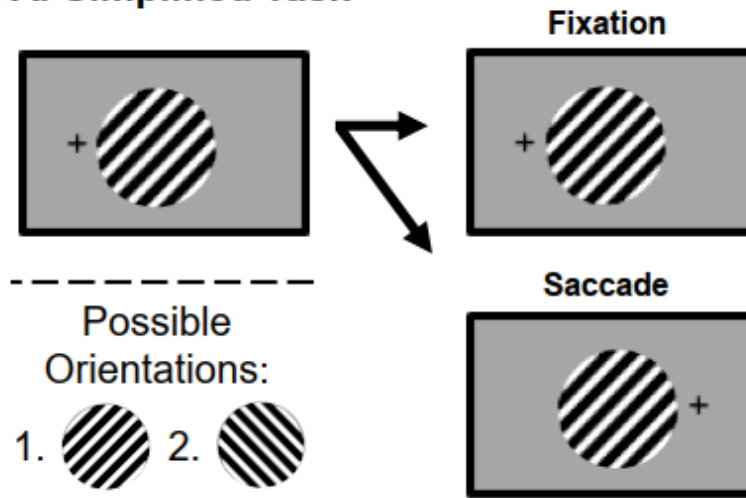
Classic fMRI Spatial Updating / Remapping Studies.

Functional magnetic resonance imaging (fMRI) experiments in the early 2000s focused on spatial updating of a point object across saccades (Medendorp et al., 2003; Merriam et al., 2003, 2007). One barrier to this is the relatively low temporal resolution of fMRI data relative to the duration of a saccade. To overcome this, investigators prolonged their event-related tasks and compared univariate activation before and after the saccade. Merriam et al. (2003) employed a single-step task (visual stimulus followed by a saccade), whereas Medendorp et al. (2003) used a double-step task, where a first saccade was followed by a second saccade or reach toward the remembered target. The results of both experiments lent strong support to the notion that the human parietal eye fields (putative monkey LIP) also update / remap gaze-centered information during saccades, in particular across hemispheres when saccades reverse the visual field of the remembered stimulus (Medendorp et al., 2003). Similar results were also obtained in occipital cortex (Merriam et al., 2007), thus bridging the earlier monkey updating works to human spatial updating (Henriques et al., 1998).

Cortical Feature Updating: An fMRIa Approach.

Demonstrating feature remapping in the human brain has proven to be a challenge, likely because it involves very subtle, transient modulations in neural firing patterns (Chen & Hafed, 2018; Subramanian & Colby, 2014), perhaps below the level detectable by standard univariate fMRI subtraction approaches. So far, it has also proven difficult to detect visual feature updating using a multi-voxel pattern analysis (MVPA) approach (Golomb & Kanwisher, 2012a), perhaps because gaze-centred feature remapping involves interactions between, rather than within, different portions of retinotopic space.

A. Simplified Task



B. Cortical Activation

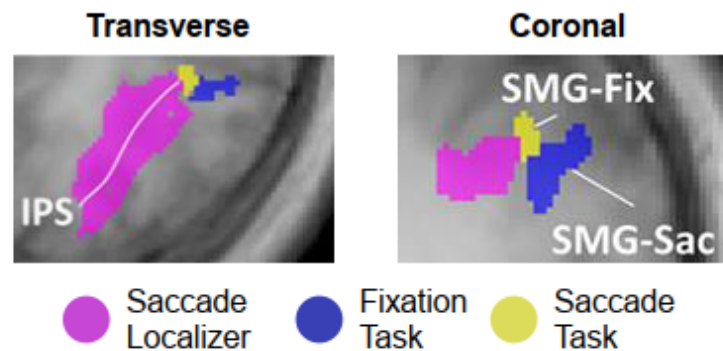


Fig. 3. Supramarginal gyrus shows transsaccadic orientation modulations. A) Depiction of simplified paradigm that was used to test the updating of object orientation within a fixation or across a saccade (Dunkley et al., 2016). B) Cortical activation presented on a transverse slice of the average brain of all participants, with activation for saccade-only activity (fuchsia; Saccade Localizer) abutting fixation-related (indigo blue; Fixation Task) and saccade-related (mustard yellow; Saccade Task) orientation updating.

For these reasons, we have employed an approach based on the fMRI adaptation (fMRIa) technique (Grill-Spector & Malach, 2001). In fMRIa, one compares the fMRI blood-oxygen-level-dependent (BOLD) response for repeated vs. different stimuli at the whole brain or region-of-interest (ROI) level, to detect changes that either reflect adaptation - suppression (less activation) or enhancement (more activation) during repetition. To adapt

this for studies of transsaccadic memory, we interposed a saccade between the two stimuli and compared this to fMRIa controls without a saccade.

