

1 **Predictive Foveal Processing in Active Vision**

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23 **Optional elements:**

24 1 Terminology item, 5 Sidebars, 1 Future Issues item

25

26 **Figures:**

27 3

28 **Abstract**

29 Humans execute rapid saccadic eye movements to inspect objects of interest in high-acuity foveal  
30 vision. Even though each saccade entails a large-scale displacement of the retinal image, vision  
31 is continuous, and we easily keep track of the location and identity of relevant stimuli. This review  
32 highlights the contribution of predictive foveal processing to visual continuity. Specifically, we  
33 summarize evidence that foveal and even foveolar vision is non-uniform and modulated by  
34 attentional allocation. We then describe a set of psychophysical and neuroimaging studies  
35 demonstrating that defining features of the eye movement target are predicted in pre-saccadic  
36 foveal vision. We explore a parsimonious implementational mechanism and propose the  
37 contribution of foveal prediction to several, seemingly unconnected phenomena that may be  
38 unified under a straightforward assumption: Peripheral saccade target features predictively alter  
39 feature tuning in high-acuity foveal vision, facilitating a smooth perceptual transition once the  
40 target shifts to the center of gaze.

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45 **Keywords:**

46 foveal vision

47 saccadic eye movements

48 trans-saccadic visual continuity

49 predictive remapping

50 pre-saccadic attention

51 **Main text**

52 In a petri dish, the human retina looks like an unremarkable fragment of tissue, not dissimilar to  
 53 a piece of discarded gum. A glance through a fluorescence microscope, however, reveals an  
 54 intricate landscape of blood vessels traversing the retinal surface like a winding network of rivers  
 55 and streams (see Kolb et al., 2020). Near the center of this network lies a small island: the  
 56 avascular foveola, where retinal tissue layers spread aside and allow light to fall directly onto a  
 57 densely packed population of cone photoreceptors (Curcio et al., 1990; Hageman & Johnson,  
 58 1991; Hendrickson, 2005; **Figure 1A; Terminology**). The resulting signals carry highly resolved  
 59 visual information, the prioritization of which is reflected in the organization of upstream neural  
 60 areas. Even though the width of the anatomical depression on the retina—the so-called fovea—  
 61 covers merely the central 5 degrees of the visual field, more than 40% of primary visual cortex  
 62 (V1) is devoted to the processing of foveal input (Perry & Cowey, 1985; Wässle et al., 1990;  
 63 Azzopardi & Cowey, 1996; in macaque monkeys). To utilize the resolution of those signals and  
 64 bring relevant information into foveal vision, humans execute rapid saccadic eye movements up  
 65 to 4 times per second, depending on the visual environment and behavioral goal (Yarbus, 1967;  
 66 Andrews & Coppola, 1999; Land et al., 1999).

67 In this review, we highlight a pivotal yet surprisingly underinvestigated aspect of visual  
 68 processing in the active observer: the characteristics of foveal vision while the eyes prepare to  
 69 move to a peripheral location. After reviewing the literature on visual perception during the  
 70 saccade preparation interval—which predominantly characterizes perceptual modulations at the  
 71 target of the imminent eye movement (**Section 1**)—we will summarize converging evidence that  
 72 even high-acuity foveolar vision is perceptually non-uniform and modulated by attentional  
 73 allocation. Crucially, we will describe a set of psychophysical and neuroimaging investigations  
 74 demonstrating that defining features of the peripheral eye movement target are anticipated in pre-  
 75 saccadic foveal vision, presumably facilitating a smooth perceptual transition once the target is  
 76 foveated (**Section 2**). Next, we will explore a parsimonious implementational mechanism that  
 77 relays peripheral input to foveal neurons via feedback and/or horizontal connections (**Section 3**),  
 78 and will demarcate foveal prediction from predictive remapping of attention pointers (Cavanagh  
 79 et al., 2010; Rolfs et al., 2011), an established account of visual continuity known to alter pre-  
 80 saccadic foveal sensitivity (**Section 4**). Finally, we will discuss which established findings foveal  
 81 prediction could contribute to or even explain (**Section 5**). For this purpose, we will collect a range  
 82 of previously observed trans-saccadic phenomena that have remained unconnected and partially  
 83 unexplained, and will propose that they can be unified under a single, straightforward assumption:  
 84 Peripheral eye movement target features are anticipated in foveal vision and predictively alter  
 85 feature tuning in the area of highest acuity.

86  
87 **Terminology**88 *Retinal topography (see Figure 1A)*89 *Foveola:* central ~1.2 degrees of visual angle (dva; 0.35 mm); avascular and rod-free90 *Fovea:* central ~5 dva (1.5 mm); width of the anatomical depression on the retina91 *Parafovea:* central ~8.3 dva (2.5 mm); thickness of the rod and cone layer drops to levels  
92 comparable to the peripheral retina93 *Perifovea:* central ~18.3 dva (5.5 mm); number of cells in the ganglion cell layer drops from 4  
94 to 1

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## 98 1. The literature on visual continuity focuses on peripheral processing

99 Each saccadic eye movement has considerable perceptual consequences beyond the foveation  
100 of relevant information (for reviews, see Rolfs & Schweitzer, 2022; Schütz & Stewart, 2025;  
101 **Sidebar 1**). During the movement, the entire visual image sweeps across the retina at velocities  
102 of up to 500–700 degrees per second (e.g., Raab, 1985; Becker, 1989), which is accompanied  
103 by a spatially widespread reduction in visual contrast sensitivity (Volkman, 1978; Burr, 1994).  
104 After saccade landing, every object in the scene is shifted in eye-centered coordinates and  
105 therefore processed by a different neuronal population in retinotopically organized brain areas.  
106 Consistent with this, stimuli presented briefly before or after a saccade are often mislocalized in  
107 space (e.g., Honda, 1985; Ross et al., 1997; Lappe et al., 2000) or time (e.g., Yarrow et al., 2001;  
108 Morrone & Burr, 2005; Hunt & Cavanagh, 2009; Klanke et al., 2025; Nörenberg et al., 2025).  
109 Saccade-contingent retinal image displacements concomitantly alter the appearance or, more  
110 precisely, the eccentricity-dependent fidelity of all objects in the visual image. The target of each  
111 large-scale eye movement in particular is perceived at a reduced peripheral resolution before the  
112 movement is executed. Upon saccade landing, the visual system receives a high-resolution foveal  
113 image which, presumably, must be matched to its poorly resolved pre-saccadic counterpart  
114 (review: Stewart et al., 2020).

115 Several mechanisms have been proposed to facilitate this transition and enable a continuous  
116 trans-saccadic percept. For instance, pre-saccadic peripheral information is assumed to be  
117 maintained in visual (working) memory (e.g., Irwin, 1991, 1992; Bays & Husain, 2008; Ohl & Rolfs,  
118 2017; 2018; 2020; Schut et al., 2017; Kong et al., 2021; Ohl et al., 2024; review: Aagten-Murphy  
119 & Bays, 2019) and subsequently integrated (e.g., Ganmor et al., 2015; Oostwoud Wijdenes et al.,  
120 2015; Wolf & Schütz, 2015; Hübner & Schütz, 2017; Stewart & Schütz, 2018; review: Stewart et  
121 al., 2020) or even fused (Paeye et al., 2017) with post-saccadic signals. Systematically altering  
122 the shape or size of the eye movement target during saccadic flight suggests that discrepancies  
123 between pre- and post-saccadic target appearances are learned and continuously recalibrated  
124 (Cox et al., 2005; Li & DiCarlo, 2008; Herwig & Schneider, 2014; Weiß et al., 2014; Herwig et al.,  
125 2015; Valsecchi & Gegenfurtner, 2016; Valsecchi et al., 2020). In addition, trans-saccadic  
126 continuity is supported by the spatial and temporal dynamics of visual signals generated during  
127 the eye movement itself. Specifically, the motion streak produced by rapid intra-saccadic image  
128 motion links the pre- and post-saccadic retinal positions of the saccade target (Schweitzer &  
129 Rolfs, 2020, 2021; Schweitzer et al., 2025; Ince et al., 2025).

