

Allocation of attention across saccades

Abbreviated title: Attention across saccades

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24 **ABSTRACT**

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26 Whenever the eyes move, spatial attention must keep track of the locations of targets as
27 they shift on the retina. This study investigated trans-saccadic updating of visual attention
28 to cued targets. While observers prepared a saccade, we flashed an irrelevant, but salient
29 color cue in their visual periphery and measured the allocation of spatial attention before
30 and after the saccade using a tilt discrimination task. We found that just before the
31 saccade, attention was allocated to the cue's future retinal location, its predictively
32 "remapped" location. Attention was sustained at the cue's location in the world across the
33 saccade, despite the change of retinal position whereas it decayed quickly at the retinal
34 location of the cue, after the eye landed. By extinguishing the color cue across the
35 saccade, we further demonstrate that the visual system relies only on predictive allocation
36 of spatial attention, as the presence of the cue after the saccade did not substantially
37 affect attentional allocation. These behavioral results support and extend physiological
38 evidence showing predictive activation of visual neurons when an attended stimulus will
39 fall in their receptive field after a saccade. Our results show that tracking of spatial
40 locations across saccades is a plausible consequence of physiological remapping.

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48 **INTRODUCTION**

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50 The average inter-saccadic interval is short, about 1/3 of a second, so in everyday
51 situations, we view, study, recognize, and track objects across many fixations. Each object
52 is therefore encoded from several locations on the retina and then processed at various
53 times by several different sets of neurons in retinotopic visual processing areas (Serenio et
54 al., 1995; Gardner et al., 2008). Clearly, every time we make an eye movement, the visual
55 system needs to account for retinal image shifts to maintain object continuity as well as the
56 stability of our visual world (Wurtz, 2008).

57 Physiological research suggests that saccade control areas may compensate for the
58 retinal image shifts caused by eye movements (Duhamel et al., 1992; Sommer and Wurtz,
59 2002; Kusunoki and Goldberg, 2003; Hall and Colby, 2011). A post-saccadic target
60 location is determined by taking into account the pre-saccadic target position and the
61 metrics of the planned saccade. This results in the shift of neural activity from neurons with
62 receptive fields encoding the pre-saccadic target position to neurons with receptive fields
63 encoding its post-saccadic position (Figure 1), an effect called remapping (Duhamel et al.,
64 1992; Nakamura and Colby, 2002; Sommer and Wurtz, 2002; Heiser and Colby, 2006).
65 Remapping is predictive and — in some areas — even observed before the saccade
66 (Duhamel et al., 1992; Kusunoki and Goldberg, 2003).

67 Remapping-related neural activity has also been demonstrated in humans
68 (Medendorp et al., 2003; Merriam et al., 2003; 2007; Parks and Corballis, 2008; 2010;
69 Medendorp, 2011) and it has been proposed that this activity could also be seen in
70 behavioral effects (Melcher and Colby, 2008; Cavanagh et al., 2010). In particular,
71 neurophysiological studies report that only attended or salient stimuli are remapped
72 (Gottlieb et al., 1998) and that saccade control areas involved in remapping are also
73 involved in control of spatial attention (Moore and Armstrong, 2003; Schall, 2004; Awh et
74 al., 2006; Bisley and Goldberg, 2010). In support of these proposals, a recent study did
75 find pre-saccadic remapping of spatial attention (Rolfs et al., 2011). In particular, these
76 authors reported pre-saccadic perceptual benefits at the location which an attended
77 stimulus would occupy only after the saccade (Rolfs et al., 2011) . These results implied
78 that remapping spatial attention or attentional pointers enables the visual system to keep
79 track of relevant objects across saccades (Cavanagh et al., 2010; Rolfs et al., 2011).

80

81

Figure 1

83 However, there has been no test yet of the assumption that the perceptual
84 processing benefits seen at the remapped location before the saccade (Rolfs et al., 2011)
85 are transferred to the spatial location of the cue after the saccade. A number of studies of
86 attentional cueing have reported that, after the saccade, spatial attention is allocated to
87 either spatial location of the attended stimulus (suggesting that attention was remapped)
88 or to the retinal location which the cue occupied before the saccade (suggesting that
89 remapping had failed or was incomplete) or to both (Golomb et al., 2008; 2010b; 2011).
90 However, those studies investigated updating of memorized locations, a process which
91 likely has a different time course than the remapping of stimuli present in the immediate
92 visual environment (see (Golomb et al., 2008) for discussion). Moreover, those studies did
93 not measure attention allocation both before and after the saccade (Golomb et al., 2008;
94 2010b; 2011), making the link between attentional remapping before the saccade (Rolfs et
95 al., 2011) and attentional effects after the saccade (Golomb et al., 2008) open to question.
96 Thus, it is unknown whether predictive remapping can be associated with spatiotopic
97 allocation of attention across saccades.

98 Additionally, most remapping studies investigated updating of spatial locations,
99 without respect to object features or identity (Duhamel et al., 1992; Nakamura and Colby,
100 2002; Sommer and Wurtz, 2002; Medendorp et al., 2003; Merriam et al., 2003; Parks and
101 Corballis, 2010; Hall and Colby, 2011). Remapping provides a predicted post-saccadic
102 location for attended objects but the prediction may have some error (Szinte and
103 Cavanagh, 2011; Szinte et al., 2012) and objects may move during a saccade. An
104 auxiliary method to establish target locations can call on checking for whether post-
105 saccadic object features match those stored in a trans-saccadic memory (Deubel et al.,
106 1996; 1998; 2010; Crapse and Sommer, 2012). This process may take some time after the
107 saccade (Zhou and Desimone, 2011), but would be a viable strategy if spatial updating
108 after the saccade takes some time to develop (Golomb et al., 2008). However, so far it is
109 not known whether visual remapping is sufficient to elicit spatiotopic attention effects after
110 the saccade or whether the visual system actively searches for particular cue features to
111 realign attention to the cue following the saccade.

