

Perspective Review:

Cortical Mechanisms for Transsaccadic Vision: Extrinsic and Intrinsic Feature Updating

Abbreviated Title: Cortical Mechanisms for Transsaccadic Vision

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48 **Abstract**

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

70 **Keywords**

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

73 **Highlights**

- 74
- 75 The role of transsaccadic vision is discussed in terms of updating and integrating
both extrinsic spatial features and intrinsic identity cues.
 - 76 Cortical mechanisms are reviewed for transsaccadic feature updating and
memory, with emphasis on recent imaging and functional connectivity analysis.
 - 77
 - 78 A conceptual model is proposed with separate mechanisms for transsaccadic
updating of extrinsic vs. intrinsic object features.

- 80 ▪ Future directions focus on conceptual progress and clinical applications.

81

82 **Introduction**

83 Humans make two to three saccades per second to align the fovea with objects of high
84 interest in the visual field (Wade et al., 2003; Yarbus, 1967). By allowing the brain to focus
85 on foveal information, rather than the entire visual field, this adaptation saves both cortical
86 space and computational costs (Herwig, 2015). However, it also creates several
87 computational challenges for the brain, with constant visual interruptions and
88 repositioning of the retina relative to the world (Binda & Morrone, 2018a; Hamker et al.,
89 2008; Ibbotson & Krekelberg, 2011; McFarland et al., 2015; Melcher & Colby, 2008;
90 Teichert et al., 2010; Wurtz, 2008). The study of transsaccadic vision is sometimes
91 regarded to be an esoteric topic, i.e., the intersection of the vision and saccade fields, but
92 the reality is that sustained fixation is largely a laboratory phenomenon. Thus,
93 transsaccadic vision *is* normal vision, so understanding its mechanisms is central to an
94 understanding of vision itself.

95 To understand transsaccadic vision, one must first agree on its purpose. Many
96 investigators have stated that the ultimate purpose of transsaccadic vision is to maintain
97 a stable percept despite eye movements (Baltaretu et al., 2023; Bridgeman et al., 1994;
98 Higgins & Rayner, 2015; Honda, 2006; Mathôt & Theeuwes, 2011; Melcher & Colby,
99 2008). While this is true from a subjective perspective, from an evolutionary viewpoint the
100 primate visual system developed in a dynamic world full of moving animals and weather
101 phenomena, now expanded to include people and vehicles, so stability in itself cannot be
102 a biological imperative. From a more objective biological viewpoint, the visual system
103 needs to identify *what* objects are, *where* they are, and do this rapidly enough to allow us
104 to interact with the world in real time (Hayhoe, 2017; Hayhoe et al., 2025; Hayhoe &
105 Ballard, 2005; Hayhoe et al., 2012; Land & Tatler, 2009). Done correctly, this ultimately
106 will lead to the subjective perception of stability when our visual surroundings are stable
107 (or not), appropriately reflecting the external reality that surrounds us.

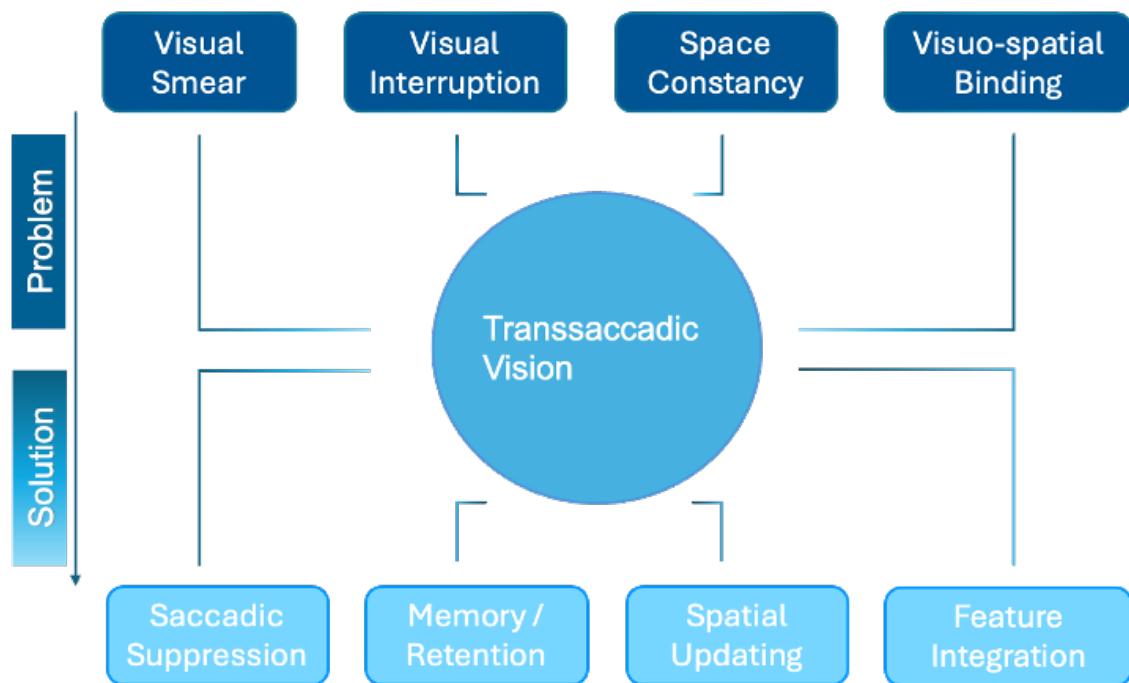
108 From this biological viewpoint, the question is, how does the visual system serve its
109 fundamental purpose in the face of constant eye movements? Just over 15 years ago,