Extrinsic (Orientation) Updating. In our first study (Dunkley et al., 2016), we presented participants with an oriented object before and after saccades (or an equivalent period of fixation) and then, required them to indicate whether the overall orientation of the object was the same or different (Fig. 3A). We, then, searched for cortical regions that showed either significant suppression or enhancement across saccades versus fixation. Two

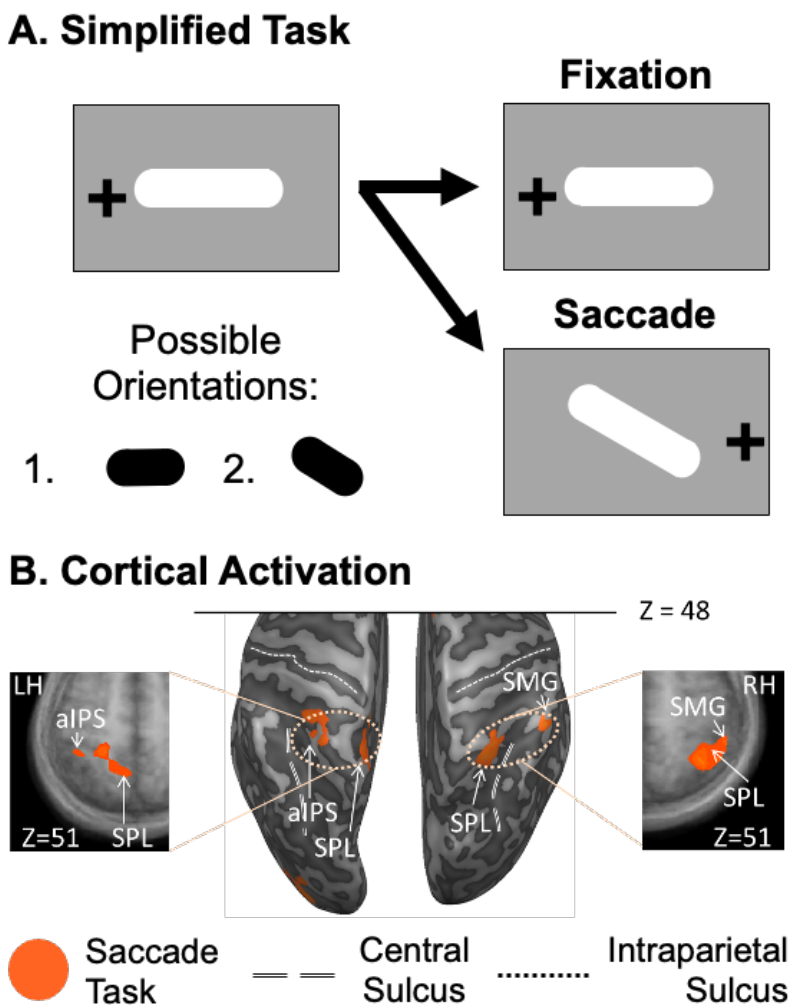


Fig. 4. Transsaccadic parietal modulations during grasp updating. A) Simplified fMRIa task that investigated the updating of object orientation of a 3D object, for fixations or across a saccade. B) The corresponding cortical activation is shown (orange; Saccade Task) for the updating of object orientation across saccades vs. fixation (Baltaretu et al., 2020). Along the inflated brain renderings (middle) are shown a transsaccadic SMG

region and traditional reach / grasp regions (anterior intraparietal sulcus, aIPS, and superior parietal lobule, SPL; review: Vesia & Crawford, 2012). These are presented in the lateral panels on transverse slices of the average brain of all participants.

areas showed significant saccade-specific effects: repetition enhancement in left extrastriate cortex (putative V4) and saccade-repetition suppression in right supramarginal gyrus (SMG), an inferior parietal area immediately lateral to the standard parietal eye field (Fig. 3B).

Further, right SMG showed the same interaction in another task involving transsaccadic orientation memory for action (Fig. 4), along with activation of other parietal areas associated with grasp (Baltaretu et al., 2020). It is noteworthy that this SMG area is very close to the site of right parietal TMS stimulation that produced transsaccadic orientation memory deficits (Prime et al., 2008) and might be considered a higher-level elaboration of monkey LIP described above (Subramanian & Colby, 2014). Considering this adjacency and possible overlap, one might consider LIP + SMG to form ‘extended parietal eye fields’. Based on these new data and the known role of LIP in spatial updating (Medendorp et al., 2003; Merriam et al., 2003), we propose that this extended parietal eye field plays a special role in *extrinsic* feature updating for both location and orientation.

Intrinsic Feature Updating. To test which brain areas are involved in the updating of *intrinsic* object features, we employed a similar fMRIa paradigm to that described above, but this time varying a feature linked to object identity, namely spatial frequency (Baltaretu et al., 2021). In this case, we identified an area in dorsomedial occipital cortex (cuneus, corresponding to parts of V1-V3) that showed significant modulations for both, including intrinsic feature modulation (repetition enhancement) and saccade > fixation modulation (Fig. 5). We did not find the significant interaction between these two signals that we observed in SMG (see previous section), but their intermingled presence in the same region still points to this region as a putative transsaccadic area. For example, intrinsic visual features and saccade signals could interact either within this site or at the level of its projections (see ‘Functional Network Analysis’ below). Comparing this to SMG suggests that 1) extrinsic versus intrinsic updating mechanisms rely on different functional anatomy, and 2) the specific mechanisms (interaction vs. multiplexing) may differ.