112 In the current study, we devised a task to investigate these two issues (Figure 2).
113 While participants planned a saccade, we induced attentional capture with the onset of an
114 irrelevant color cue (Müller and Rabbitt, 1989; Nakayama and Mackeben, 1989; Carrasco
115 and Yeshurun, 2009; Schreij et al., 2010), as it is known that neural representations of
116 attended objects are remapped across saccades (Gottlieb et al., 1998). We measured the

117 allocation of spatial attention at different locations and at different times before and after
118 the saccade by using a probe discrimination task in which participants had to report a
119 Gabor orientation change. Indeed, improvements in probe discrimination can be used as a
120 direct measure of attention allocation (Deubel and Schneider, 1996; Ling and Carrasco,
121 2006; Neggers et al., 2007; Gersch et al., 2009; Carrasco, 2011; Jonikaitis and Deubel,
122 2011; Rolfs and Carrasco, 2012). With this novel design we could determine whether
123 spatial attention is predictively remapped before the saccade, and whether, after the
124 saccade, it is allocated to the spatial location of the cue, to the retinotopic location of the
125 cue, or both. By varying the onset of the tilted Gabor test with respect to the saccade, we
126 measured when those attentional benefits appeared or disappeared. In addition to
127 examining the allocation of attention across saccades, we manipulated the status of the
128 attention-capturing color cue, either keeping it onscreen after the saccade or removing it
129 during the saccade. This manipulation allowed us to investigate whether the allocation of
130 attention after the saccade depends on the continuing presence of the color cue. In
131 particular, the presence of the color cue after the saccade could facilitate spatiotopic
132 attentional benefits, as the visual system could use the cue to position attention after the
133 saccade. If the presence of the color cue after the saccade facilitates attentional allocation,
134 we should observe an increase of the attentional benefit following the saccade as
135 information about the cue's location builds up.

136 -----
137 Figure 2
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140 **MATERIALS AND METHODS**

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142 **Participants**

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144 Fifteen participants (age between 21 and 29 years, 5 females, normal or corrected-to-
145 normal vision) took part in the experiment (11 participants completed the Transient-cue
146 task, 14 completed the Sustained-cue task, 10 completed both). All except for two of the
147 authors (DJ, MS) were naive as to the purpose of the study. The experiments were
148 undertaken with the understanding and written consent of each subject and were
149 conducted in accordance with the Declaration of Helsinki.

150

151 **Setup**

152

153 Participants sat in a quiet and dimly illuminated room. We recorded right-eye gaze position
154 with an SR Research EyeLink 1000 desktop mounted eye-tracker, calibrated before each
155 new block and whenever necessary. Participants' head movements were minimized using
156 adjustable chin and forehead rests, allowing for an accuracy of recorded gaze position
157 that is finer than 0.25° at a sampling rate of 1000 Hz. Stimulus presentation and response
158 collection was controlled by an Apple computer and implemented in Matlab (MathWorks,
159 Natick, MA, USA) using Psychophysics and EYELINK toolboxes (Watson and Pelli, 1983;
160 Brainard, 1997; Cornelissen et al., 2002). Stimuli were presented at a viewing distance of
161 60 cm, on gamma-linearized screens, a 21-inch Sony GDM-F500R (1280 x 1024 pixels,
162 vertical refresh rate of 85 Hz) in Munich, or a 22-inch Compaq P1220 (1024 x 768 pixels,
163 vertical refresh rate of 120 Hz) in Paris.

164

165 **Procedure**

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167 ***Main task***

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169 Figure 2 depicts the display configuration. During each trial, participants performed two
170 tasks, a saccade task and a probe discrimination task. A trial started with participants
171 fixating a central fixation target forming a “bull’s eye” (radius 0.75°) on a gray background
172 (mean luminance 39 cd/m^2). We presented two potential saccade targets – filled black
173 circles (radius 0.75°) – 8° to the left and to the right of the fixation. After a fixation period
174 (mean = 1 s, SD. = 300 ms, cutoff at 3.3 SD.), the fixation target disappeared, and the
175 “bull’s-eye” replaced one of the two potential saccade targets. If participants did not make
176 a correct saccade within 700 ms following saccade target appearance, we repeated the
177 trial later during the same experimental session.

178 In addition, six discrimination-task-related objects (radius 2°) formed two rows
179 composed of three objects each, 6° above and below the fixation and the two saccade
180 target locations. The objects consisted of a stream of flickering stimuli, composed of
181 vertical Gabor patches (frequency: 2.5 cpd; 100% contrast; random phase; standard
182 deviation of Gaussian window: 1.1° ; mean luminance 40 cd/m^2) alternating with noise
183 masks (each pixel’s gray value from gaussian distribution; M: 0.5; STD: 0.5; cut-off at 0,
184 black, and 1, white; mean luminance 40 cd/m^2), every 24–25 ms (3 frames at 120 Hz
185 refresh rate or 2 frames at 85 Hz refresh rate depending on the setup used). Between 100

186 ms before and 600 ms after saccade target onset (time selected randomly from a uniform
187 distribution), a probe appeared randomly at one of the six locations, with equal probability.
188 At that location and time, the Gabor changed orientation for one period of 24–25 ms
189 followed again by a mask. We selected the probe orientation based on a threshold
190 procedure explained below. Once the probe had appeared, no more Gabor patches
191 followed at any of the locations and the noise masks now alternated with blanks. 700 ms
192 after saccade target onset, all objects disappeared and the participant reported the probe
193 orientation (clockwise or counterclockwise from vertical) followed by a response feedback
194 (a beep if incorrect). We stressed that the main task was to make accurate and fast
195 saccades, and told participants not to worry if they did not see the probe.