110 Melcher and Colby (2008) published a landmark review that outlined several principles of
111 transsaccadic perception based on the knowledge we had at that time. A few years later,
112 our current lab proposed more specific cortical mechanisms based on the transcranial
113 magnetic stimulation (TMS) data available at that time (Prime et al., 2011). However,
114 considerable advances have been achieved since then. Here, we update this topic by
115 reviewing the computational challenges associated with transsaccadic vision and the
116 psychophysical, neurophysiological and neuroimaging evidence for specific mechanisms,
117 with a focus on our recent transsaccadic adaptation studies (Baltaretu et al., 2020, 2021,
118 2023; Dunkley et al., 2016; Tomou et al., 2025). This evidence leads us to argue that there
119 are separate cortical mechanisms for transsaccadic updating, approximately
120 corresponding to the 'what' and 'where' functions described above.

121 **The Computational Problem(s) of Transsaccadic Vision.**

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

124 **Visual Smear / Suppression.** Saccades cause retinal motion relative to the world, which
125 could result in blurred vision and/or confusion between self-generated and external
126 motion (Campbell & Wurtz, 1978; Castet & Masson, 2000; Idrees et al., 2020; Ilg &
127 Hoffmann, 1993; Judge et al., 1980; Shioiri & Cavanagh, 1989). In theory, efference
128 copies (the internal sense of eye motion from the motor system) could cancel this motion
129 to offer continuous visual perception during saccades (Helmholtz, 2013; Sherrington,
130 1918; Sommer & Wurtz, 2008; Subramanian et al., 2019; Sun & Goldberg, 2016; von
131 Holst & Mittelstaedt, 1950). However, this is biologically limited by the ability of the visual
132 system to process high speeds of motion and generate perfectly calibrated efference
133 copies in space and time (Castet & Masson, 2000; Shioiri & Cavanagh, 1989). As a result,
134 perisaccadic vision (vision during saccade execution) is blurred and thus suppressed
135 through both passive and active mechanisms, leaving most people effectively blind during
136 saccades (Bremmer et al., 2009; Castet & Masson, 2000; Diamond et al., 2000; Higgins
137 & Rayner, 2015; Kleiser et al., 2004; Matin, 1974; W. Richards, 1969; Schweitzer et al.,
138 2025; Shioiri & Cavanagh, 1989; Thilo et al., 2004; Wurtz, 2008; Zimmermann, 2020;
139 though, see also Idrees et al., 2020). This gives rise to a second problem:



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

145

146 **Visual Interruption / Transsaccadic Memory.** Saccades frequently interrupt vision for
 147 30-100 ms (Bahill et al., 1975; Enderle, 2005). Then, an additional ~100-200 ms is
 148 required to transmit and process visual information in the cortex (Amano et al., 2006;
 149 Hegde, 2008; Lamme & Roelfsema, 2000; Matin, 1974; Matin et al., 1993; Ross et al.,
 150 2001; Wutz et al., 2016; Yoshor et al., 2007). If the brain simply discarded all the
 151 information from previous fixations (O'Regan & Noe, 2001), this would render humans
 152 effectively blind half the time – a dangerous situation for any species. Fortunately, it
 153 appears that at least some important information is retained (i.e., remembered) and
 154 available for predictive processing at the new gaze position (Blackmore et al., 1995; Burr
 155 et al., 1994; Kong et al., 2021; Prime et al., 2007, 2010, 2011; Tanaka et al., 2014), at
 156 least until visual information can be processed (see next section for details).

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

159 visual information entering the retina will not be in spatial register with the original visual
160 information (Crespi et al., 2011; Geng et al., 2008; Graef et al., 2001; Jonikaitis &
161 Belopolsky, 2014; Luabeya et al., 2024; Shafer-Skelton et al., 2017). This requires some
162 additional mechanism to *spatially update* information across fixations (Deubel et al., 2010;
163 Hamker et al., 2011; Klier & Angelaki, 2008; Mohsenzadeh et al., 2016; White & Snyder,
164 2007). In subsequent sections of this review, we will consider several potential
165 mechanisms that have been proposed to solve this problem.

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

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

181 **Psychophysical Evidence for Transsaccadic Memory and Integration.**

182 **Memory Capacity.** In the past, opinions about the capacity of transsaccadic memory
183 have varied wildly from essentially nothing (Bridgeman et al., 1975; Bridgeman & Mayer,
184 1983; Bridgeman & Stark, 1979; O’Regan & No, 2001) to highly detailed information
185 (Castelhano & Henderson, 2005; Henderson & Hollingworth, 2003; Parker & Tas, 2025).
186 The current consensus is that transsaccadic memory (maintenance of visuospatial
187 information across eye movements) is attention-dependent and has a limited capacity
188 similar to visual working memory, and likely shares many of the same mechanisms (Awh

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

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

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

219 1997; Mullette-Gillman et al., 2005; Pouget et al., 2002; Smith & Crawford, 2005), there
220 is relatively little physiological evidence that this mechanism is dominant in the visual
221 system. A popular alternative is that limited amounts of spatial information can be updated
222 (see neural mechanisms below) (Andersen et al., 1985; Cavanaugh et al., 2016; Colby et
223 al., 1995; Duhamel et al., 1992; Gancarz & Grossberg, 1999; Henriques et al., 1998; Lee
224 & Tehovnik, 1995; Mays & Sparks, 1980b; Sparks, 1989). Network modeling studies have
225 shown that visual information can then be transformed into motor frames without the need
226 for intermediate spatial frames (Blohm et al., 2009; Smith & Crawford, 2001, 2005).