130 The most extensive body of literature on visual continuity, however, characterizes pre-saccadic  
131 attentional modulations at the target of an imminent saccade: In the vast majority of these  
132 investigations (pioneered by Kowler et al., 1995; Deubel & Schneider, 1996), observers are cued  
133 to execute an eye movement to a peripheral target. Sometime during the latency between the  
134 saccade prompt and the onset of the movement, a perceptual probe may appear at the target  
135 location. After saccade landing, observers report the task-relevant probe property, such as its  
136 presence/absence or orientation (review: Li et al., 2021). Characteristically, observers' detection  
137 and discrimination performances start ramping up around 60 ms after movement cue onset and  
138 continue to increase as the peripheral probe appears in later and later stages of saccade  
139 preparation (e.g., Montagnini & Castet, 2007; Deubel, 2008; Rolfs et al., 2011; Rolfs & Carrasco,  
140 2012; Hanning et al., 2019; Kroell & Rolfs, 2021). These findings motivated the now firmly  
141 established conclusion that visuospatial attention shifts to the saccade target before the eyes  
142 begin to move.

143 Beyond yielding general performance improvements, pre-saccadic attention boosts the  
144 perceived contrast of the saccade target (Rolfs & Carrasco, 2012) and progressively tunes

145 peripheral sensitivities around its features (Li et al., 2016; Ohl et al., 2017). Pre-saccadic attention  
146 may even reconcile pre- and post-saccadic target views by increasing the perceived resolution of  
147 the peripheral target stimulus (Li et al., 2016; 2019; Kroell & Rolfs, 2021; Kwak et al., 2023). The  
148 coupling between eye movement preparation and attentional allocation is considered obligatory  
149 (Kowler et al., 1995; Deubel & Schneider, 1996; Moore & Fallah, 2001), and perceptual correlates  
150 of pre-saccadic attention generalize across various task and stimulus parameters (Zhao et al.,  
151 2013). All in all, numerous investigations suggest that the target of a saccadic eye movement is  
152 transiently prioritized over all remaining locations in the visual field. This attentional prioritization  
153 is assumed to shield the perception of the target against saccade-induced visual disruptions.

154

### 155 **Sidebar 1: Eye movements are inherently beneficial for vision**

156 *Despite their transiently disruptive consequences, eye movements are inherently beneficial and*  
157 *even necessary for vision. Certain oculomotor behaviors such as the optokinetic nystagmus and*  
158 *the vestibulo-ocular reflex evolved to stabilize retinal input against world/body motion (Lencer et*  
159 *al., 2019). Conversely, some degree of image motion is required to maintain a stable percept:*  
160 *Small-scale drift movements and microsaccades prevent adaptation-induced image fading*  
161 *(Ditchburn & Ginsborg, 1952). By reformatting spatial patterns into spatiotemporal signals, drift*  
162 *additionally boosts sensitivity for fine details (Rucci & Poletti, 2007), allowing visual acuity to*  
163 *exceed limits predicted from photoreceptor spacing alone (Witten et al., 2024). Even afoveate*  
164 *animals with nearly uniform acuity such as mice (Giovannetti & Rancz, 2024) and fruit flies (Fenk*  
165 *et al., 2022) move their eyes. In mice, these movements are just large enough to provide neurons*  
166 *with uncorrelated pre- and post-saccadic input, eliminating unsystematic sources of noise*  
167 *(Samonds et al., 2018). Strikingly, certain visual sensors can only gather information while they*  
168 *move: Jumping spiders, whose ‘scanning eyes’ have narrow vertical retinas spanning only 6*  
169 *photoreceptors (Land & Fernald, 1992), sweep objects with oscillatory eye movements to obtain*  
170 *a cohesive image despite the restricted window they can encode in one snapshot.*

171

## 172 **2. Overlooked in plain sight: Redirecting the spotlight to pre-saccadic foveal vision**

173 While perceptual modulations at the saccade target have been studied extensively, considerably  
174 less is known about the concurrent development of perception in another highly relevant part of  
175 the visual field: the pre-saccadic foveal location (with the exceptions of Rolfs et al., 2011, Ludwig  
176 et al., 2014, and Hanning & Deubel, 2022, discussed in later sections). This knowledge gap can  
177 partially be attributed to methodological constraints. When humans or non-human primates  
178 attempt to maintain fixation, their eyes continue to move, albeit on a very small scale (review:  
179 Rolfs, 2009). These fixational eye movements (i.e., microsaccades, drift and tremor) generate a  
180 continuous yet irregular shift of the retinal image which, unless accounted for, interferes with  
181 reverse-correlation based estimations of foveal receptive fields (RFs) in electrophysiological  
182 studies (Yates et al., 2023). Psychophysical investigations of foveal processing face a different  
183 set of constraints: The employed performance measure must be sensitive enough to reveal  
184 variations of high-acuity vision in simple keyboard responses. At the same time, and in the active  
185 observer in particular, the performance probe must be inconspicuous enough not to interfere with  
186 saccade programming despite appearing in the very center of gaze. In neurophysiology, recent  
187 advances combining high-precision Dual-Purkinje eye tracking with a free viewing approach have  
188 started to allow for foveal RF estimations (Yates et al., 2023). In behavioral studies, dynamic 1/f  
189 noise paradigms have been employed to measure peripheral and foveal detection performances  
190 without detrimental effects on saccade programming or attentional allocation (Hanning et al.,  
191 2019; Hanning & Deubel, 2023). Beyond these methodological considerations, perhaps most

192 detrimental to the study of pre-saccadic foveal processing is the assumption that high-acuity  
193 vision is largely uninfluenced by ongoing motor processes; much like the lens of a microscope,  
194 foveal vision is presumed to reflect the ground truth of our environment. Nonetheless, studies  
195 employing (digital) Dual-Purkinje eye tracking (e.g., Poletti & Rucci, 2016; Wu et al., 2023), gaze-  
196 contingent stimulus presentation techniques (Santini et al., 2007) and adaptive optics scanning  
197 laser ophthalmoscopy (e.g., Roorda et al., 2002; **Sidebar 2**) suggest that foveal perception is  
198 considerably more intricate than classically assumed.

199

### 200 **Sidebar 2: Tools and techniques for studying foveolar vision in the moving eye**

201 *Fixational eye movements subtly yet continuously reposition stimuli on the foveolar cone mosaic.*  
202 *To ensure that a targeted foveolar location is reliably stimulated despite ongoing eye motion,*  
203 *oculomotor activity must not only be recorded but explicitly accounted for. A combination of state-*  
204 *of-the-art eyetracking and presentation techniques enables this remarkable level of experimental*  
205 *control. (Digital) Dual-Purkinje Image eyetrackers derive eye rotation from the spatial separation*  
206 *and relative motion of light reflecting from two surfaces within the eye: the front of the cornea and*  
207 *the back of the lens (the first and fourth Purkinje image; Wu et al., 2023). The resulting high-*  
208 *precision gaze estimates have been successfully combined with minimum-delay stimulus updates*  
209 *(Santini et al., 2007). At an even finer scale, a high-resolution retinal imaging technique known*  
210 *as Adaptive Optics Scanning Laser Ophthalmoscopy (Roorda et al., 2002) corrects for the eye's*  
211 *optical aberrations using deformable mirrors and enables the visualization and targeted*  
212 *stimulation of individual photoreceptors. Over the past decades, these methods have provided*  
213 *insights into in-vivo foveolar processing and the highly coordinated interplay between small-scale*  
214 *oculomotor behavior, retinal anatomy and visual acuity.*