196 The probe discrimination task served as our measure of attention allocation. We
197 summoned attention by presenting an attention-capturing cue (Müller and Rabbitt, 1989;
198 Nakayama and Mackeben, 1989; Carrasco and Yeshurun, 2009; Schreij et al., 2010), an
199 abrupt color onset stimulus presented above or below central fixation. Specifically, 70 ms
200 after saccade target appearance, the Gaussian envelope covering the cued Gabor patch
201 changed color to green (mean luminance of Gabor + green Gaussian envelope 34 cd/m²).
202 Participants were asked to ignore this color onset, as the onset location did not predict the
203 location of the probe. In the Transient-cue task, we removed the color cue during the
204 saccade (i.e., the Gabor patch returned to gray); in the Sustained-cue task, the color cue
205 remained onscreen after the saccade, until the end of the trial.

206 Participants ran a minimum of five one-hour sessions for each of the tasks (if
207 observers performed both tasks, the Sustained-cue condition preceded the Transient-cue
208 condition), each session consisting of at least 480 trials. Before starting the experiment
209 each participant completed a training session (usually taking 15 minutes).

210

211 ***Threshold procedure***

212

213 *Baseline.* Before each session, we evaluated the probe tilt angles that gave a criterion
214 82% correct performance for each probe locations when cued with a 100% valid color cue
215 and these baseline probe angles were determined for the various eccentricities (pre- and
216 post saccade) and presentation times needed to cover the possible probe conditions
217 during the main experiment. The purpose of this baseline was to establish the
218 performance level that is achieved with attention allocated to the probe location as much
219 as possible (100% valid cue) so that in the main experiment, performance that reached
220 this level for the baseline probe orientation indicates a strong engagement of attention. We

221 used interleaved QUEST staircases (Watson and Pelli, 1983), varying the probe
222 orientation at different locations until participants reached a desired 82% correct
223 discrimination performance. Just like in the main experiment, we asked participants to
224 make a saccade, and 70 ms after the saccade target onset, a cue (abrupt color change)
225 appeared. The cue location could be any of the 6 object locations and probes appeared
226 always at the cued location. In the threshold procedure, therefore, the cue was 100%
227 valid, instructing participants where to shift attention. Three staircases were evaluated for
228 probes presented 100 ms after the cue onset, corresponding to the pre-saccadic period
229 (about 50 ms before the saccade started). A first staircase was for probes above and
230 below the fixation target (eccentricity 6°, average tilt angle across participants: 17°); a
231 second for the probes above and below the saccade target (eccentricity 10°, tilt ~ 20°);
232 third for the probes presented opposite of the saccade target (eccentricity 10°, tilt ~ 20°).
233 We also measured three other staircases for probes presented 450 ms after cue onset,
234 corresponding to the post-saccadic period. Post-saccadic probes had different
235 eccentricities and thus different orientation thresholds (eccentricities 6°, 10°, 17.1°; tilt
236 ~14°, ~20°, ~24°). Only trials in which a correct saccade occurred were used for the
237 threshold procedure.

238 *Main task.* During the main task, we used the probe orientations based on the 82%
239 thresholds measured in this threshold mapping task. To do so, we tracked online eye
240 position, and depending on both probe eccentricity and whether the saccade started or
241 not, we presented the corresponding baseline probe orientation. This threshold procedure
242 equated baseline probe discrimination performance even if eccentricity of probes changed
243 across saccades, allowing us to compare probe discrimination across eccentricities as well
244 as before and after the saccade. This procedure ensures that 82% correct discrimination in
245 the main task means strong attentional modulation, values below that correspond to
246 weaker attentional effects and 50% corresponds to chance performance.

247

248 **Data analysis**

249

250 We detected saccades offline using an algorithm based on two-dimensional eye velocity
251 (Engbert and Mergenthaler, 2006), computed from subsequent samples in the eye position
252 series. The thresholds for peak velocity and minimum duration used for saccade detection
253 were 3.0 SD and 20 ms, respectively. To create the saccade landing error map (Figure
254 3b), we used a kernel density estimation based on linear diffusion processes (Botev et al.,
255 2010).

256 We discarded trials where the saccade latency was below 100 ms or above 500 ms.
257 We only analyzed trials in which the saccade landed within a 2° radius around its goal. In
258 total we accepted 92% trials: 0.5% of all trials were rejected due to blinks, 7% due to
259 inaccurate saccades and 0.1% due to participants looking at the color onset location.

260 The performance in the probe discrimination task is expressed as the percentage of
261 correct orientation discriminations. As the probe appeared at a random time, we binned
262 probe presentation times into 100 ms time bins before and after the saccade for further
263 analysis. In pre-saccadic analyses, each bin contained all probes whose presentation
264 ended in a given 100 ms interval; in post-saccadic analyses, each bin contained all probes
265 whose presentation started in a given 100 ms interval. This analysis thus excluded all
266 probes overlapping with the saccade in time. On average for each participant a bin
267 contained around 60 trials (distributions of trials for different conditions are shown in Figure
268 5 & 6). Since there were two response alternatives, the chance level of probe
269 discrimination was at 50%. For the analysis of probe discrimination performance, we
270 pooled data across saccade directions. Statistical analyses included repeated-measure
271 analyses of variance; and direct comparisons between different time bins were done with
272 paired t-tests. Transient-cue and Sustained-cue tasks were compared to each other using
273 a mixed effects ANOVA, which allows for comparisons of conditions containing partly
274 overlapping participant pools.