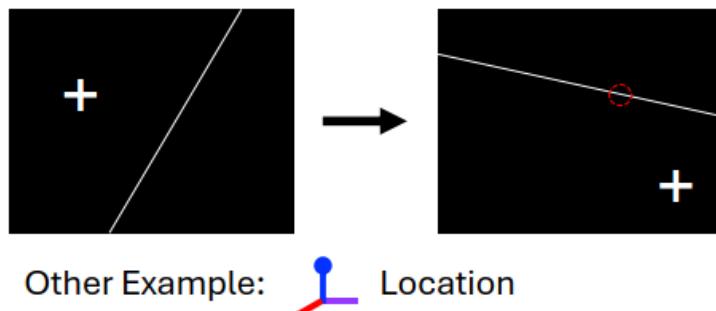
227 Visual landmarks (i.e., allocentric cues) are also known to augment this transformation
228 process (Byrne et al., 2010; Byrne & Crawford, 2010; Golomb et al., 2010; Lisi et al.,
229 2015). Landmarks appear to be most important when they are close to the target (Deubel,
230 2004), embedded in context (Germeyns et al., 2004), when target reliability is low (Byrne
231 & Crawford, 2010; Hayhoe et al., 1992; Karn et al., 1997), and for longer-term stability
232 (Boon et al., 2018; Chen et al., 2014). Note that these mechanisms are not mutually
233 exclusive: transsaccadic integration is thought to integrate target, saccade, and landmark
234 information in an optimal fashion (Byrne et al., 2010; Niemeier et al., 2003, 2007).

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

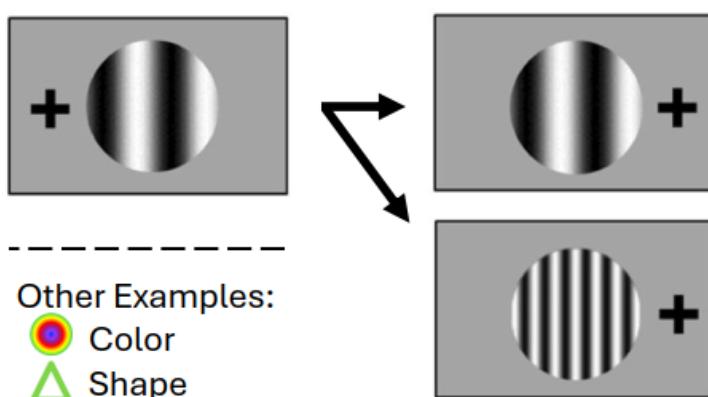
244 An uptick in progress has been made to better understand the processing of intrinsic
245 features (Goktepe & Schütz, 2023; He et al., 2017; Hübner & Schütz, 2021a, 2021b;
246 McConkie & Currie, 1996; Moussaoui et al., 2025; Parker & Tas, 2025; Schütz & Souto,
247 2015; Sharvashidze et al., 2024; Tas & Parker, 2023; Wagner & Schütz, 2023; Wittenberg
248 et al., 2008; Wolf et al., 2019), despite being less understood compared to spatial

249 updating. Features, such as color, have been shown to draw saccades toward
250 postsaccadic targets that match those of presaccadic cues (Hollingworth et al., 2013),
251 suggesting an interaction between saccades and color perception (Bompas & O'Regan,
252 2006; Sperling et al., 2008). Changes in surface features and spatial frequency across

A. Extrinsic Spatial Features



B. Intrinsic Identity Features



253

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

261

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

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

271 **Primate Neurophysiology.**

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

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

289 One more recent study suggested that the predictive signals might not be as spatially
290 specific as originally assumed (Zirnsak & Moore, 2014). This appears to be different for
291 different cells (Hartmann et al., 2017; Neupane et al., 2016), and might depend on the
292 task-relevance of the stimulus. Response field activation for task-relevant stimuli (e.g.,
293 those required for action) disperses during saccades (Colby et al., 1995; Gottlieb et al.,
294 1998; Kusunoki et al., 2000; Mohsenzadeh et al., 2016; Sommer & Wurtz, 2008; Sun &

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

298 Less is known about the transsaccadic neurophysiology of updating other visual features.
299 Most spatial updating studies did not consider features beyond location (Duhamel et al.,
300 1992; Gottlieb & Goldberg, 1999; Hartmann et al., 2017; Kusunoki et al., 2000; Neupane
301 et al., 2016; Umeno & Goldberg, 2001; Walker et al., 1995). Two notable exceptions are
302 that LIP shows modest transsaccadic updating of shape-related information
303 (Subramanian & Colby, 2014) and the superior colliculus appears to retain and update
304 orientation information across saccades (Chen & Hafed, 2018; Fracasso et al., 2023), but
305 it is widely believed that these updating processes contribute to transsaccadic feature
306 updating (Khayat et al., 2004; Melcher & Colby, 2008; Prime et al., 2008, 2011; X. Wang
307 et al., 2024).