215

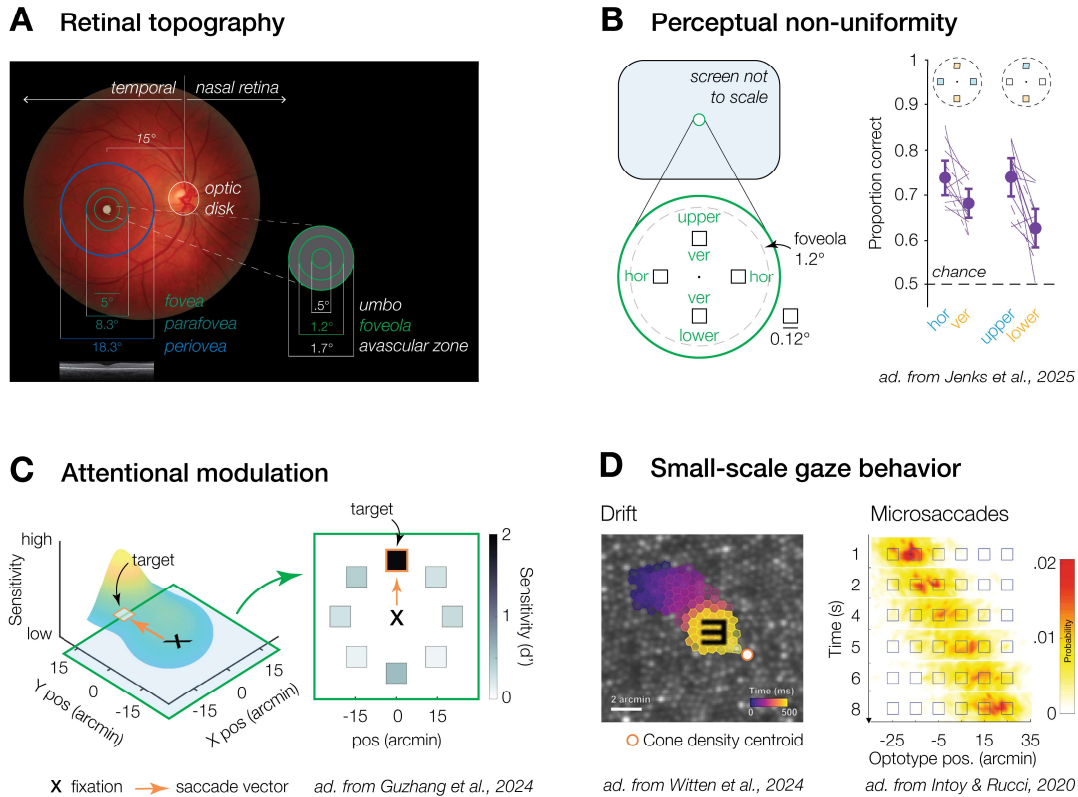
216

## 216 **2.1 Foveolar vision is perceptually non-uniform and modulated by attention**

217 To start, foveal visual processing is non-uniform on both an anatomical and functional level.  
218 The foveal region, classically defined as the width of the anatomical depression on the retina  
219 (e.g., Hendrickson, 2005; Kolb, 2020; **Figure 1A**), contains an even smaller area known as the  
220 foveola. The foveola spans the central ~1.2 degree of visual angle (dva; 0.35 mm; Curcio et al.,  
221 1990; Hendrickson, 2005) and is devoid of capillaries and rod photoreceptors. The density of  
222 color-sensitive cone photoreceptors exhibits a sharp peak near the foveolar center, declines  
223 steeply within the surrounding 0.3–0.6 dva and, by ~1 dva (0.3 mm) eccentricity, is more than  
224 halved (Curcio et al., 1990; Song et al., 2011; Zhang et al., 2015). These and additional  
225 anatomical and functional non-uniformities in downstream neurons (Kupers et al., 2022) give rise  
226 to substantial acuity variations within the foveal and even foveolar region. High-acuity judgments  
227 are impaired when stimuli are presented less than 0.2 dva from the center of fixation (Poletti et  
228 al., 2013), with generally higher discrimination accuracies along the horizontal than the vertical  
229 meridian (Jenks et al., 2025; **Figure 1B**). In addition, and in marked contrast to parafoveal vision  
230 (Jenks et al., 2025; review of extra-foveal polar angle asymmetries: Himmelberg et al., 2023),  
231 stimuli presented just 0.3 dva above the line of sight are more accurately discriminated than  
232 stimuli positioned equidistantly below it.

233 Despite its exceptionally high overall acuity, this perceptual topography can be reshaped by  
234 attentional allocation. Exogenous (Zhang et al., 2021) and valid endogenous (Poletti et al., 2017)  
235 attention cues transiently increase the accuracy of discrimination judgments for stimuli presented  
236 0.2–0.3 dva from fixation, mirroring selective attention effects conventionally observed in the  
237 parafoveal and peripheral visual field. Moreover, instructed microsaccades to targets at 0.3 dva  
238 eccentricity are preceded by sensitivity modulations that strongly resemble pre-saccadic attention

239 shifts (Shelchkova & Poletti, 2020; Guzhang et al., 2023; **Figure 1C**). Strikingly, perceptual  
 240 enhancement at the microsaccade target is associated with sensitivity costs in the opposite  
 241 foveolar hemifield (Shelchkova & Poletti, 2020) and even in the very center of fixation (Guzhang  
 242 et al., 2023).



268 **Figure 1.** Retinal topography (A) and dynamics of foveolar vision (B-D). **A:** Spatial location and extent of key retinal  
 269 structures overlaid on an in vivo photograph of a healthy right eye. **B:** Foveolar perceptual non-uniformity. Observers’  
 270 sensitivity to small stimuli presented within the foveola is higher along the horizontal (‘hor’) than the vertical (‘ver’)  
 271 meridian, and higher above than below the line of sight. **C:** Foveolar attentional modulations. During microsaccade  
 272 preparation, attention shifts to the target location, increasing observers’ sensitivity. **D.** Repositioning of foveolar vision  
 273 through ocular drift (left) and microsaccades (right). Directed ocular drift gradually moves a to-be discriminated optotype  
 274 towards the retinal area with highest cone density. Microsaccades rapidly center gaze on the currently relevant optotype  
 275 during self-timed sequential discrimination. **Credit line:** Panel A adapted  
 276 from <https://commons.wikimedia.org/wiki/File:Macula.svg> by Zywxw99 including photo by Danny Hope (CC BY 2.0).  
 277 Optical coherence tomography image of a healthy human retina (bottom left) from Kermany et al. (2018) (CC BY 4.0).  
 278 Panel B adapted from Jenks, Carrasco, & Poletti (2025) (CC BY 4.0). Panel C adapted with permission from Guzhang  
 279 et al. (2024) (CC BY-NC-ND 4.0). Panel D adapted from Witten et al. (2024) and Intoy and Rucci (2020) (CC BY 4.0).  
 280

281 Beyond altering the small-scale distribution of visuospatial attention, microsaccades leverage  
 282 foveolar acuity in a task-efficient manner by compensating for perceptual non-uniformities: While  
 283 solving a foveolar needle-threading task, observers execute spontaneous microsaccades that  
 284 direct the high-acuity foveolar center to the momentarily most relevant part of the display (Ko et  
 285 al., 2010; see Intoy & Rucci, 2020 and Shelchkova et al., 2019 for comparable findings in optotype  
 286 discrimination and face scanning tasks, respectively; **Figure 1D**). Similarly, the direction of small-  
 287 scale ocular drift movements flexibly adapts to current task demands (Lin et al., 2023) as well as  
 288 anatomical properties of the foveolar region: A study combining high-resolution retinal imaging  
 289 and microscopic photo-stimulation of single cone photoreceptors demonstrated that small-scale

290 ocular drift movements adaptively steer minute stimuli towards the foveolar region with highest  
291 cone density (Witten et al., 2024; **Figure 1D**). Consistent with this, eliminating the beneficial effect  
292 of fixational eye movements by stabilizing the retinal image impairs discrimination performance  
293 at eccentricities as small as 0.2 dva (Poletti et al., 2013).

294 In brief, visual processing in the fovea and foveola is far from saturated; instead, an inherently  
295 non-uniform perceptual topography is dynamically modulated by attentional deployment and  
296 effectively repositioned through small-scale oculomotor activity.

297

## 298 **2.2 Foveal cortex contributes to peripheral discrimination during passive fixation**

299 Beyond its indisputable importance for high-acuity vision, foveal processing assumes another,  
300 more unexpected role: Evidence from functional magnetic resonance imaging (fMRI; Williams et  
301 al., 2008; Fan et al., 2016; Constantino et al., 2025), brain stimulation (Chambers et al., 2013),  
302 and psychophysical (Fan et al., 2016; Weldon et al., 2016; Yu & Shim, 2016; review: Oletto et al.,  
303 2023) studies suggests that neurons with foveal RFs contribute to the discrimination of stimuli  
304 presented in the visual periphery. Williams and colleagues (2008) recorded fMRI activity while  
305 fixating observers performed a shape discrimination task on two novel objects presented at 7 dva  
306 eccentricity. Surprisingly, voxels in the region of V1 that conventionally encodes foveal visual  
307 stimulation carried information about the category of the peripherally presented shapes (for  
308 convergent findings using orientation signals and naturalistic stimuli, see Fan et al., 2016, and  
309 Constantino et al., 2025, respectively). Object category was selectively decodable from the  
310 cortical area processing  $\pm 2$  dva around the center of gaze. Foveal activation was robustly elicited  
311 by different stimulus arrangements, not caused by the foveation of either object through eye  
312 movements and correlated with observers' peripheral discrimination performance. In short,  
313 neurons in foveal retinotopic cortex responded to stimuli far outside their RFs, irrespective of the  
314 precise location of these signals in the visual scene.