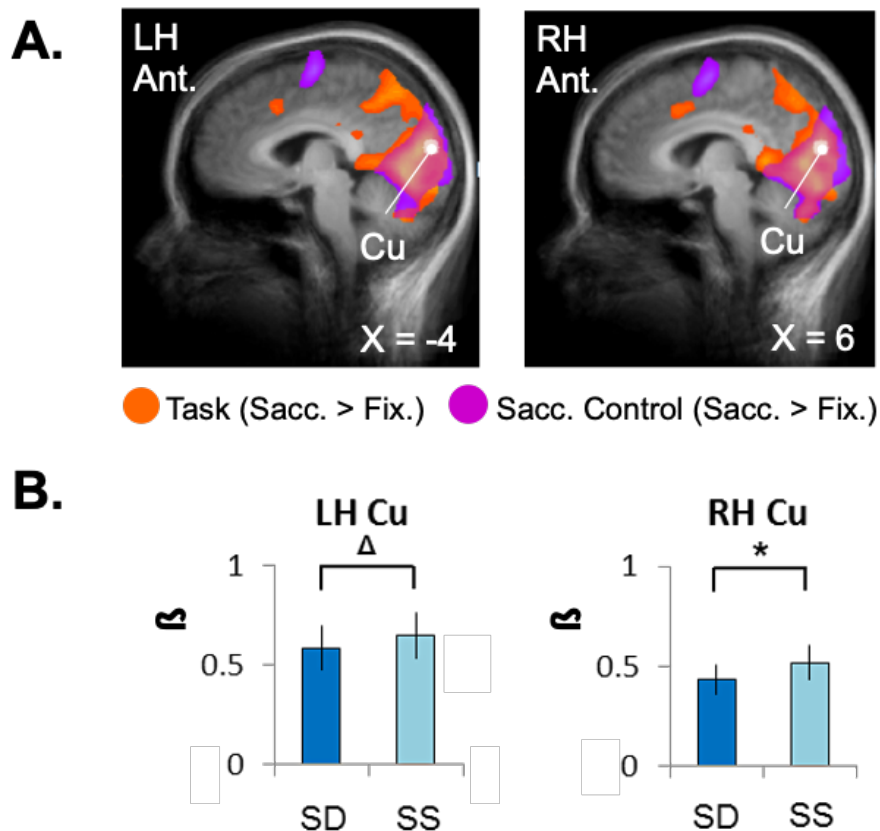


Fig. 5. Cuneus shows both saccade and spatial frequency modulations. A) Cortical activations are presented for saccade-sensitive modulations (orange; Saccade > Fixation Task), which are different from saccade-only modulations (fuchsia; Saccade Localizer Task). Highlighted is cuneus (Cu), presented in the left (left panel) and right (right panel) hemispheres, which shows eye movement sensitivity and intrinsic object feature (spatial frequency) updating (Baltaretu et al., 2021). B) Beta weights are shown for the saccade conditions (change in spatial frequency – saccade different, SD; repetition of spatial frequency – saccade same, SS), which demonstrate enhancement in right cuneus (and a trend in left cuneus).

Multiple Feature Updating. Based on the preceding fMRIa findings, we hypothesized that SMG is involved in spatial updating of object orientation (an extrinsic spatial property), whereas dorsomedial occipital cortex could play a special role in combining saccade and feature information for updating object identity (an intrinsic feature). To test this hypothesis and extend it to the situation where multiple features are updated, we asked participants to remember both extrinsic stimulus orientation and shape (another

important intrinsic feature) across saccades (Baltaretu et al., 2023). We found results (Fig. 6) resembling the sum of our previous single-feature experiments: saccade-specific adaptation in SMG and combined shape / saccade modulations in cuneus. This suggests that the mechanisms for updating extrinsic spatial cues and intrinsic identity cues are likely simultaneously active for transsaccadic vision in real-world conditions.