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

316 **TMS Studies.**

317 Online transcranial magnetic stimulation (TMS) provides a safe way to disrupt local
318 cortical processing in humans during transsaccadic behaviors (Table 1). For example,
319 Morris et al. (2007) showed that online TMS pulses over parietal cortex during saccades
320 can disrupt the updating of location information. Perisaccadic single-pulse TMS over right
321 inferior parietal cortex reduced the memory capacity of stimulus orientation from the usual
322 3-4 objects to just one, consistent with a loss of spatial information (Prime et al., 2008).
323 This was interpreted as a loss of the saccadic updating signals, but there was still a
324 weaker effect during fixation that might suggest a broader role (see 'cortical feature

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

328

329 **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

330

331 In similar TMS experiments, unilateral stimulation over early visual cortex (EVC) disrupted
332 transsaccadic updating of visual orientation, but only when the saccade brought the
333 remembered stimulus *into* the visual field corresponding to the TMS-stimulated cortical
334 hemisphere (Malik et al., 2015). TMS stimulation over dorsolateral prefrontal cortex
335 (dlPFC) produced more complex effects, including either increased or decreased
336 performance, depending on the timing of the pulse relative to saccade onset and the
337 hemisphere stimulated (Tanaka et al., 2014). This is consistent with the distinction
338 between spatially-specific mechanisms in early visual cortex versus more complex top-
339 down control and working memory related processes in prefrontal cortex (Barbey et al.,
340 2013; Funahashi, 2014; Grimault et al., 2009; Johnson et al., 2007; Levy & Goldman-
341 Rakic, 1999; Pierrot-Deseilligny et al., 2003; Rossi et al., 2009; Tanaka et al., 2014).

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

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

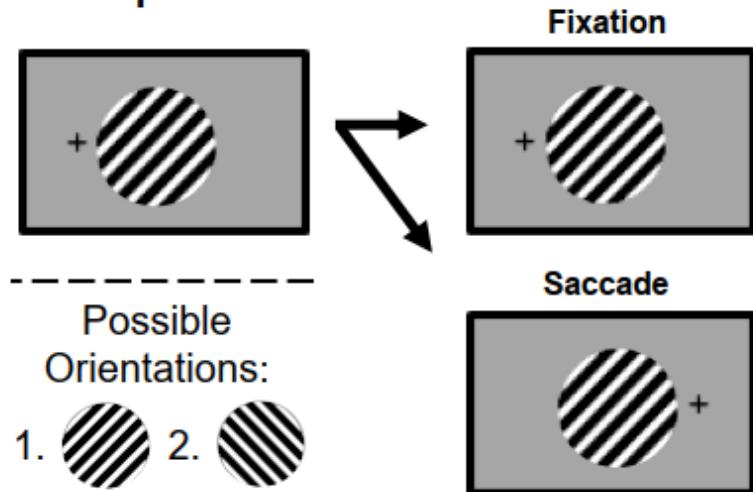
347 **Classic fMRI Spatial Updating / Remapping Studies.**

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

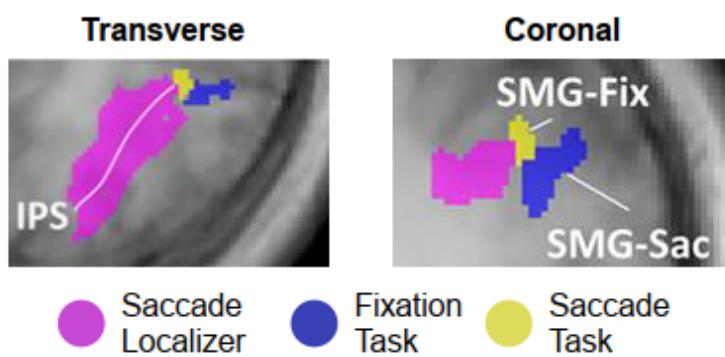
362 **Cortical Feature Updating: An fMRIa Approach.**