315 Causal evidence for an involvement of foveal cortex in peripheral processing was provided  
316 with transcranial magnetic stimulation (TMS, Chambers et al., 2013): Peripheral object  
317 discrimination was impaired  $\sim 350$ – $400$  ms after double-pulse TMS to the posterior calcarine  
318 sulcus, that is, to the earliest cortical processing site of visual information occupying the central  
319 visual field (Dow et al., 1981). Foveal discrimination was impaired immediately (50–100 ms) after  
320 pulse application, suggesting that the same area encoded foveal and peripheral information in  
321 succession. Most psychophysical investigations follow a similar logic (review: Oletto et al., 2023):  
322 Disrupting foveal processing by presenting a distractor in the center of gaze should impair  
323 peripheral performance if foveal processing contributes to peripheral discrimination at that  
324 moment in time. Indeed, using a category discrimination task identical to Williams et al. (2008),  
325 Fan and colleagues (2016) demonstrate that foveal noise presented 250 ms after the to-be  
326 discriminated peripheral objects impaired discrimination performance. Foveal distractors had no  
327 effect when the peripheral objects contained only low spatial frequency information or when  
328 observers estimated the speed of peripherally moving dots. The authors concluded that foveal  
329 cortex is flexibly engaged whenever high-resolution spatial processing of peripheral information  
330 is required (see **Sidebar 3**).

331 In all of these studies, observers were instructed to maintain fixation (with the exception of  
332 Experiment 3 in Fan et al., 2016). In more active viewing conditions, however, the same  
333 mechanism could gain a predictive quality: Before an imminent saccadic eye movement, critical  
334 features of the peripheral target are available for foveal processing. Executing the eye movement  
335 will bring the target into foveal vision. In actively behaving observers, therefore, peripheral-to-

336 foveal feature interactions would anticipate incoming information in retinotopic coordinates and  
337 support trans-saccadic visual continuity.

338

339 **Sidebar 3: What is the advantage of processing peripheral stimuli in foveal cortex?**

340 *Foveal neurons cannot increase the sharpness of peripheral signals that are poorly resolved to*  
341 *begin with (at least without the contribution of visual memory, see Mynick et al., 2025). Just like*  
342 *no simple editing tool can unblur a picture captured on a low-resolution camera, the peripheral*  
343 *resolution of a stimulus should impose an upper limit on the resolution of its foveal counterpart.*  
344 *Nonetheless, foveal vision has been proposed as a ‘high-resolution buffer’ (Weldon et al., 2016;*  
345 *paraphrased in Fan et al., 2016) to which peripheral information is relayed for improved*  
346 *processing. If not its acuity, then what characteristics of foveal vision may be harnessed in these*  
347 *cases? Is peripheral information outsourced to the vast population of foveal neurons to provide*  
348 *robust encoding? Or are foveally processed stimuli more readily available for action programming*  
349 *and execution? The finding that foveal retinotopic cortex is activated during haptic exploration in*  
350 *the dark (Monaco et al., 2017) may support this idea. Alternatively, peripheral-to-foveal feature*  
351 *interactions may provide a coarse visual anticipation of saccade target features—a process so*  
352 *entrained that it may spill over to passive fixation tasks.*

353

354

**2.3 Saccade target features are anticipated in foveal vision**

355 Foveal vision undergoes pronounced, feature-nonspecific sensitivity modulations during  
356 saccade preparation: Detection performance for foveally presented orientation signals decreases  
357 markedly while observers plan a saccade towards the peripheral target (Hanning & Deubel,  
358 2022). This general decrease in foveal performance develops continuously throughout the  
359 saccade preparation interval, manifesting as early as 200 ms before eye movement onset (Kroell  
360 & Rolfs, 2022; **Figure 2A**). Similar to small-scale gaze shifts (see **Section 2.1**), these  
361 observations likely reflect modulations of the pre-saccadic attentional landscape: The ongoing  
362 motor program is accompanied with a shift of attention towards the eye movement target and  
363 away from the current center of gaze (but see Ludwig et al., 2013, for an account of parallel  
364 peripheral and foveal sampling). To measure feature-specific modulations of pre-saccadic foveal  
365 vision, Kroell & Rolfs (2022) asked observers to monitor the appearance of a foveal orientation  
366 signal (the probe) while preparing a saccade to a second orientation signal presented peripherally  
367 (the target). Target and probe were generated by applying local orientation filters to dynamic, full-  
368 screen 1/f noise (see Hanning & Deubel, 2022) and could either have the same orientation  
369 (congruent) or two different orientations (incongruent). Starting 175 ms before saccade onset,  
370 observers detected the foveal probe more readily if it had the same orientation as the eye  
371 movement target (**Figure 2A**). This feature-specific enhancement was spatially confined to a  
372 small area (~5.5 dva horizontally) around the pre-saccadic center of fixation (**Figure 2B**),  
373 significantly more pronounced than during passive fixation (see **Sidebar 4**), and scaled with the  
374 signal-to-noise ratio of orientation information at the target location (Kroell & Rolfs, 2025). In trials  
375 in which no foveal probe was presented, reverse correlations revealed that observers reacted  
376 systematically to incidental orientation signals in the foveal noise (**Figure 2C**): For observers to  
377 perceive the target orientation in their pre-saccadic center of gaze, a high incidence of target-like  
378 orientation information was required. The spatial frequency range of these orientation signals was  
379 similar to the spatial frequency range that observers should have been able to resolve at the  
380 peripheral target location (Kroell & Rolfs, 2021). Perceiving the non-target orientation in the foveal  
381 noise required both, evidence for the non-target orientation and an absence of evidence for the

382 target orientation. In other words, the foveal noise needed to look as target-dissimilar as possible  
383 for observers to be able to perceive a competing orientation in their center of gaze.

384 Further evidence for pre-saccadic foveal feature predictions is provided by  
385 electroencephalographic (EEG) and fMRI investigations. Moran and colleagues (2024) applied  
386 multivariate decoding methods to EEG data and demonstrate that spatial frequency information  
387 presented in the proximity of a saccade target can be correctly classified at all parafoveal locations  
388 during the saccade preparation interval, irrespective of the precise saccade endpoint (see also  
389 Kroell & Rolfs, 2022). Knapen and colleagues (2016) demonstrate that during saccade  
390 preparation, foveal voxels in areas V1, V2 and V3 exhibit increased phase-preference similarity  
391 with voxels encoding a rotating wedge at the target of an impending eye movement (**Figure 2D**).  
392 Strikingly, the dimensions of the synchronized foveal region matched the target stimulus in both  
393 orientation and size, suggesting that key spatial properties were preserved despite pronounced  
394 discrepancies in peripheral and foveal RF sizes. Kämmer and colleagues (2025) demonstrate  
395 that the identity of naturalistic objects presented at the saccade target location can be decoded  
396 from foveal voxels in V1, V2 and V3 (**Figure 2E**). Cross-decoding to an instructed fixation  
397 condition revealed a shared representational format between bottom-up foveal stimulation and  
398 the pre-saccadically predicted signal: In contrast to the lateral occipital area (LO), decoding  
399 accuracy in foveal V1 relied on shape rather than category information—both for foveally  
400 presented stimuli and pre-saccadic foveal predictions. All in all, the pre-saccadic decrease in  
401 foveal sensitivity, and the concurrent encoding of target-like feature information, suggest a  
402 pronounced shift in the functional role of foveal vision: Bottom-up sensory sampling is attenuated  
403 and internal, action-relevant feature predictions transiently dominate processing.