275

276 **Results**

277

278 The average saccade latency was 210 ± 32 ms (mean \pm SEM) in the Sustained-cue
279 task and 228 ± 56 ms in the Transient-cue task. These latencies match those observed in
280 other studies investigating attentional allocation and saccade planning (Deubel and
281 Schneider, 1996; Golomb et al., 2008; Jonikaitis and Deubel, 2011; Rolfs et al., 2011;
282 Rolfs and Carrasco, 2012), suggesting that the appearance of the color cue did not have a
283 major impact on saccade latencies. Additionally, as our display consisted of several
284 flickering stimulus streams starting well before the appearance of the saccade target, the
285 probe onset itself did not stand out from these background events and so did not disrupt
286 saccade planning. Figure 3a shows that average saccade latencies for probes presented
287 at different locations and at different times after the saccade target onset are largely
288 similar. Repeated measures ANOVAs did not show an effect of either probe position with
289 respect to the saccade target or probe presentation time and this for both tasks (all $p >$
290 0.05). Figure 3b shows saccade accuracy. Average saccadic errors (as measured in

291 distance from the saccade target center at 8° eccentricity) across participants was $0.23^\circ \pm$
292 0.03° in the Sustained-cue task and $0.25^\circ \pm 0.05^\circ$ in the Transient-cue task. Finally, as
293 observed in Figure 3c, saccade landing position did not vary as a function of the probe
294 presentation time, or probe position for either of the tasks (all $p > 0.05$).

295 -----

296 Figure 3

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298

299 Next we analyzed performance in the probe discrimination task. To do so, we
300 computed probe discrimination performance as the percentage of correct discrimination
301 responses for probes appearing within specified 100 ms time bins locked either to the
302 color cue onset (Figure 4) or to the saccade onset (Figure 5 and 6). For each trial we
303 defined 3 positions of interest (cue location, remapping & future retinotopic trace) as well
304 their 3 respective controls, mirrored relative to the saccade vector. We then evaluated the
305 temporal dynamics of attention allocation at these locations, by comparing the actual
306 position with their control for the different time bins. Figure 4 shows probe discrimination
307 performance at the cued location and at its control location for two experimental conditions
308 (for this comparison, we looked at the discrimination performance observed for the 10
309 participants who did both conditions). For both Sustained-cue and Transient-cue
310 conditions, we observed the typical effect of transient spatial attention, that is
311 discrimination performance improved at the cue location, reaching a maximum around 50-
312 150 ms after the cue onset, and then decreased (Müller and Rabbitt, 1989; Nakayama and
313 Mackeben, 1989).

314 -----

315 Figure 4

316 -----

317 Next we analyzed discrimination performance over time before and after the
318 saccade, first for the Sustained-cue (see Figure 5) and then for the Transient-cue
319 conditions (see Figure 6). The upper panels of Figure 5 show probe discrimination
320 performance, whereas the lower panels show the total number of trials used in each time
321 bin by dividing them with respect to whether the color cue was already shown (post-cue
322 trials, plotted upwards) or not (pre-cue trials, plotted downwards). The earliest pre-
323 saccadic time bin (300-200 ms before the saccade) contains mostly pre-cue trials; the

324 latest time bin (100-0 ms before the saccade) contains mostly post-cue trials; the
325 intermediate time bin (200-100 ms before the saccade) contains a mix of both. Figure 5b
326 shows that in the Sustained-cue condition, before the saccade began, probe discrimination
327 improved markedly at the cue location with respect to its control location. A repeated-
328 measures ANOVA (with probe time and its location as main factors), showed that probe
329 discrimination performance before saccade onset was affected by time ($F(2,26) = 15.40$; p
330 < 0.001), probe location ($F(1,13) = 34.36$ $p < 0.001$) and the interaction between the two
331 factors ($F(2,26) = 12.75$, $p < 0.001$). Probe discrimination performance increased strongly
332 at the cue location as compared to control location for probes presented up to 200 ms
333 before the saccade (200-100 ms before saccade, $t(13) = 2.62$, $p < 0.05$; 100-0 ms before
334 saccade, $t(13) = 9.78$, $p < 0.001$, filled squares in Figure 5b mark statistically significant
335 comparisons).

336 Figure 5b also shows the discrimination performance for probes presented after the
337 saccade has landed. Probe discrimination performance remained higher at the cued
338 location than at the cue control location after the saccade. Repeated-measures ANOVA
339 showed the main effect of the probe location ($F(1,13) = 11.97$, $p < 0.01$) and an effect of
340 time was approaching significance ($F(3,39) = 2.68$, $p = 0.06$); the interaction was not
341 significant $F(3,39) = 1.33$, $p = 0.27$. Paired t-tests showed that probe discrimination at the
342 cue location was significantly better than that at the control location 0 – 200 ms after the
343 saccade (0-100 ms after saccade, $t(13) = 2.72$, $p < 0.05$; 100-200 ms after saccade, $t(13)$
344 $= 2.77$, $p < 0.01$). Combined, these results show that the cue improved discrimination
345 performance at its location, and that this benefit is sustained, as a spatiotopic attentional
346 benefit, across the saccade.

347 -----

348 Figure 5

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350 Next, we analyzed probe discrimination performance at other locations in the visual
351 field. The first set of locations we analyzed were the locations above and below the
352 saccade target (Figure 2a). Before the saccade starts, these two locations are not directly
353 relevant for the saccade task nor are they related to the cue location, even though it
354 has been suggested that one of those locations is the location to which predictive
355 remapping is directed (Mathôt and Theeuwes, 2010), a view that is no longer maintained
356 (remapping is directed in the opposite direction see Fig 1a; (Krauzlis and Nummela, 2011;
357 Mathôt and Theeuwes, 2011; Rolfs et al., 2011)). After the saccade ends, this location on