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

A. Simplified Task



B. Cortical Activation



370

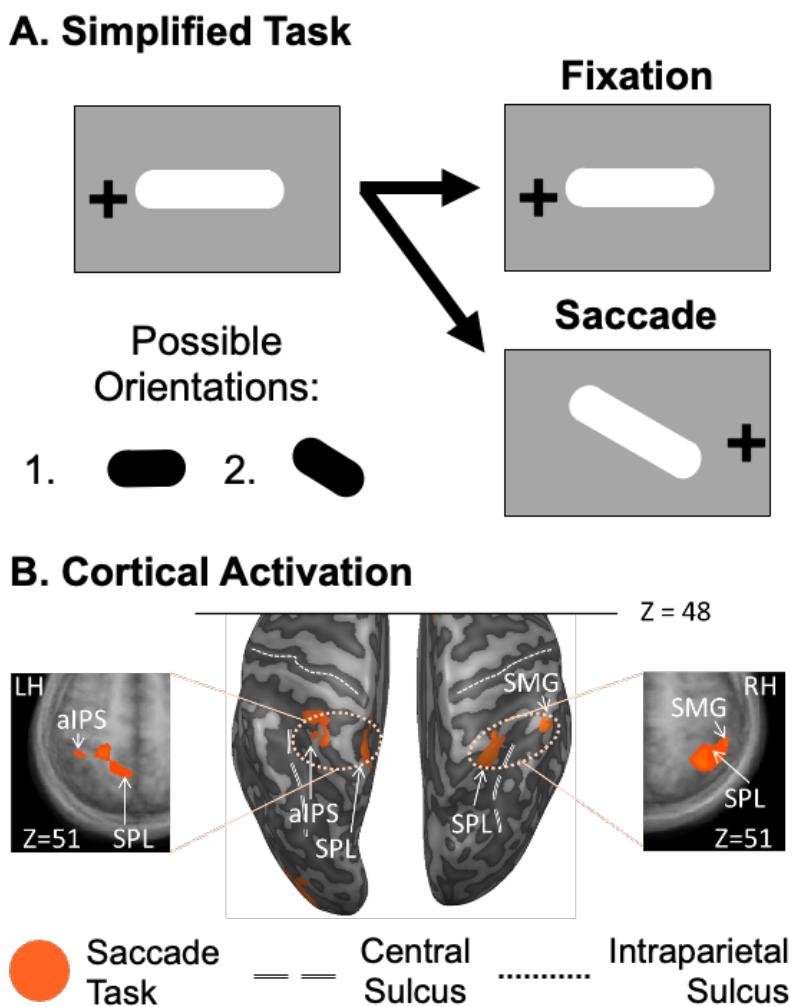
371 **Fig. 3.** Supramarginal gyrus shows transsaccadic orientation modulations. A) Depiction
372 of simplified paradigm that was used to test the updating of object orientation within a
373 fixation or across a saccade (Dunkley et al., 2016). B) Cortical activation presented on a
374 transverse slice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

377

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

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

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



390

391 **Fig. 4.** Transsaccadic parietal modulations during grasp updating. A) Simplified fMRIa
392 task that investigated the updating of object orientation of a 3D object, for fixations or
393 across a saccade. B) The corresponding cortical activation is shown (orange; Saccade
394 Task) for the updating of object orientation across saccades vs. fixation (Baltaretu et al.,
395 2020). Along the inflated brain renderings (middle) are shown a transsaccadic SMG

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

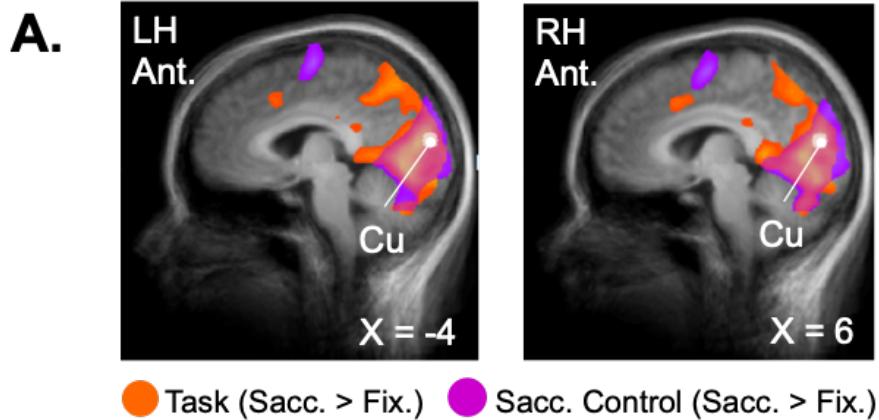
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400 areas showed significant saccade-specific effects: repetition enhancement in left
401 extrastriate cortex (putative V4) and saccade-repetition suppression in right
402 supramarginal gyrus (SMG), an inferior parietal area immediately lateral to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

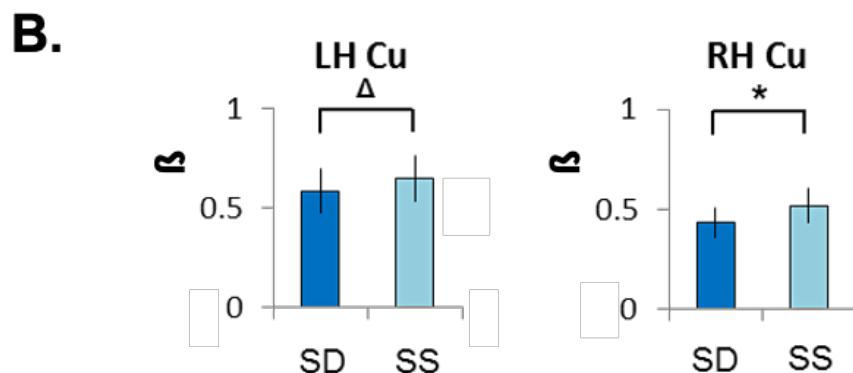
404 Further, right SMG showed the same interaction in another task involving transsaccadic
405 orientation memory for action (Fig. 4), along with activation of other parietal areas
406 associated with grasp (Baltaretu et al., 2020). It is noteworthy that this SMG area is very
407 close to the site of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

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

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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).