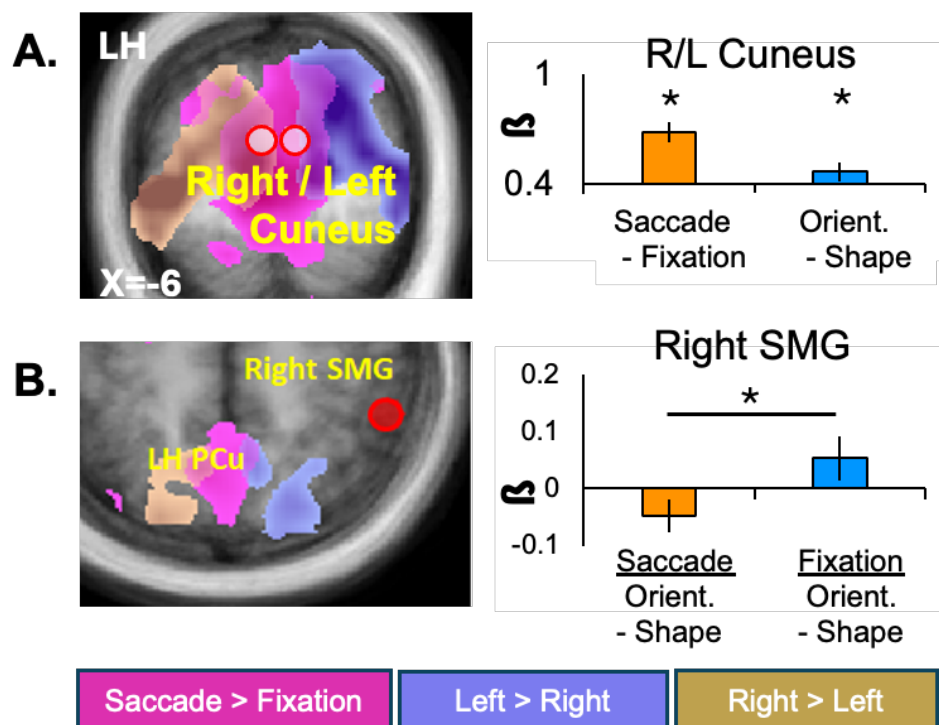


Fig. 6. SMG and cuneus are both modulated when shape and orientation are updated across saccades. A) Cortical activations are extracted (Baltaretu et al., 2023) from right and left cuneus (red circles; shown in the coronal slice of the average brain of all participants; left panel). The related beta weights are plotted as a function of eye movement (Saccade – Fixation) and intrinsic feature changes (Orientation – Shape) which show a significant effect of both saccade and feature updating in cuneus. B) SMG ROI shown on the transverse slice (red circle; left panel) from which beta weights were extracted and plotted as a function of feature changes in the Saccade (orange; Saccade: Orientation – Shape) and Fixation (blue; Fixation: Orientation – Shape) conditions. These show interaction effects of saccade and intrinsic feature updating signals in right SMG.

Functional Network Analysis.

Seed Region Analysis. Another important criterion for any area involved in transsaccadic vision is that it should share signals with other areas needed to form a complete ‘updating circuit’, which should depend on the nature of the task. To test this, we used the ROIs cited in the previous section as ‘seed areas’ for functional connectivity analysis, i.e., correlations of event-related BOLD time series data with other areas through time. One