358 the display now corresponds to the retinotopic trace location for attentional benefits, i.e.
359 the retinal location the cue had previously occupied (Golomb et al., 2008; 2010a; 2010b;
360 2011). A retinotopic trace exists only after the saccade, thus in the pre-saccadic period we
361 refer to that location as the “future retinotopic trace location”. Probe discrimination
362 performance increased at both the future retinotopic trace location and at its control
363 location (Figure 5c; effect of time was significant $F(2,26) = 5.54, p < 0.01$), but there was
364 no significant difference between the two locations ($F(1,13) = 0.93, p = 0.35$), nor an
365 interaction between the two factors ($F(2,26) = 0.44, p = 0.65$). Paired t-tests showed no
366 significant differences between the two locations at any time point before the saccade (all
367 $p > 0.05$). Thus, probe discrimination increased at both locations with a similar time course
368 and magnitude, probably due to their proximity to the saccade target (Gersch et al., 2009).
369 This discrimination performance prior to the saccade therefore fails to show the advantage
370 reported by Mathôt and Theeuwes (Mathôt and Theeuwes, 2010). A possible explanation
371 for this discrepancy is that Mathôt and Theeuwes’s stimulus created a strong perception of
372 apparent motion between the pre-saccadic cue and the attentional probe. A recent
373 replication of their experiment revealed general reaction time benefits along the path
374 connecting the cue and target (as compared to eccentricity-matched control locations)
375 strengthening this conjecture (Harrison et al., 2012).

376 After the saccade, performance at the retinotopic trace location and its control
377 (Golomb et al., 2008) was affected by probe presentation time ($F(3,39) = 3.53, p < 0.05$)
378 but not by probe position ($F(1,13) = 0.90, p = 0.35$) and probe position did not interact with
379 probe timing ($F(3,39) = 1.28, p = 0.29$). Nevertheless, planned t-tests showed that probe
380 discrimination at the retinotopic trace location was better than at its control location ($t(13) =$
381 $2.25, p < 0.05$) over the interval 0-100 ms after the saccade but not beyond. In other
382 words, there was a short-lived performance advantage at the retinotopic trace location
383 after the saccade in support of earlier reports by Golomb and colleagues (Golomb et al.,
384 2008; 2010a; 2010b; 2011).

385 Finally, we analyzed the two locations on the other side of the saccade goal. These
386 two locations were related neither to the saccade target nor to the cue, and were in the
387 opposite visual hemifield from the saccade target. However, before the saccade starts, the
388 location at the same vertical position as the cue is the location on the retina that the cue
389 will occupy after the saccade (see Figure 2a) and is therefore the remapped location of the
390 cue (Duhamel et al., 1992; Kusunoki and Goldberg, 2003; Hall and Colby, 2011; Krauzlis
391 and Nummela, 2011; Rolfs et al., 2011). Thus, our pre-saccadic analysis was centered
392 upon finding whether the spatial attention captured by the color cue is predictively

393 remapped to this location before the saccade (Figure 5a). This would put in place the
394 attention that would subsequently align with the cued location after the saccade supporting
395 the post-saccadic perceptual benefits that we found there (post-saccadic cue location). A
396 repeated-measures ANOVA showed a significant effect of probe position ($F(1,13) = 20.17$,
397 $p < 0.001$); the probe presentation time effect was marginally significant ($F(3,39) = 3.18$, p
398 $= 0.06$); the interaction between the two factors was not significant ($F(3,39) = 0.68$, $p =$
399 0.51). Paired t-tests revealed that probe discrimination was better at the remapped
400 location than at the control location in time intervals 200-100 ms before saccade onset
401 ($t(13) = 3.12$, $p < 0.01$) and 100 to 0 ms before saccade onset ($t(13) = 5.45$, $p < 0.001$).

402 After the saccade was finished, these two locations on the screen, furthest from the
403 saccade target have no relevance for the effects of either the abrupt onset or the saccade
404 planning. The data show that the post-saccadic probe discrimination was still affected by
405 probe position ($F(1,13) = 9.78$, $p < 0.01$) but not by probe presentation time ($F(3,39) =$
406 1.17 , $p = 0.33$), and that there was no interaction ($F(3,39) = 0.82$, $p > 0.48$). The main
407 effect of probe position was unexpected, and turned out not to hold up in the Transient-cue
408 condition (see below).

409 Discrimination performance in the Transient-cue condition (Figure 6) where the cue
410 was presented only before the saccade, showed largely similar effects. Discrimination at
411 the cue and cue control locations before the saccade depended on probe presentation
412 time ($F(2,20) = 12.37$, $p < 0.01$) and probe location ($F(1,10) = 15.51$, $p < 0.01$), but there
413 was no interaction between these two factors ($F(2,20) = 2.36$, $p = 0.12$). We obtained the
414 same results after the saccade (probe presentation time, $F(3,30) = 12.01$, $p < 0.01$; probe
415 position, $F(1,10) = 5.18$, $p < 0.05$, interaction, $F(2,20) = 0.06$, $p = 0.97$). Thus, probe
416 discrimination was better at the spatial cue position both, before and after the saccade. In
417 particular, probe discrimination at the cue location was better than at the control location
418 for the first 100 ms after the saccade ($t(10) = 2.06$, $p < 0.05$). Again, we did not observe
419 any benefits at the future retinotopic trace location before the saccade (probe position,
420 $F(1,10) = 0.28$, $p = 0.60$; probe time, $F(2,20) = 3.22$, $p = 0.06$; interaction, $F(2,20) = 0.14$, p
421 $= 0.86$). As in the Sustained-cue experiment, during the first 100 ms following the saccade,
422 discrimination performance was better at the retinotopic trace location than at the control
423 location ($t(10) = 3.36$, $p < 0.01$; probe position, $F(1,10) = 0.30$, $p = 0.59$; probe time,
424 $F(3,30) = 8.68$, $p < 0.01$; interaction, $F(3,30) = 4.37$, $p < 0.05$). Thus, in the Transient-cue
425 condition we replicated the attentional retinotopic trace benefits observed in the Sustained-
426 cue condition. Finally, we observed a benefit at the remapped location before the saccade

427 (probe position, $F(1,10) = 21.32, p < 0.001$; time, $F(2,20) = 1.05, p=0.36$; interaction,
428 $F(2,20) = 1.81, p = 0.18$), but not after (all $ps > 0.05$).