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405 **Sidebar 4: Are pre-saccadic foveal predictions fundamentally different from peripheral-to-**  
406 **foveal feature interactions during fixation?**

407 *Peripheral object information has been decoded from foveal voxels while observers withheld gaze*  
408 *shifts towards the peripheral stimulus (e.g., Williams et al., 2008). By directly comparing fixation*  
409 *and saccade preparation conditions, Kroell & Rolfs (2022) demonstrated that congruency effects*  
410 *develop faster and are significantly more pronounced when observers subsequently saccade to*  
411 *the peripheral orientation signal. The attentional process selecting the peripheral stimulus (rapid*  
412 *pre-saccadic attention during saccade preparation and slower covert attention during fixation)*  
413 *may govern the time course and, once averaged across time, the magnitude of foveal congruency*  
414 *effects. Moreover, the appearance of a task-relevant peripheral stimulus may trigger the initiation*  
415 *of a saccade preparation program. Even when the movement is withheld, pre-motor perceptual*  
416 *and attentional processes are likely engaged to some degree. In other words, the emergence of*  
417 *a phenomenon during fixation does not preclude its involvement in active vision; rather, any*  
418 *mechanism manifesting during fixation may have evolved to support perception in its most natural*  
419 *behavioral context: the preparation and imminent execution of an eye movement.*

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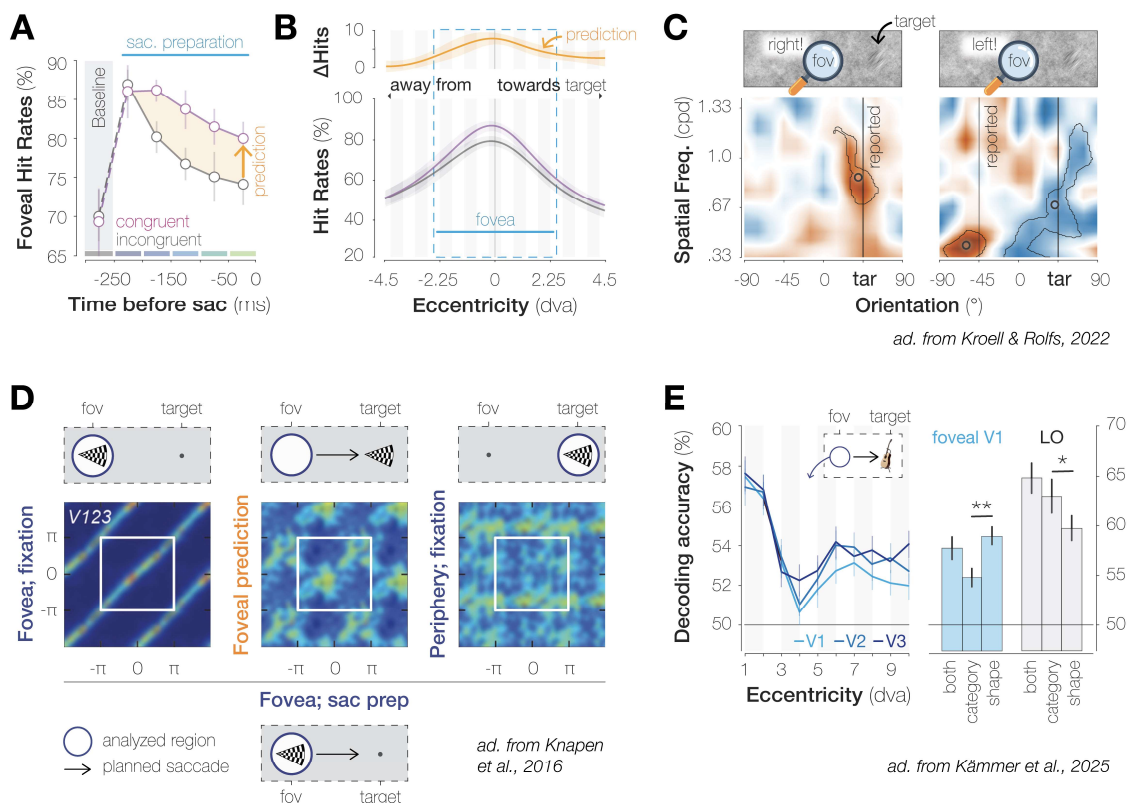
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**Figure 2.** Psychophysical (A-C) and neuroimaging (D-E) evidence for pre-saccadic foveal feature predictions. **A.** While preparing a saccade to a peripheral orientation signal, observers exhibit higher Hit Rates for foveal probes with target-congruent orientation. **B.** The difference in Hit Rates is spatially specific and peaks in the center of fixation. **C.** Reverse correlations on incidental noise properties reveal that congruent False Alarms are triggered by foveal ('fov') signals that match the saccade target in orientation and perceived spatial frequency content ('Spatial Freq.'). Red and blue color values signify above- and below-average incidence of a certain orientation x spatial frequency combination in the foveal noise. **D.** fMRI investigation demonstrating increased phase preference similarity (manifesting as a diagonal pattern in the phase matrix) between foveal and peripheral voxels if, and only if, a saccade is subsequently executed towards the peripheral target. Stimulus configuration insets illustrate the compared conditions on the x-axis (same for all panels) and y-axis (depicted above each panel). The checkerboard stimulus indicates the location of the rotating wedge employed to induce phase preference in a certain region of retinotopic cortex. **E.** fMRI investigation demonstrating that naturalistic saccade target objects can be decoded from foveal voxels in V1, V2 and V3. Unlike in mid-level visual areas (lateral occipital area; LO), V1 decoding performance relied on the shape of the saccade target rather than its category. **Credit line:** Panels A-C adapted from Kroell and Rolfs (2022) (CC BY 4.0). Panel D adapted from Knapen et al. (2016) (CC BY 4.0). Panel E adapted from Kämmer et al. (2025) (CC BY 4.0).

### 3. Potential neural mechanisms of foveal prediction

In their seminal study, Williams and colleagues (2008) propose that cortical feedback connections may underlie the decodability of peripheral object identity from foveal voxels. In follow-up fMRI (Fan et al., 2016; Kämmer et al., 2025) and psychophysical (review: Oletto et al., 2023) investigations, convergent findings were suggested to reflect a 'foveal feedback' process. Yet, the precise neural implementation, including the putatively involved areas and necessary anatomical preconditions, has never been explicitly characterized (with the recent exception of Constantino et al., 2025). Indeed, a hierarchical feedback mechanism appears appealing: Relevant peripheral input is processed in a bottom-up fashion until it reaches higher-order visual areas in which features and feature conjunctions are encoded by neurons with large RFs (such

483 as areas V4 or TE; Nandy et al., 2017; Kobatake & Tanaka, 1994). These higher-order regions  
484 may then relay feature information to foveal neurons in early visual cortex, presumably even V1  
485 as previously suggested (Williams et al., 2008; Chambers et al., 2013; Kämmer et al., 2025). Fed-  
486 back information may subsequently combine with feedforward visual signals, enhancing  
487 congruent foveal input or, potentially, generating a periphery-like foveal percept in the absence  
488 of bottom-up stimulation. For hierarchical, corticocortical feedback to constitute a viable  
489 mechanism of foveal prediction, at least three preconditions must be fulfilled: (1) the selection of  
490 relevant peripheral information in mid- or high-level visual areas, (2) selective feedback to lower-  
491 level neurons sharing the same feature preference (feature-specific feedback), and (3) selective  
492 feedback to neurons with foveal RFs (spatially specific feedback).

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### 3.1 Selection of relevant information

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### 3.2 Feature-specific feedback

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A second precondition is that neurons in feedback-sending areas must relay selected inputs to foveal neurons with a similar feature preference. Anatomical and physiological evidence in early visual cortex of macaque, marmoset and owl monkeys (e.g., Shmuel et al., 2005; Federer et al., 2021; review: Angelucci & Bressloff, 2006) as well as tree shrews (Zhang et al., 2018) indicates that a large subset of visual feedback neurons primarily project to target cells with matched feature selectivity. Arguably, feature-matched feedback may even be necessary to maintain the integrity of bottom-up encoding by preventing an ambiguous drive on single neurons (but see Stettler et al., 2002; review: Briggs, 2020). Less is known about the feature-specificity of feedback projections from neurons in mid-level visual areas, which are tuned to more complex visual patterns. Studies in macaques demonstrate that the feature preference of V4 cells (Jeurissen et al., 2024) as well as task-induced attentional allocation (Ferro et al., 2021) can modulate the dynamics of feedback to V1. Moreover, a computational model based on recordings in macaque V4 proposes that during saccade preparation, higher-level areas such as TE or TEO relay spatially global feature information to V4 neurons, modulating their responses to oriented probes according to the orientation of the saccade target stimulus (Burrows et al., 2014; see also Hamker & Zirnsak, 2006). Direct anatomical or electrophysiological evidence for feature-selective feedback from mid- to high-level cortical areas, however, remains to be established.