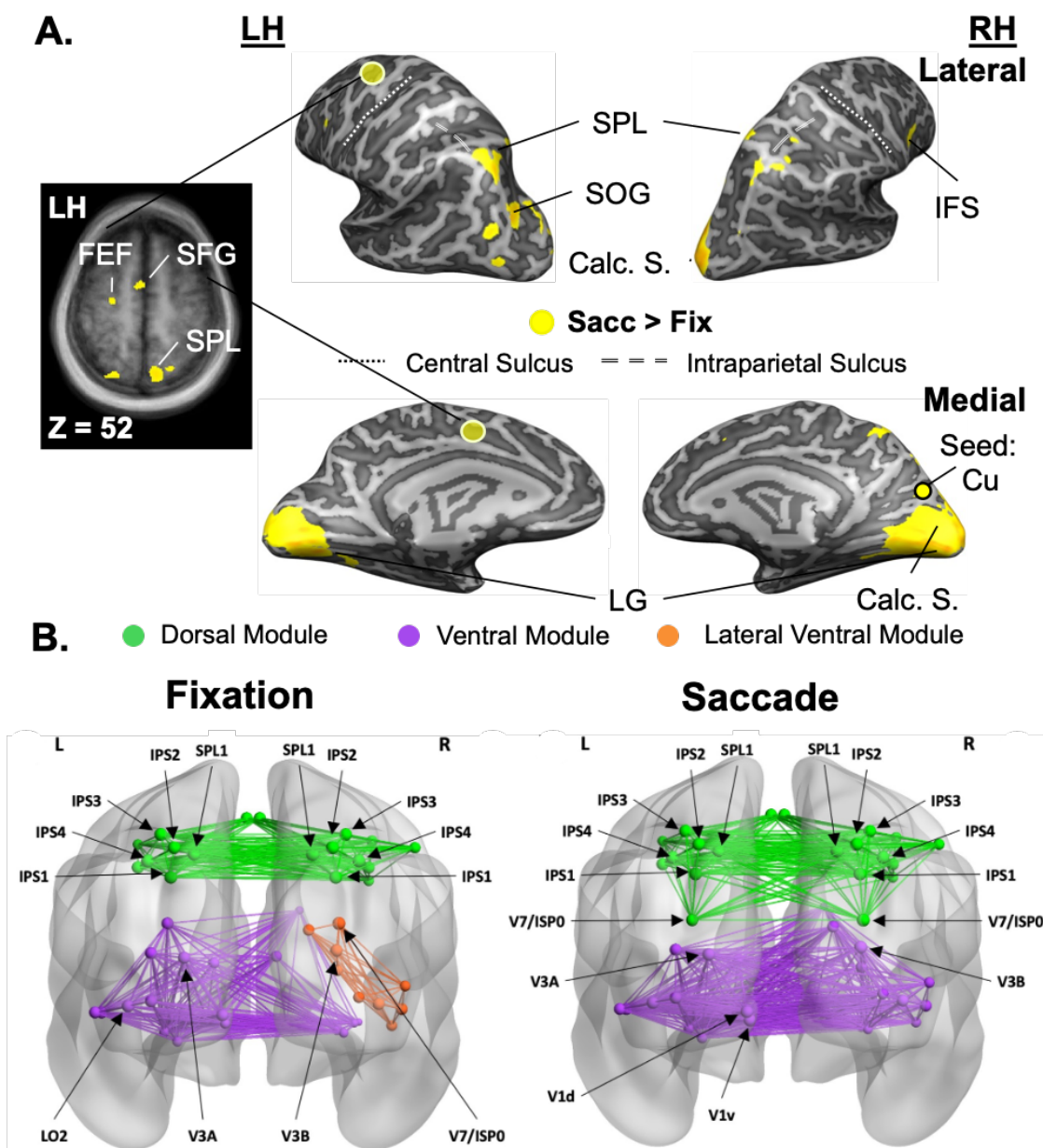


Fig. 7. Functional cortical networks for transsaccadic integration. A) Cortical activation shows functional correlations for Saccade > Fixation conditions (yellow) with cuneus as the seed region (Baltaretu et al., 2023). On the inflated brain renderings and lateral transverse slice (left panel), saccade-related modulations are shown between cuneus and early-to-mid visual regions (Calc. S., LG, and SOG), sensorimotor parietal (SPL), and frontal eye and working memory (SFG, FEF, and IFS) regions. B) Using graph theory analysis (Tomou et al., 2025), separate, dorsal / ventral modules are shown to exist for Fixation-related updating (left panel), with two distinct ventral modules (one spanning both hemispheres, purple, and one lateralized to the right hemisphere, orange). The two ventral modules merge to account for saccade-related updating in the Saccade condition (right panel). Abbreviations: FEF, frontal eye fields; SFG, superior frontal gyrus; IFS, inferior frontal sulcus; SPL, superior parietal lobule; SOG, superior occipital gyrus; Calc. S., calcarine sulcus; LG, lingual gyrus; Cu, cuneus; IPS(0 - 4), intraparietal sulcus (regions 0 - 4); V1d, dorsal visual area 1; V1v, ventral visual area 1; V3A/B, visual areas A/B; V7, visual area 7; LO2, lateral occipital area 2.

would expect signals in a putative transsaccadic vision area to correlate with signals in gaze areas that might provide the efference copy for the saccade signal, and (depending on the task) other visual areas, higher-level perception areas, working memory areas, and / or motor areas for action.

For example, when participants only had to remember and compare object features across saccades (Baltaretu et al., 2023), cuneus showed functional connectivity with areas that would be expected to support such processes (Fig. 7A). Similarly, occipital visual areas (V1, LG, SOG), parietal and frontal areas associated with saccades (FEF, SEF, SPL), and prefrontal cortex (SFG, IFS). When participants also had to update orientation to aim grasp movements (Baltaretu et al., 2020), SMG signals still correlated with the FEF, as well as areas associated with visually-guided grasp (SPL, aIPS). The main point here is that these correlations make sense in terms of the context: the role of the specific seed areas (cuneus and SMG, respectively) and the specific tasks in which they were engaged.

Modularity Analysis. The limitation of seed region analysis is that it only examines the functional connectivity of one brain region at a time. In more sophisticated forms of functional connectivity analysis, such as graph theory analysis, it is possible to analyze large numbers of cortical 'nodes' to understand the simultaneous relationships between all of their signals. To this end, Tomou et al. (2025) re-examined the fMRI data from our

shape / orientation updating task (Baltaretu et al., 2023), in order to better understand how functional networks change across eye movement types and support feature updating. To do this, Tomou et al. (2025) performed a Newman modularity analysis (Newman, 2006) to determine which cortical nodes tend to cluster together.

In the fixation version of this task (Fig. 7B, left panel), nodes from the extended visual system were divided along dorsal-ventral lines (a bilateral parieto-frontal module and two ventral occipito-temporal modules). In addition, the ventral modules were lateralized, with one spanning all of left visual cortex and parts of right visual cortex and the other confined to lateral, right visual cortex. In the context of the current review, it is noteworthy that the dorsal module contained the extended parietal eye fields (LIP + SMG) and frontal eye fields, whereas the left ventral module contained both sides of cuneus, suggesting that these extrinsic / intrinsic updating centres existing within broader 'home' modules.