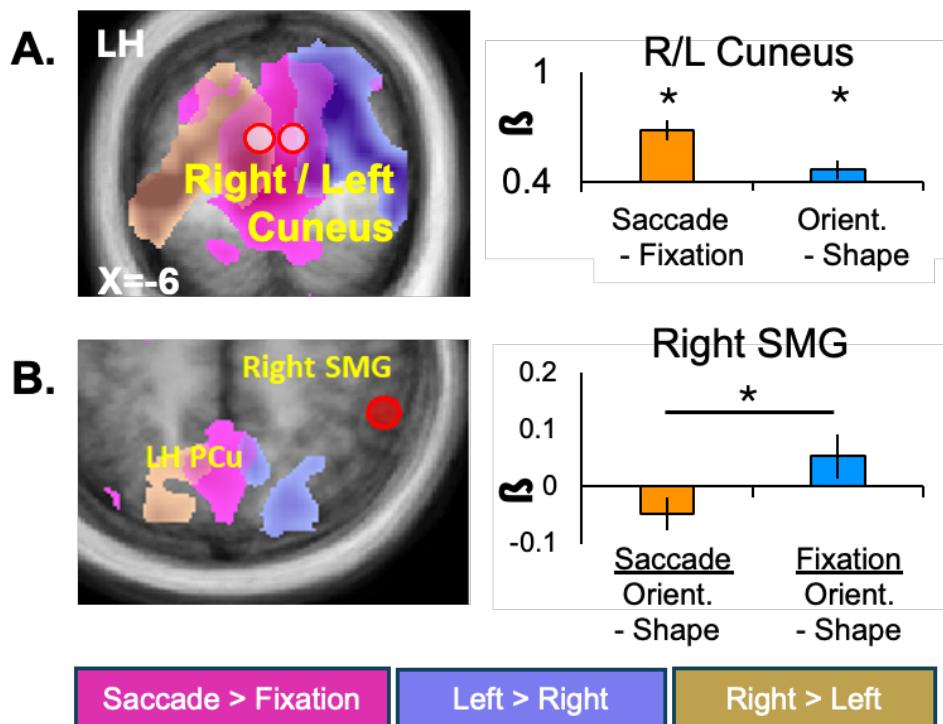
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Multiple Feature Updating. Based on the preceding fMRIa findings, we hypothesized that SMG is involved in spatial updating of object orientation (an extrinsic spatial property), whereas dorsomedial occipital cortex could play a special role in combining 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

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

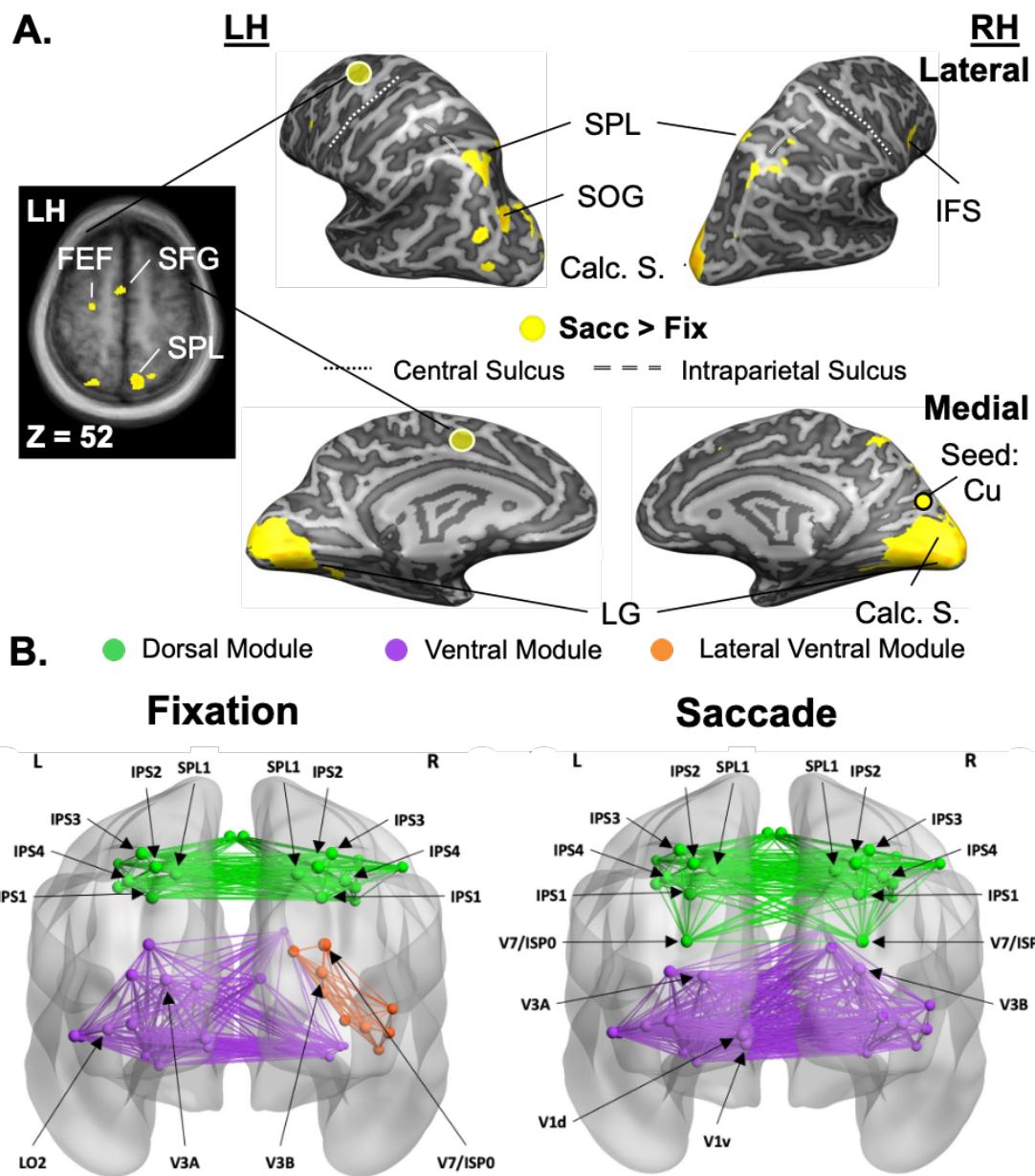
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485 **Functional Network Analysis.**