429 To evaluate whether the presence of the color cue after the saccade affected the
430 allocation of spatial attention, we compared Sustained-cue and Transient-cue tasks
431 directly, using mixed effects ANOVA with three factors – probe presentation time, position
432 and task. If cue presence after the saccade had an effect on the discrimination benefit at
433 the cue location as compared to the control location, then one would observe an
434 interaction between the three factors. We found no interaction neither between the probe
435 presentation time and position ($F(3,69) = 0.73, p = 0.43$), nor an interaction between task,
436 position and time ($F(3,69) = 0.78, p = 0.36$). Thus, the presence or absence of an attention
437 capturing cue after the saccade did not affect the attentional benefits at the cue location.
438 This means that feature-based information did not affect discrimination benefits observed
439 at the cue location after the saccade.

440

441 **DISCUSSION**

442

443 We investigated the remapping of spatial attention across saccadic eye movements and
444 report the following findings. First, performance at the cue location increased substantially,
445 relative to its control, demonstrating the classic attentional benefit of a task-irrelevant onset
446 (see Carrasco, 2011, for a review; Theeuwes, 1994; Yantis and Hillstrom, 1994).
447 Importantly, before the saccade, the discrimination performance also increased at the
448 remapped location of the onset cue, which demonstrates with behavioral measures the
449 remapping of attention captured by a salient stimulus. This remapping of attention
450 occurred regardless of whether the cue disappeared or stayed onscreen across the
451 saccade. After the saccade, we observed a short-lived improvement in performance at the
452 retinotopic location that the cue occupied before the saccade. This retinotopic trace of
453 attention dissipated within the first 100 ms after the saccade. Moreover, an attentional
454 benefit at the cue location on the screen persisted after the saccade, meaning that
455 transient attention, invoked at the “remapped” location by an abrupt onset stimulus before
456 saccade, is correctly allocated to its intended spatiotopic location immediately after the
457 saccade. This effect occurs because the retinal image shift during the saccade brings the
458 cue’s location into alignment with the remapped location, thus creating a spatiotopic
459 attentional benefit. And this effect was seen whether or not the color cue was present
460 after the saccade.

461 Our findings demonstrate plausible behavioral consequences of the remapping of
462 neural activity reported in neurophysiological studies (see Figure 7). Neural responses to
463 stimuli appearing outside of neurons' visual receptive fields, but at locations that those
464 receptive fields will occupy after the saccade, have been observed in several areas
465 involved in saccade planning – the frontal eye fields (Umeno and Goldberg, 1997;
466 Sommer and Wurtz, 2006), the lateral intraparietal cortex (Duhamel et al., 1992; Kusunoki
467 and Goldberg, 2003; Heiser and Colby, 2006), and the superior colliculus (Walker et al.,
468 1995; Churan et al., 2011). Such remapping of visual activity has also been observed in a
469 number of human fMRI (Medendorp et al., 2003; Merriam et al., 2003) and EEG studies
470 (Parks and Corballis, 2008; 2010; Peterburs et al., 2011). While fMRI studies, due to the
471 sluggishness of signal, demonstrate remapping of memorized stimuli after the saccade
472 (Medendorp et al., 2003; Merriam et al., 2003; 2007), EEG and single cell recording
473 studies demonstrate predictive remapping of attended stimuli, before the saccades
474 (Duhamel et al., 1992; Kusunoki and Goldberg, 2003; Parks and Corballis, 2008; 2010).

475 The role of attention in remapping has been frequently discounted (Duhamel et al.,
476 1992; Sommer and Wurtz, 2006; Hall and Colby, 2011; Melcher, 2011). However, our
477 result is in agreement with the established physiology of attention and eye movements.
478 Frontal and parietal areas as well as the superior colliculus, all of which show predictive
479 remapping activity (Duhamel et al., 1992; Walker et al., 1995; Kusunoki and Goldberg,
480 2003; Sommer and Wurtz, 2006), are also involved in attentional shifts (Schall, 2002;
481 Bisley and Goldberg, 2003; 2010; Liu et al., 2010; Lovejoy and Krauzlis, 2010).
482 Consequently, we argue that it is the locations of spatial attention —attentional pointers —
483 that are remapped across saccade (Cavanagh et al., 2010). Indeed, typically, remapping
484 occurs only for attended stimuli (Gottlieb et al., 1998) and both behavioral and
485 neurophysiological studies demonstrate that saccade targets, which are strongly attended
486 to, are remapped regardless of whether participants plan a single saccade (Collins et al.,
487 2009; Rolfs et al., 2011), or sequences of saccades (Sommer and Wurtz, 2002; Ostendorf
488 et al., 2010; Rolfs et al., 2011). Finally, several studies have shown that the location of
489 hand movement targets is also remapped across eye movements (Medendorp and
490 Crawford, 2002; van Pelt and Medendorp, 2008), an expected finding given that planning
491 hand movements to an object leads to the automatic allocation of spatial attention to reach
492 targets (Baldauf and Deubel, 2008; 2010; Jonikaitis et al., 2010; Jonikaitis and Deubel,
493 2011).

494 Our study demonstrates both the remapping of spatially cued attention before the
495 saccade and allocation of attention at the cue's location in the world after the saccade.