### 530 3.3 Spatially specific feedback

531 The third precondition is that feature information must be relayed selectively from neurons  
532 encoding the peripheral saccade target to neurons with foveal RFs. Since corticocortical feedback  
533 projections in macaque monkeys predominantly travel along feedforward connections, they target  
534 lower-level neurons whose RFs are centered on the same retinotopic visual field location  
535 (Angelucci et al., 2002; Shmuel et al., 2005). Nonetheless, retrograde labeling revealed that V1  
536 neurons receive input from cells in higher visual areas that encode regions of visual space up to  
537 5 times (V2) to 25 times (MT) larger than their own RFs (Angelucci et al., 2002; review: Angelucci  
538 & Bressloff, 2006). In other words, foveal V1 neurons indeed receive information from regions  
539 outside their classical RFs through feedback connections. While this observation is equally true  
540 for neurons with peripheral RFs, neuroimaging and psychophysical investigations in humans  
541 suggest a crucial importance of feedback signals for foveal vision in particular. In fMRI studies,  
542 deep convolutional neural networks consistently fail to predict the activation of foveal voxels from  
543 the properties of foveally presented stimuli. Voxel-to-voxel models which allow for top-down  
544 interactions between voxels in different areas dramatically improve foveal decodability (Mell et  
545 al., 2021). Relying on psychophysical data, the central-peripheral dichotomy (Zhaoping, 2014;  
546 2017; 2019) proposes that top-down feedback is especially pronounced in foveal vision and loses  
547 efficacy in the peripheral visual field. If this spatial selectivity cannot be accomplished solely by  
548 foveally targeted feedback connections, other processes—such as horizontal connections and  
549 the allocation of spatial attention—may support the focalization of a spatially global feature signal:

550 Horizontal connections in macaque V1 have been shown to extend the effective RF size of  
551 neurons by a factor of almost 3 (depending on RF size definitions, see Angelucci et al., 2002)  
552 and, in cortical space, are slightly direction-biased towards foveal neurons. Using voltage-  
553 sensitive dye imaging in macaque V1, Bouhnik, Korch and Slovín (2025) demonstrate a  
554 concurrent activation increase at the target of a microsaccade (<1 dva amplitude) and the center  
555 of fixation—an effect that could be explained by spatially targeted horizontal connectivity patterns.  
556 Before large-scale saccades, the spatial range of horizontal connections is likely insufficient to  
557 transfer signals from the periphery to the fovea (but see Constantino et al., 2025, for an account  
558 of seemingly long-range, peripheral-to-foveal horizontal connectivity in human V1). Yet, horizontal  
559 connections are known to interact with feedback projections to support longer-range visual  
560 computations such as contour detection and figure-ground segmentation. For instance, by  
561 applying Granger causality analyses to simultaneous V1 and V4 recordings in behaving  
562 macaques, Liang and colleagues (2017) demonstrate that removing the influence of V4 feedback  
563 substantially reduced lateral interactions in V1 and vice versa. In the case of foveal prediction, it  
564 can be speculated that lateral connectivity patterns direct spatially broad feedback signals  
565 towards foveal neurons (**Figure 3A**).

566 Alternatively, the deployment of visuospatial attention is known to alter the contrast threshold  
567 and/or gain of single neurons in a stable retinotopic reference frame (macaque V1 and V4:  
568 McAdams & Maunsell, 1999; macaque V4: Reynolds et al., 2000; Williford & Maunsell, 2006;  
569 macaque MT: Martínez-Trujillo & Treue, 2002; human psychophysics: White et al., 2015).  
570 Spatially non-selective feature signals would thus be amplified differentially across the visual field,  
571 depending on the attentional prioritization of its target neurons' RF locations (**Figure 3B**). It is  
572 conceivable that the fovea as the region of highest acuity is assigned a permanent attention  
573 pointer, amplifying the modulatory power of any signal relayed to the corresponding neural  
574 population. Moreover, the preparation of a saccadic eye movement introduces a profound  
575 reorganization of the spatial attentional landscape: Attention not only shifts towards the eye  
576 movement target, but also in the opposite direction of the saccade vector, to the retinotopic

577 location that the target will occupy upon eye movement landing (e.g., Cavanagh et al., 2010; Rolfs  
578 et al., 2011; see **Section 4**). For saccades with accurate landing points, this mechanism would  
579 predictively remap attention to the foveal region (Collins et al., 2019).

580 So far, this section has explored the plausibility of a corticocortical feedback mechanism as  
581 implied in seminal foveal decoding studies (e.g., Williams et al., 2008). Given that subcortical  
582 structures are involved in both visual and oculomotor processing, they may provide an alternative  
583 or complementary route for foveal feature predictions. In particular, corticothalamic connections  
584 between V1 and the lateral geniculate nucleus have been suggested to convey attention- and  
585 context-related signals (macaques: Vanduffel et al., 2000; McAlonan et al., 2008; humans:  
586 O'Connor et al., 2002; Ling et al. 2015). More recent work identifies the superior colliculus (SC)—  
587 a midbrain structure conventionally linked to oculomotor control—as a particularly promising  
588 candidate region. In macaques, saccadic eye movement commands in motor-related SC neurons  
589 are tuned to visual features of the movement target (Baumann et al., 2023) and may relay these  
590 features to cortical visual areas. Furthermore, recordings from foveal SC neurons suggest that  
591 they respond to intra-saccadic changes in saccade target appearance, even though the target  
592 only entered their RFs after movement offset (Zhang et al., 2025). These findings raise the  
593 intriguing possibility that pre-saccadic foveal predictions could be implemented by subcortical  
594 circuits exclusively.

595 All in all, neurophysiological investigations in non-human primates demonstrate that neurons  
596 in mid-level visual areas can selectively process prioritized stimuli in their large RFs (Treue,  
597 2001). Anatomical evidence on feedback connectivity patterns between macaque V2 and V1  
598 suggests that feedback-sending neurons project primarily to lower-level neurons with similar  
599 feature preference (review: Angelucci & Bressloff, 2006). Neuroimaging and psychophysical  
600 evidence in human observers indicates that feedback connections play a particularly important  
601 role in foveal vision, yet the neural implementation of this spatial specificity remains speculative.  
602 Future investigations employing neurophysiological and anatomical tracing protocols in non-  
603 human primates and high-resolution neuroimaging in humans are required to clarify if foveally  
604 specific perceptual modulations are implemented through feedback projections targeting the  
605 fovea in particular, adaptive horizontal connectivity in cortical or subcortical areas, attention-  
606 governed local gain modulations, or a combination of these mechanisms.

607

#### 608 **4. How does foveal prediction differ from predictive remapping of attention pointers?**

609 One influential interpretation conceptualizes attention as assigning “pointers” to behaviorally  
610 relevant locations in retinotopic space—that is, internal markers indicating where in the visual  
611 field processing should be enhanced (Cavanagh et al., 2010). During saccade preparation,  
612 attention has been shown to shift in the opposite direction of the saccade vector. This process is  
613 known as predictive remapping of attention pointers and can be conceptualized as an anticipatory  
614 shift of spatial priority to the retinotopic locations that attended objects will occupy upon eye  
615 movement landing (Rolfs et al., 2011; Szinte et al., 2018). Before accurate saccades, the attention  
616 pointer highlighting the eye movement target should be predictively remapped to the pre-saccadic  
617 center of gaze. Nonetheless, predictive remapping of attention and foveal prediction should have  
618 fundamentally different implementational characteristics. Their respective perceptual  
619 consequences can be harnessed to distinguish between both mechanisms (**Figure 3D-F**).

620

#### 621 **4.1 Predictive remapping of attention pointers: an overview**

622 A landmark finding in visual neuroscience is that neurons in the lateral intraparietal area (LIP)  
623 respond to stimuli that will fall into their RFs after an impending saccade (Duhamel et al., 1992).

624 Similar dynamics have since been reported in several cortical and subcortical structures involved  
625 in gaze control and attention, including the LIP (Kusunoki & Goldberg, 2003; Merriam et al., 2003;  
626 Medendorp et al., 2003), the frontal eye fields (FEF; Umeno & Goldberg, 1997; Sommer & Wurtz,  
627 2002), the SC (Walker et al., 1995), and visual cortex (Nakamura & Colby, 2002; Merriam et al.,  
628 2007; Neupane et al., 2016; Knapen et al., 2016). While many of these studies did not  
629 exhaustively map RFs immediately before and during saccades—which is required to establish  
630 the true diversity of neural sensitivity shifts linked to an impending eye movement (Zirnsak &  
631 Moore, 2014)—the key finding by Duhamel et al. (1992) was initially interpreted as transient RF  
632 shifts *in the direction of the saccade* (reviews: Wurtz, 2008; Burr & Morrone, 2011; Golomb &  
633 Mazer, 2021).