When saccades caused the retinal fields of the stimuli to reverse left-for-right (Fig. 7B, right panel), the two ventral modules 'joined' together, perhaps due to a combination of updating and sensory signals (Tomou et al., 2025). Finally, during the saccade task, bilateral IPS (near PEF / SMG) and right V3B (lateral to cuneus) were important 'betweenness centrality hubs' (i.e., reflective of regions that bridge together multiple, different clusters; Freeman et al., 1991; Newman, 2005), suggesting a role for communicating between modules.

In summary, our extrinsic and intrinsic updating centres appear to fall within separate dorsal / ventral network modules, with increased bilateral communication during saccades. Taken together with our earlier seed network analysis, this suggests that although these extrinsic / intrinsic updating centres can be placed within specific 'home' network modules, they can also access broader task-dependent functional connectivity.

Discussion

Synthesis. In a dynamic world where perception is disrupted with each saccade, we somehow overcome the imposed challenges in acting and achieving our goals. As reviewed above, this is thought to involve the retention, updating, and integration of visual information across saccades (Fig. 1). Earlier neuroimaging experiments focused on the

spatial updating question (Medendorp et al., 2003; Merriam et al., 2003, 2007) and TMS experiments suggested that spatial updating also supports transsaccadic memory of object orientation (Prime et al., 2008, 2010). However, it was not known whether different cortical mechanisms exist for the retention, updating, and integration of different object features.

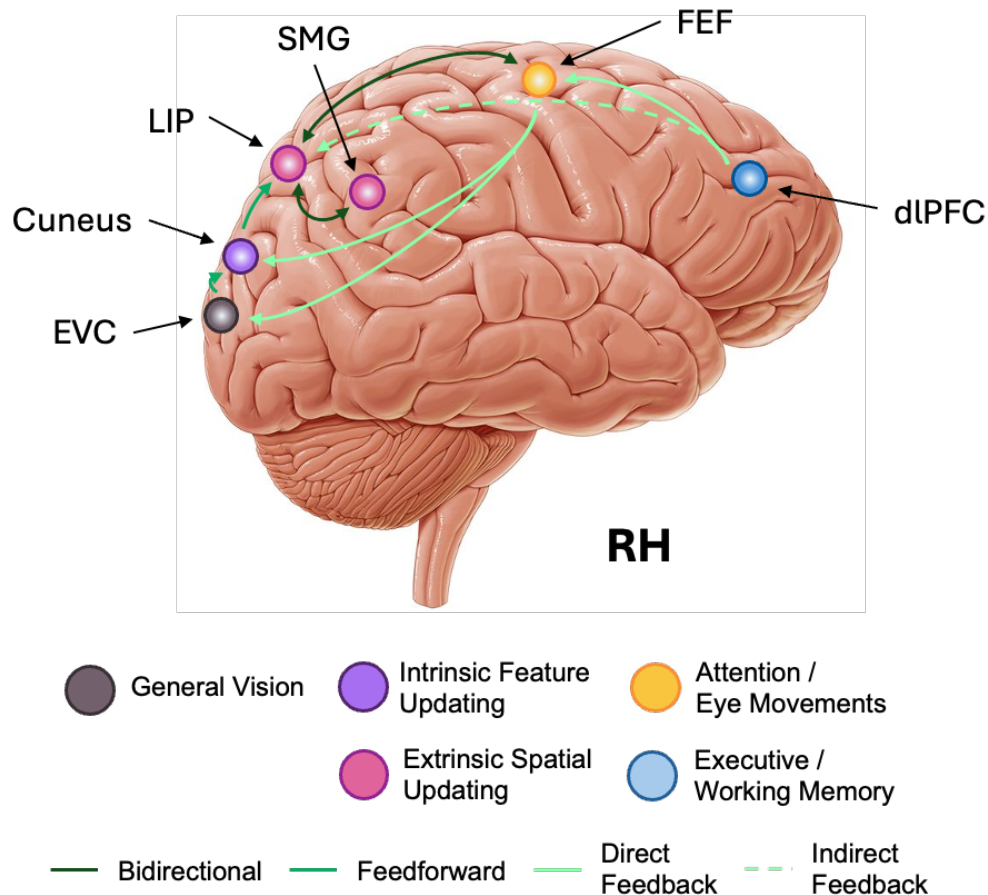


Fig. 8. Conceptual model of transsaccadic vision. Visual (feature) information is processed in early visual cortex (EVC). From there, intrinsic object features (e.g., spatial frequency, color, and shape) are combined with gaze-contingent signals in cuneus. Simultaneously, early visual information can also be passed along into parietal cortex for extrinsic object perception – LIP for saccade-related processing which are fed into SMG for the combinations of eye movement and extrinsic object feature information. LIP and FEF take presaccadic signals to effectuate eye movements, and then use this information for additional updating signals – further refined through executive / working memory signals emanating from dlPFC. This streamlined network of regions can handle both intrinsic and extrinsic object feature updating across saccades, resulting in transsaccadic vision.