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



491

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

507
508 would expect signals in a putative transsaccadic vision area to correlate with signals in
509 gaze areas that might provide the efference copy for the saccade signal, and (depending
510 on the task) other visual areas, higher-level perception areas, working memory areas,
511 and / or motor areas for action.

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

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

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

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

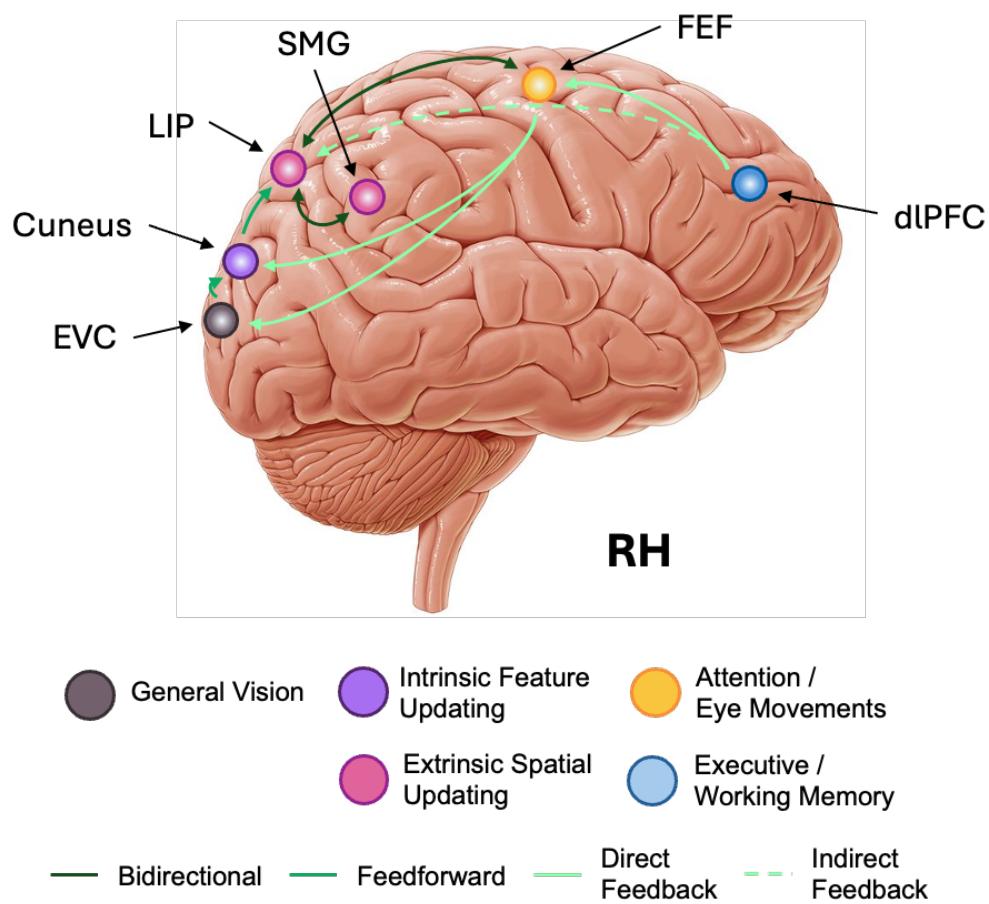
539 When saccades caused the retinal fields of the stimuli to reverse left-for-right (Fig. 7B,
540 right panel), the two ventral modules 'joined' together, perhaps due to a combination of
541 updating and sensory signals (Tomou et al., 2025). Finally, during the saccade task,
542 bilateral IPS (near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

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

551 **Discussion**

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

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



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

586 Given that our surroundings are composed of numerous, complex objects, each with
587 various features, vision scientists have found it useful to make a fundamental distinction
588 between perception of what and where objects are (Goodale, 2011; Goodale & Milner,
589 1992; Goodale & Haffenden, 1998; Mishkin et al., 1983). Here, we have expanded this to
590 the notion of *extrinsic* spatial properties (i.e., object location, orientation, motion) and
591 *intrinsic* cues (e.g., shape, texture, color) to object identity. Specifically, we propose that
592 the brain possesses separate mechanisms for extrinsic vs. intrinsic feature updating, with
593 posterior parietal cortex (specifically, LIP and SMG) playing a special role in the former,
594 and occipital cortex (specifically, the cuneus region) playing an important role in the latter
595 (Dunkley et al. 2016; Baltaretu et al. 2020, 2021, 2023; Tomou et al. 2025). This emerged
596 in both our fMRI-based ROI analysis (Figs. 3-6), their functional connectivity within
597 broader dorsal / ventral network modules (Fig. 7B, and their engagement of other regions
598 that appear to support spatial updating for specific task-related outcomes (e.g., Fig. 7A).