496 This lends support to the hypothesis that the remapping of visual attention contributes to
497 spatiotopic attention allocation across saccades: even though the object is present in the
498 receptive fields of different visual neurons before and after saccade, the transfer of
499 attention from the cued location to the remapped location before the saccade will bring
500 that attention back to the cue's spatial location once the saccade lands (Cavanagh et al.,
501 2010). Importantly, we observed discrimination benefits for the first 100 ms after the
502 saccade, regardless of whether the color cue was still present in the visual field or not. If
503 perceptual benefits during the first 100 ms after the saccade had occurred contingent on
504 the presence of the color cue across the two fixations, then spatiotopic cueing effects
505 should have been observed only when the cue was visible after the saccade, and not
506 when it was erased. Instead, we observed that removing the color cue during the saccade
507 had little or no effect on attentional benefits at the cue location after the saccade,
508 suggesting that spatiotopic benefits across saccades mainly depend on spatial attention
509 that was appropriately remapped before the saccade landing.

510 If the cued location had to be rediscovered following the saccade, we would expect
511 some delay in the appearance of the attentional benefits. For example, recent single cell
512 recording studies show that after a saccade, visual selectivity to attended features such as
513 color or shape which were present before the saccade takes around 100 ms to build up in
514 attention modulated visual areas V4 and FEF (Bichot et al., 2005; Zhou and Desimone,
515 2011). Moreover, recent evidence suggests that FEF neurons detect a stimulus that
516 changes across a saccade (including changes in location, color, or size) but this selectivity
517 also takes some time to develop (Crapse and Sommer, 2012). Thus, if the visual system
518 had to detect feature information following the saccade to localize spatial attention,
519 spatiotopic benefits would take more time to emerge than is observed in single cell
520 recording studies of remapping (Duhamel et al., 1992; Kusunoki and Goldberg, 2003).
521 Even though we do not discount that feature-based visual processing could potentially aid
522 in localizing objects in some situations after the saccade, our data demonstrate that
523 predictive remapping of attended targets and spatiotopic attentional allocation after the
524 saccades is the default mode of function in the visual system, even when there are no task
525 demands to update information across saccades, and even when the unique feature of an
526 object is extinguished during the saccade.

527 Our findings address current controversies concerning the distribution of spatial
528 attention after saccades. Golomb and colleagues have reported that after a saccade, there
529 is a strong attentional benefit at the retinotopic location that had been occupied by a
530 memorized stimulus before the saccade (retinotopic trace location), and that in some

531 cases it took up to a 100 ms for spatiotopic attention effects to occur (Golomb et al., 2008;
532 2010a; 2010b). Our results confirm the presence of the retinotopic trace after the saccade,
533 however we also observed clear spatiotopic effects immediately after the saccade.
534 Contrary to our task, the studies of Golomb and colleagues used location memory to
535 investigate spatiotopic and retinotopic processing benefits after the saccade. The time
536 course of spatial updating across saccades for memorized locations might be different, as
537 there is no urgency for the visual system to update information about the stimulus which
538 has already disappeared from the visual field. Additionally, those studies did not measure
539 attention allocation before the saccade, which leaves open the possibility that there is no
540 pre-saccadic remapping of attention in a location memory task. This is in contrast to the
541 pre-saccadic remapping of spatial attention in response to an attention-grabbing, currently
542 visible stimulus. Future research would need to compare both situations directly.

543 Our design is similar to neurophysiological studies which demonstrate that abrupt
544 onset stimuli are remapped (Duhamel et al., 1992; Sommer and Wurtz, 2002; Kusunoki
545 and Goldberg, 2003; Merriam et al., 2003). The findings from neurophysiological studies
546 and our current results indicate that salient, attention-capturing stimuli are automatically
547 remapped across saccades, even in cases when there is no task-related benefit to do so.
548 However, less is known about whether remapping also occurs for voluntary attentional
549 shifts. Studies that investigated spatial attention allocation before saccades found that
550 voluntary attention shift to locations that are not saccade targets is impaired (Kowler et al.,
551 1995; Deubel and Schneider, 1996; Deubel, 2008). The competition between voluntary
552 and saccade-triggered attention shifts could influence the nature and timing of the
553 remapped of voluntary attention across saccades. To our knowledge, this question has not
554 been investigated.

555 Our results, combined with those of previous studies, portray a dynamic picture of
556 attention allocation before and after saccadic eye movements. Attention drawn to salient
557 objects before a saccade is remapped around the time the eyes move in the opposite
558 direction of the saccade. As a consequence, attention is continuously allocated to the
559 spatial locations of attended objects in the world across saccades, correcting for the large
560 position shifts that eye movements cause for these objects on the retina and throughout
561 retinotopic cortices. Moreover, the retinal positions of attended pre-saccadic stimuli shows
562 brief attentional benefits after a saccade (Golomb et al., 2008), suggesting that these
563 benefits cannot be immediately extinguished. Combined, such spatial updating of attention
564 may help quickly follow attended targets, despite perpetual eye movements.

565

566

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737 **Figures**

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739 **Figure 1.** Predictive remapping. While the observer is preparing a saccade from the
740 lighthouse window to the white bird, a flash captures his or her attention. This flash is
741 registered by a population of neurons with receptive fields at that location (RF1: black
742 dashed circle in panel a). However, after the saccade, the receptive fields of those
743 neurons are at an irrelevant location; corresponding to the retinotopic trace of the flash
744 (RF1: black dashed circle in panel b). To keep track of this potentially relevant visual
745 event, the visual system needs to relocalize, or remap, the attention captured by the flash
746 to the retinotopic location the flash will have after the saccade. This remapping aids visual
747 stability by pre-activating, before and during the saccade, a population of neurons with
748 receptive fields at the retinal location (RF2: white dashed circle in panel a) which will
749 match the location of the flash after the saccade (RF2: white dashed circle in panel b).