634 An alternative explanation posits that LIP, FEF, and SC serve as priority maps that predictively  
635 update attentional states rather than shifting RFs per se. According to this account, the findings  
636 of Duhamel and colleagues (1992) reflect a predictive shift of feature-nonspecific neural activity  
637 *in the opposite direction of the saccade*, to neurons encoding the post-saccadic location of the  
638 attended saccade target (Cavanagh et al., 2010; Marino & Mazer, 2016; Rolfs & Szinte, 2016;  
639 **Figure 3C**). Predictive remapping is thus formalized as an updating of attentional pointers in  
640 retinotopic coordinates, informed by corollary discharge signals representing the direction and  
641 amplitude of the impending saccade. Several findings support the link between remapping and  
642 spatial attention: the pre-saccadic reorganization of LIP activity depends on stimulus salience and  
643 behavioral relevance (Gottlieb et al., 1998), is sensitive to manipulations of attentional state  
644 (Marino & Mazer, 2018; Yao et al., 2018), and can shift entire priority maps during saccade  
645 preparation (Mirpour & Bisley, 2012). From a functional standpoint, predictive spatial updating  
646 enables the trans-saccadic tracking of relevant targets (Howe et al., 2011; Rolfs et al., 2011) by  
647 establishing attentional continuity in visual cortex (Marino & Mazer, 2018; Yao et al., 2018).

648 Psychophysical studies in humans converge on the interpretation that attention predictively  
649 shifts to the future retinotopic location of attended targets before saccade onset (Rolfs et al., 2011;  
650 Jonikaitis et al., 2013; Puntiroli et al., 2015; Szinte et al., 2015; 2018; Wilmott & Michel, 2021).  
651 For example, while observers plan a sequence of two saccades, the retinal location that will  
652 contain the second target after completion of the first saccade is already attended before that first  
653 saccade begins (Rolfs et al., 2011). Crucially, spatial priority signals must first be established  
654 before they can be remapped—that is, attention must be allocated to relevant locations prior to  
655 the execution of the first movement (Szinte et al., 2018; **Sidebar 5**). After the saccade, both  
656 behavioral facilitation and neural activity transiently persist at the pre-saccadic retinotopic position  
657 (Golomb et al., 2008; 2010). This persistence motivated the dual-spotlight model (Golomb, 2019)  
658 which proposes that remapping involves a pre-activation of the upcoming retinal locus before  
659 disengagement from the current one, producing a brief overlap period that supports trans-  
660 saccadic continuity without requiring a transfer of feature information. Computational accounts  
661 formalize these mechanisms as recurrent parietal–visual interactions (Bergelt & Hamker, 2019;  
662 Casarotti et al., 2012). These models reproduce both predictive remapping of attention and  
663 retinotopic persistence, providing a unified explanation for behavioral and neurophysiological  
664 findings without incorporating a shift in neuronal RF locations. Critically, the attention-pointer  
665 based explanation of remapping does not require the remapping of visual feature information  
666 (review: Golomb & Mazer, 2021).

667 In sum, three characteristics of predictive remapping of attention pointers (Cavanagh et al.,  
668 2010; Rolfs et al., 2011; Szinte et al., 2018) can be emphasized. First, it relies on a priority map,  
669 that is, a retinotopically organized overview of relevant locations in the visual field. Since the  
670 vector of the imminent saccade determines the spatial direction and magnitude of remapping, this  
671 priority map must have access to efference copy information. Second, multiple attention pointers

672 highlighting several relevant locations can be remapped at once. Third, predictive attentional  
673 remapping constitutes a purely spatial updating mechanism that tracks relevant locations across  
674 saccades, without a concomitant transfer of feature information. Any feature information within  
675 the highlighted spatial regions enters the visual system in a feedforward fashion.

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#### 677 **Sidebar 5: The prerequisites of predictive remapping of attention**

678 *Predictive remapping of attention pointers across saccades (Cavanagh et al., 2010; Rolfs et al.,*  
679 *2011) requires a shift of activity in the opposite direction of the upcoming saccade, consistent with*  
680 *early demonstrations of vector-parallel remapping (Duhamel et al., 1992). This view was*  
681 *challenged by neurophysiological studies reporting pre-saccadic RF shifts that converge toward*  
682 *the saccade goal (Zirnsak et al., 2014; Neupane et al., 2016), raising doubts about the functional*  
683 *role of remapping for updating attention (review: Zirnsak & Moore, 2014). Crucially, however,*  
684 *these studies did not manipulate attention at non-target locations (e.g., through transient cues or*  
685 *behaviorally relevant stimuli; Gottlieb et al., 1998). Szinte et al. (2018) showed that predictive*  
686 *remapping of attention only emerges when a peripheral location is already attended before*  
687 *saccade execution, aligning this mechanism with known dynamics of spatial attention. Similarly,*  
688 *in double-step saccade tasks, remapping of the second saccade target occurs only when that*  
689 *target receives attention prior to the first saccade (Rolfs et al., 2011). Consistent with this*  
690 *prerequisite, neurophysiological studies that directly manipulated attention observed rapid,*  
691 *vector-parallel updating of attentional signals in areas V4 (Marino & Mazer, 2018) and MT (Yao*  
692 *et al., 2018).*

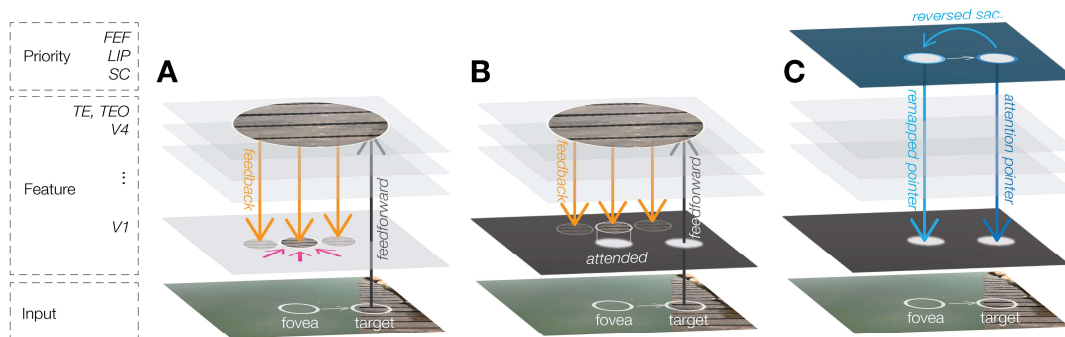
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#### 694 **4.2 Distinction from foveal prediction**

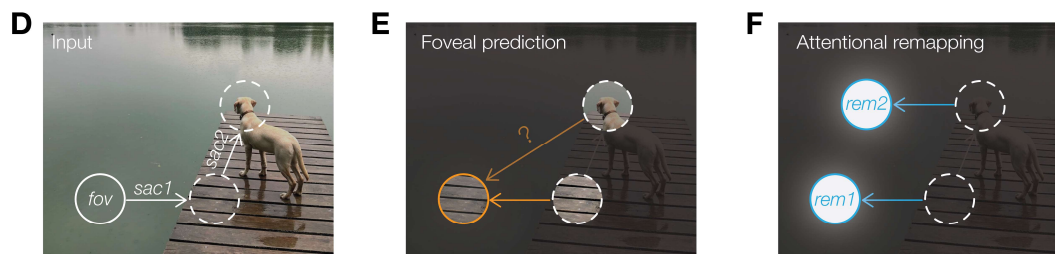
695 Foveal prediction, by contrast, should primarily rely on an interaction between feature-selective  
696 brain regions. No priority map or efference copy signal is required; regardless of where the  
697 imminent eye movement is directed, feature information is invariably relayed to foveal retinotopic  
698 cortex. In accordance with this, pre-saccadic feature predictions are aligned to the center of  
699 fixation, irrespective of the precise eye movement vector (Kroell & Rolfs, 2022; Moran et al.,  
700 2024). Attention pointers, by contrast, are remapped to the post-saccadic retinal stimulus location,  
701 which, depending on saccadic over- or undershoots, is slightly displaced from the pre-saccadic  
702 center of fixation (Collins et al., 2009). Consequently, both predictive remapping and foveal  
703 prediction transiently uncouple the location and identity of the saccade target stimulus, yet in  
704 distinct ways. Predictive remapping of attention pointers involves a purely spatial shift of relevant  
705 locations from a prioritized to a pre-saccadically irrelevant region in space. While this shift  
706 successfully anticipates the post-saccadic retinal location of the attended target, it may entail a  
707 brief prioritization of target stimulus and irrelevant features at the remapped location in rapid  
708 succession. Foveal prediction transfers feature-specific activation from peripheral to foveal  
709 neurons at the cost of transiently detaching these features from their spatial location. These  
710 characteristics generate predictions that can be used to experimentally distinguish between both  
711 accounts. Unlike foveal congruency effects, the peripheral increase in discrimination performance  
712 demonstrated by Rolfs and colleagues (2011) should affect any information within the remapped  
713 focus of attention without relating to the features of the first or second saccade target (**Figure 3F**).  
714 Moreover, it is unclear whether and how attending to two relevant locations before the first eye  
715 movement affects foveal congruency effects (**Figure 3E**). If attention selects relevant objects for  
716 feedback, visual information at both attended target locations may be fed back as a temporally  
717 sequenced or even combined signal. The temporal priority and relative weighting of inputs from

718 separate locations may be manipulated experimentally by varying the eccentricity, contrast or  
 719 frame-to-frame reliability of feature information at both attended locations.