Given that our surroundings are composed of numerous, complex objects, each with various features, vision scientists have found it useful to make a fundamental distinction between perception of what and where objects are (Goodale, 2011; Goodale & Milner, 1992; Goodale & Haffenden, 1998; Mishkin et al., 1983). Here, we have expanded this to the notion of *extrinsic* spatial properties (i.e., object location, orientation, motion) and *intrinsic* cues (e.g., shape, texture, color) to object identity. Specifically, we propose that the brain possesses separate mechanisms for extrinsic vs. intrinsic feature updating, with posterior parietal cortex (specifically, LIP and SMG) playing a special role in the former, and occipital cortex (specifically, the cuneus region) playing an important role in the latter (Dunkley et al. 2016; Baltaretu et al. 2020, 2021, 2023; Tomou et al. 2025). This emerged in both our fMRIa-based ROI analysis (Figs. 3-6), their functional connectivity within broader dorsal / ventral network modules (Fig. 7B, and their engagement of other regions that appear to support spatial updating for specific task-related outcomes (e.g., Fig. 7A).

Figure 8 integrates these newer ideas with the previous literature to provide a simple conceptual model of cortical transsaccadic updating / integration within two parallel streams, interconnected through feedback, lateral, and feedforward connections with the broader transsaccadic network (Hamker, 2003, 2005; Prime et al., 2011). At the level of occipital cortex, early visual cortex already shows signs of gaze-centered updating signals, likely due to recurrent signals from higher levels of the system (Hartmann et al., 2017; Malik et al., 2015; Merriam et al., 2007; Nakamura & Colby, 2002; Neupane et al., 2016). Our thesis is that cuneus then plays a special role in bringing together signals related to intrinsic object features (e.g., shape, spatial frequency) with saccade signals, and relays this to a network of areas involved in transsaccadic updating and integration of object identity (Baltaretu et al., 2021; Merriam et al., 2007; Nakamura & Colby, 2002; Ploran et al., 2007; Schiavetto et al., 2002; Watson et al., 2016).

Concurrently, the extended parietal eye fields (LIP and SMG) appear to be involved in updating object location and orientation, respectively, and communicate this information to areas involved in visual perception and / or movement control, depending on the task (Andersen et al., 1992; Bracewell et al., 1996; Colby et al., 1995; Huk et al., 2017; Medendorp et al., 2003; Nakamura et al., 2001; Prime et al., 2008, 2011; Subramanian &

Colby, 2014; Vesia et al., 2010). FEF and possibly LIP are thought to provide the saccade efference copy for spatial updating (Duhamel et al., 1992; Goldberg & Bruce, 1990; Gottlieb & Goldberg, 1999; Klier & Angelaki, 2008; Merriam et al., 2003; Prime et al., 2008; Sommer & Wurtz, 2008; Umeno & Goldberg, 2001; Wang et al., 2024), although this may involve sub-cortical structures as well.

Finally, dlPFC may contribute to both maintenance of visual memory in these circuits and in cognitive control for tasks involving top-down instruction (Barbey et al., 2013; Brosnan & Wiegand, 2017; Cameron et al., 2015; Ding et al., 2009; Funahashi, 2014; Grimault et al., 2009; Johnson et al., 2007; Levy & Goldman-Rakic, 1999; Pierrot-Deseilligny et al., 2003; Rossi et al., 2009; Takeda & Funahashi, 2002; Tanaka et al., 2014). With its role in both working memory (left hemisphere) and reasoning abilities (right hemisphere; Barbey et al., 2013), once a future target has been identified, it likely holds onto relevant visual information, sends signals back to LIP (Pierrot-Deseilligny et al., 2003; Wang et al., 2025) for visuospatial processing (remapping) and upcoming saccade preparation, finally refined, but ultimately executed by FEF (Cameron et al., 2015; Ding et al., 2009; Sajad et al., 2015). Additionally, dlPFC has been shown to guide visual attention, even further back in cortex - in early visual cortex (Katsuki & Constantinidis, 2012). These connections are potentially able to support extrinsic feature updating through a frontoparietal pathway (via SMG) and intrinsic feature updating through a frontooccipital pathway (via cuneus).