599 Figure 8 integrates these newer ideas with the previous literature to provide a simple
600 conceptual model of cortical transsaccadic updating / integration within two parallel
601 streams, interconnected through feedback, lateral, and feedforward connections with the
602 broader transsaccadic network (Hamker, 2003, 2005; Prime et al., 2011). At the level of
603 occipital cortex, early visual cortex already shows signs of gaze-centered updating
604 signals, likely due to recurrent signals from higher levels of the system (Hartmann et al.,
605 2017; Malik et al., 2015; Merriam et al., 2007; Nakamura & Colby, 2002; Neupane et al.,
606 2016). Our thesis is that cuneus then plays a special role in bringing together signals
607 related to intrinsic object features (e.g., shape, spatial frequency) with saccade signals,
608 and relays this to a network of areas involved in transsaccadic updating and integration
609 of object identity (Baltaretu et al., 2021; Merriam et al., 2007; Nakamura & Colby, 2002;
610 Ploran et al., 2007; Schiavetto et al., 2002; Watson et al., 2016).

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

616 Colby, 2014; Vesia et al., 2010). FEF and possibly LIP are thought to provide the saccade
617 efference copy for spatial updating (Duhamel et al., 1992; Goldberg & Bruce, 1990;
618 Gottlieb & Goldberg, 1999; Klier & Angelaki, 2008; Merriam et al., 2003; Prime et al.,
619 2008; Sommer & Wurtz, 2008; Umeno & Goldberg, 2001; Wang et al., 2024), although
620 this may involve sub-cortical structures as well.

621 Finally, dlPFC may contribute to both maintenance of visual memory in these circuits and
622 in cognitive control for tasks involving top-down instruction (Barbey et al., 2013; Brosnan
623 & Wiegand, 2017; Cameron et al., 2015; Ding et al., 2009; Funahashi, 2014; Grimault et
624 al., 2009; Johnson et al., 2007; Levy & Goldman-Rakic, 1999; Pierrot-Deseilligny et al.,
625 2003; Rossi et al., 2009; Takeda & Funahashi, 2002; Tanaka et al., 2014). With its role in
626 both working memory (left hemisphere) and reasoning abilities (right hemisphere; Barbey
627 et al., 2013), once a future target has been identified, it likely holds onto relevant visual
628 information, sends signals back to LIP (Pierrot-Deseilligny et al., 2003; Wang et al., 2025)
629 for visuospatial processing (remapping) and upcoming saccade preparation, finally
630 refined, but ultimately executed by FEF (Cameron et al., 2015; Ding et al., 2009; Sajad et
631 al., 2015). Additionally, dlPFC has been shown to guide visual attention, even further back
632 in cortex - in early visual cortex (Katsuki & Constantinidis, 2012). These connections are
633 potentially able to support extrinsic feature updating through a frontoparietal pathway (via
634 SMG) and intrinsic feature updating through a frontooccipital pathway (via cuneus).

635 **Limitations and Future Directions.** This review and our thesis are clearly subject to
636 several limitations. First, our two-stream theory of transsaccadic cortical processing is
637 based on a limited set of studies examining extrinsic (location, orientation) and intrinsic
638 (spatial frequency, shape) cues. These results need to be replicated and expanded to
639 account for motion processing (which may involve other areas such as MT+) and the
640 various other cues to object identity (Crouzet & Serre, 2011; Donderi, 2006; Leeds et al.,
641 2014; Palmeri & Gauthier, 2004). Second, cortical modulations related to attention, which
642 we only mentioned in passing, are also known to play an important role in transsaccadic
643 vision (Awh et al., 2006; Awh & Jonides, 2001; Bichot et al., 2005; Crapse & Sommer,
644 2012; Dowd & Golomb, 2019, 2020; Jonikaitis et al., 2013; Theeuwes et al., 2009; Zhou
645 & Desimone, 2011). Third, we mainly focused on egocentric updating mechanisms, and

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

651 One technique that can potentially address some of these limitations is multiunit
652 recordings from various sites (McFarland et al., 2015; Seo et al., 2024). Our hope is that
653 the framework provided in Figure 8 might inspire such experiments. Further, advances in
654 source localization with human EEG and MEG still lag the spatial resolution of fMRI, but
655 provide virtually unlimited temporal resolution. For example, EEG and MEG have recently
656 been used to test the cortical dynamics of predictive updating (Fabius et al., 2020;
657 Kurtzberg & Vaughan, 1982; Parks & Corballis, 2008; Peterburs et al., 2011; Richards,
658 2003), and graph theory analysis of source-localized EEG signals has been used to track
659 the functional networks of visual and saccade signals through time (Ghaderi et al., 2023).
660 The latter included transsaccadic memory of an oriented grating and found functional
661 connectivity between SMG and visual and frontal cortex consistent with our model.

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

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

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

687 **Conclusions**

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

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708

709 **Declarations of Interest.**

710 The authors have no declarations of interest to make.

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