722 **Neural implementation of foveal prediction (A-B) and attentional remapping (C)**



734 **Perceptual consequences of foveal prediction (E) and attentional remapping (F)**



746 **Figure 3.** Potential neural implementation (A-C) and perceptual consequences (D-F) of pre-saccadic foveal  
 747 prediction and predictive remapping of attentional pointers. **A**, Mid- to high-level neurons with large RFs covering the  
 748 fovea and saccade target relay prioritized target features to lower-order neurons with foveal RFs (and matched  
 749 feature selectivity; see text). Since this feedback mechanism alone would simultaneously target neurons with  
 750 neighboring, non-foveal RFs, short-range horizontal connections (pink arrows) may converge fed-back inputs onto  
 751 foveal neurons. **B**, Spatially broad feedback signals may impinge on a non-uniform attentional landscape, which  
 752 increases the gain of feature input relayed to neurons at the predictively remapped target location—the fovea. **C**.  
 753 Predictive attentional remapping involves the updating of a spatial priority map according to the characteristics of  
 754 the ongoing motor program: the attention pointer highlighting the target location is predictively shifted along the  
 755 axis of the imminent movement, yet in the opposite direction. **D**, Example scenario in which an observer plans a  
 756 quick sequence of two saccades: from the water (fov) to the wood panels on the dock (sac1), to the dog's head  
 757 (sac2). **E**, Before the first saccade, the orientation of the wood panels is predicted in pre-saccadic foveal vision.  
 758 Future research needs to establish if the features of the second attended target are predicted simultaneously. **F**.  
 759 Complementing foveal feature predictions, attention pointers highlighting both target locations are remapped  
 760 predictively, reaching the retinal locations they will occupy after saccade offset (rem1 and rem2) before the first  
 761 saccade is completed. This purely attentional updating mechanism establishes spatial continuity without involving  
 762 a transfer of feature information. **Credit line:** The photograph used as an example image in all panels was taken  
 763 by the author LMK.

764  
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 766 **5. Which trans-saccadic phenomena could foveal prediction be contributing to?**

767 The pre- and early post-saccadic intervals of the oculomotor cycle are accompanied by a range  
 768 of spatial and temporal misperceptions (see **Section 1**). For instance, when estimating the time  
 769 at which their eyes land on a target stimulus, observers' judgments reliably precede the veridical  
 770 saccade offset (Deubel et al., 1999; Hunt & Cavanagh, 2009; Yan et al., 2025). When the same  
 771 stimulus is passively moved into observers' center of gaze during instructed fixation, temporal  
 772 estimates lag behind the true time of foveation (Hunt & Cavanagh, 2009). Foveal prediction

773 appears capable of accounting for these findings: anticipating the target in their center of gaze  
774 may lead observers to pre-date the time point of foveation.

775 Moreover, during instructed fixation, two stimuli presented in rapid succession at the same  
776 spatial location are fused into a single percept (color: Efron, 1967; Vernier stimuli: Herzog & Koch,  
777 2001; Scharnowski et al., 2007a; 2007b). Paeye and colleagues (2017) provide evidence for  
778 perceptual fusion across saccadic eye movements and, thus, across separate retinal locations.  
779 They presented a vertical line at the saccade target location and, upon saccade initiation,  
780 replaced it with three horizontal lines of lower contrast. Observers reported a fused percept of the  
781 pre-saccadic peripheral and post-saccadic foveal stimulus, that is, a vertical line on top of three  
782 horizontal ones, on ~65% of trials. The same percentage was obtained when both stimuli were  
783 successively presented in observers' center of gaze during instructed fixation. The authors  
784 conclude that predictively remapped attention pointers (Cavanagh et al., 2010) may be linked to  
785 object identity information. Foveal prediction provides an alternative explanation that does not  
786 require a reframing of the predictive remapping account: The pre-saccadic stimulus may have  
787 been predicted in foveal vision. Upon landing, the same population of foveal neurons processed  
788 the post-saccadic stimulus and both inputs were fused, just like they would have been if  
789 successively presented in observers' center of gaze during fixation. Similarly, changing the visual  
790 properties of the saccade target stimulus during saccadic flight impairs post-saccadic target  
791 processing on both a behavioral (Huber-Huber et al., 2019; Buonocore et al., 2020) and neural  
792 (Edwards et al., 2018; Huber-Huber et al., 2019; Buonocore et al., 2020) level—a phenomenon  
793 termed the extrafoveal preview effect (review: Huber-Huber et al., 2021). A parsimonious  
794 explanation of these findings is that pre-saccadic peripheral and post-saccadic foveal inputs are  
795 processed by the same neuronal population which signals a prediction error once target features  
796 are altered (see Zhang et al., 2025).

797 Future investigations could establish the contribution of foveal prediction to other classical  
798 phenomena that rely on a combination of pre-saccadic peripheral and post-saccadic foveal inputs,  
799 such as trans-saccadic integration (review: Stewart et al., 2020), learning (Weiß et al., 2014), and  
800 blanking (e.g., Deubel et al., 2002; Grzeczowski et al., 2020; 2024). A defining characteristic of  
801 foveal-prediction-mediated feature interactions would be their spatial specificity: Foveal prediction  
802 should selectively promote feature interactions between the target and the pre-saccadic center of  
803 gaze, but not between two exclusively peripheral locations.

804

## 805 **Summary points**

- 806 1. Humans execute rapid saccadic eye movements to inspect objects of interest in high-  
807 acuity foveal vision. Even though each saccade entails a large, rapid shift of the retinal  
808 image, we keep track of the position and identity of relevant stimuli.
- 809 2. Previous research on trans-saccadic continuity has focused on *peripheral* sensitivity  
810 modulations: During saccade preparation, attention deterministically shifts to the eye  
811 movement target, shielding its perception against saccade-induced disruptions.
- 812 3. *Foveal* vision has long been assumed to be unaffected by motor or attentional processes.  
813 Yet, studies employing high-precision eyetracking demonstrate that an inherently non-  
814 uniform foveal and even foveolar perceptual landscape is modulated by attention and  
815 effectively repositioned through small-scale oculomotor activity.
- 816 4. Behavioral and neuroimaging evidence suggests that foveal vision supports trans-  
817 saccadic continuity: Defining features of the saccade target are anticipated in pre-saccadic  
818 foveal vision, enabling a smooth perceptual transition once the target is truly foveated.

- 819 5. Foveal prediction differs from predictive attentional remapping: While attentional  
820 remapping entails a predictive shift of one or several *spatial* attention pointers, foveal  
821 prediction involves a targeted *feature* transfer between two invariant locations: the  
822 saccade target and pre-saccadic center of gaze.
- 823 6. Foveal prediction may contribute to a range of established trans-saccadic phenomena  
824 such as temporal misjudgments of saccade offset, trans-saccadic fusion, extra-foveal  
825 preview effects, trans-saccadic integration, learning, and blanking.

826

**827 Future Issues**

- 828 1. What neural mechanisms underlie foveally confined perceptual modulations? Potential  
829 candidates include feedback projections targeting the fovea in particular, adaptive  
830 horizontal connectivity within cortical or subcortical circuits, attention-driven local gain  
831 modulations, or a combination of these mechanisms.
- 832 2. Which features are predicted before sequences of saccades, when multiple saccade  
833 targets are attended simultaneously?
- 834 3. Does foveal prediction benefit post-saccadic perception or gaze behavior? For instance,  
835 are corrective saccades to an intra-saccadically displaced target executed more readily if  
836 its features could be successfully predicted?
- 837 4. Can careful experimental designs gauge the contribution of foveal prediction to  
838 established phenomena such as trans-saccadic fusion, blanking or learning?
- 839 5. Does foveal prediction adapt to foveal vision loss caused by, for instance, macular  
840 degeneration? If so, how and on which timescale?
- 841 6. Do feature predictions precede eye movements in afoveate animals with close-to uniform  
842 visual acuity? If so, what are their spatial dynamics?
- 843

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848

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