Limitations and Future Directions. This review and our thesis are clearly subject to several limitations. First, our two-stream theory of transsaccadic cortical processing is based on a limited set of studies examining extrinsic (location, orientation) and intrinsic (spatial frequency, shape) cues. These results need to be replicated and expanded to account for motion processing (which may involve other areas such as MT+) and the various other cues to object identity (Crouzet & Serre, 2011; Donderi, 2006; Leeds et al., 2014; Palmeri & Gauthier, 2004). Second, cortical modulations related to attention, which we only mentioned in passing, are also known to play an important role in transsaccadic vision (Awh et al., 2006; Awh & Jonides, 2001; Bichot et al., 2005; Crapse & Sommer, 2012; Dowd & Golomb, 2019, 2020; Jonikaitis et al., 2013; Theeuwes et al., 2009; Zhou & Desimone, 2011). Third, we mainly focused on egocentric updating mechanisms, and

only touched briefly on the role and mechanisms related to landmark-centered coding (Bharmauria et al., 2025). Fourth, our focus on fMRI results brings the inevitable problem that this technique has poor temporal resolution, whereas perisaccadic signals are transient. And finally, so far, we have made no attempt to relate these signals to specific cellular events.

One technique that can potentially address some of these limitations is multiunit recordings from various sites (McFarland et al., 2015; Seo et al., 2024). Our hope is that the framework provided in Figure 8 might inspire such experiments. Further, advances in source localization with human EEG and MEG still lag the spatial resolution of fMRI, but provide virtually unlimited temporal resolution. For example, EEG and MEG have recently been used to test the cortical dynamics of predictive updating (Fabius et al., 2020; Kurtzberg & Vaughan, 1982; Parks & Corballis, 2008; Peterburs et al., 2011; Richards, 2003), and graph theory analysis of source-localized EEG signals has been used to track the functional networks of visual and saccade signals through time (Ghaderi et al., 2023). The latter included transsaccadic memory of an oriented grating and found functional connectivity between SMG and visual and frontal cortex consistent with our model.

Finally, a conceptual limitation of the current scheme creates an additional ‘binding problem’ (Dowd & Golomb, 2020; Treisman, 1996; Treisman & Sato, 1990) –the integration of extrinsic and intrinsic signals– but only addresses it at a superficial connectionist level, without providing specific mechanisms. The techniques discussed above (specifically EEG, MEG, and local field potentials from neurophysiology) also provide the opportunity to consider the role of ensemble population oscillations in ‘binding’ information across saccades (Chen & Golomb, 2023; Chiu & Golomb, 2025; Doucet et al., 2020; Dowd & Golomb, 2019; Golomb et al., 2014; Keren et al., 2010; Kovacs & Harris, 2019; Lu & Golomb, 2023; Monosov et al., 2008; Shafer-Skelton et al., 2017). Based on our model, we would predict both SMG and cuneus to show synchronized oscillations when updating of both extrinsic and intrinsic features is required.

Potential Clinical Applications. Any model will ultimately be judged not only by its explanatory power, but also by its application potential. Failures in transsaccadic spatial updating have been implicated in a number of brain disorders, including optic ataxia

(Cheviet et al., 2021; Khan et al., 2005), thalamic stroke (Ostendorf et al., 2010), right parietal damage (Pisella, 2017; Ten Brink et al., 2019), frontal cortex damage (Duhamel et al., 1992), and schizophrenia (Bansal et al., 2019). While most of these studies have focused on spatial updating of location and fit well with the parietal stream of our conceptual model, the transsaccadic updating of intrinsic features has been less tested. Our model would suggest that cuneus damage would give rise to specific deficits in transsaccadic object identification. Toward this end, TMS provides a useful bridge from neuroimaging and neuropsychology results and has already implicated frontal and posterior parietal cortex (Collins & Jacquet, 2018) in updating object orientation (Prime et al., 2011); but, to our knowledge, TMS over cuneus has not been tested during paradigms that involve transsaccadic feature updating.

Conclusions

Saccades are both necessary and problematic for vision. However, these problems are mostly overcome through the mechanisms of transsaccadic vision – an associated set of processes for perception, oculomotor execution, attention, working memory, and executive control. Here, we make a case for distinguishing between transsaccadic vision for two distinct feature categories: extrinsic spatial cues vs. intrinsic cues to object identity. After reviewing the general state of knowledge on the cortical mechanisms for transsaccadic vision we further propose two separate cortical mechanisms: a parietal mechanism for extrinsic spatial feature updating, and an occipital mechanism for updating intrinsic identity cues, along with their functional circuitry. We suggest that future work should focus on understanding how these object properties are bound together, identify the complete functional networks that support this, and provide possible reinterpretations and avenues for clinical application. Given that saccades are inextricable from real-world visual behavior, solving these questions is tantamount to understanding vision itself.

Acknowledgments.

We thank Vishal Bharmuria, Nedim Göktepe, Gaelle Luabeya, Veronica Nacher, Kathrin Pabst, Jessica Parker, and Cristina Rubino for helpful comments on this manuscript. This work was supported by the National Science and Engineering Research Council of Canada (NSERC), the Vision: Science to Applications (VISTA) program (supported in part

706 by the Canada Foundation for Research Excellence Fund), an Ontario Graduate
707 Scholarship (to BRB) and a York Research Chair (to JDC).

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709 **Declarations of Interest.**

710 The authors have no declarations of interest to make.

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