750 **Figure 2.** Experimental procedure. (a) *Display setup.* Participants were instructed to shift
751 their gaze to the saccade target (ST), which could appear to the right or to the left of the
752 fixation target (FT). We presented six visual streams composed of alternating Gabor and
753 noise patches above and below the FT and ST. Shortly after the onset of the ST, an
754 attentional cue (green) appeared directly above or below the FT. At different times relative
755 to the saccadic eye movement, a probe (tilted Gabor) appeared within one of the six visual
756 streams and participants reported its orientation. Relative to the position of the cue and to
757 the saccade direction, the probe could appear at the “remapped cue location” (blue frame),
758 the “cue location” (red frame), the “future retinotopic trace location” (black frame) or at their
759 respective control locations mirrored across the horizontal meridian (respective light
760 colors). The schematic is not to scale and the colored frames were not visible during the
761 experiment. (b) *Visual streams.* As a function of the locations of the probe and of the cue,
762 the visual streams could be one of four different streams. The “Distractor stream” was
763 composed of vertical Gabors alternating with noise masks. The “Probe stream” was
764 identical, except that at a random time one tilted Gabor appeared. The “Distractor stream
765 + Sustained-cue”, “Distractor stream + Transient-cue”, “Probe stream + Sustained-cue”
766 and “Probe stream + Transient-cue” streams were similar to the ones described above
767 except that 70 ms after the ST onset all Gabors within these streams were green. Note
768 that no Gabors were shown within any streams after the probe presentation, while the
769 green color stayed on only in the Sustained-cue condition. (c) *Stimulus timing.* The FT
770 disappeared first with the onset of the ST, followed 70 ms later by the cue. The saccade
771 started with an average latency of 210 ms. The probe appeared either before the saccade
772 (pre-saccadic probe) or after the saccade (post-saccadic probe). Horizontal arrows denote
773 the time interval during which the probe could appear.

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777 **Figure 3.** (a) *Saccade latency* as a function of probe presentation time and probe
778 locations. Colors indicate the probe locations with respect to saccade target and onset
779 cue, as described in the small legend icon. Error bars indicate SEM. (b) *Saccade accuracy*
780 for all saccade directions and probe locations. Redder colors represent higher incidence of
781 saccades to that location. (c) *Saccade amplitude* as a function of probe presentation time
782 and probe location. Same conventions as in panel a. All three panels show data from the
783 Sustained-cue condition. Data from the Transient-cue (not displayed) condition were not
784 statistically different.

785 **Figure 4.** Probe discrimination performance at the cue location before and after the color
786 cue onset for Sustained-cue and Transient-cue conditions. Colors indicate the probe
787 locations as described in the small legend icons for each panel. We computed
788 performance in temporal bins separated by 100 ms. For a given temporal bin, filled
789 symbols indicate significant differences between a location of interest and its control,
790 based on repeated-measures t-tests taken separately for the sustained and the transient-
791 cue condition.
792
793

794 **Figure 5.** Probe discrimination performance before and after saccades for the Sustained-
795 cue condition is shown in the upper panels. (a) Performance for probes presented at the
796 remapped location and its control, (b), at the cue location and its control, and, (c), at the
797 future retinotopic trace location and its control. Colors indicate the probe locations as
798 described in the small legend icons for each panel. We computed performance in temporal
799 bins separated by 100 ms both for probes appearing before the saccade started and for
800 probes appearing after the saccade finished. For a given temporal bin, filled symbols
801 indicate significant differences between a location of interest and its control, based on
802 repeated-measures t-tests. Numbers of trials when probe was shown either before the
803 color cue (pre-cue trials, plotted downwards) or after the color cue (post-cue trials, plotted
804 upwards) are shown in the lower panels. Same color conventions as in the upper panels.
805 The number of pre-cue and post-cue trials for each bin sums up to the total number of
806 trials available for that time bin. Error bars are SEM.
807

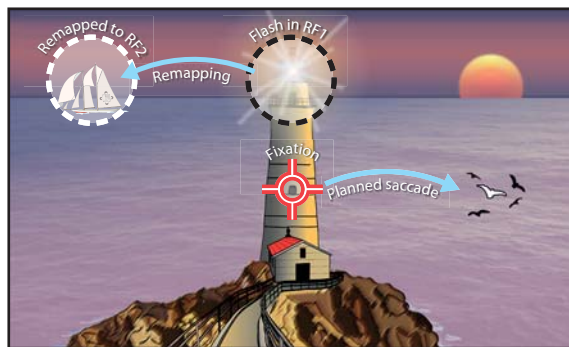
808 **Figure 6.** Probe discrimination performance before and after saccades for the Transient
809 cue condition. All conventions are the same as in Figure 5.

810 **Figure 7.** Remapping in neurophysiology and behavior. While the observer is preparing a
811 saccade from the lighthouse window to the white bird, a flash captures his or her attention
812 (visual scene, b). Both electrophysiological (a) and behavioral (c) studies investigated how
813 the visual system tracks an attention-capturing stimulus, here the flash, despite intervening
814 eye movements. (a) In electrophysiological studies of predictive remapping, an attention-
815 capturing cue is presented at a location (marked by an asterisk) that falls outside the
816 neuron's Receptive Field (solid circle). Just before the saccade onset, the neuron
817 becomes responsive to the attention-capturing cue, if the receptive field of that neuron will
818 fall on the cued location *after* the saccade. This finding has been interpreted as a receptive
819 field shift *in the direction of the saccade*, here marked by the arrow, to what has been
820 termed the cell's Future Receptive Field (dotted circle). (c) In the current study we
821 presented an attention-capturing cue (a green Gaussian blob) and measured
822 discrimination performance at the location indicated by the tilted Gabor patch. We interpret
823 the increased perceptual discrimination performance as predictive remapping of visual
824 attention *in the direction opposite the saccade*, marked by the arrow. Both
825 neurophysiological and behavioral studies measured locations or receptive fields that
826 maintain the same relationship – the attention-grabbing stimulus is presented at one
827 location, and the response is measured at the location or receptive field where the cued
828 location will land after the saccade. These are two equivalent descriptions of the same
829 process that we argue is best described as a transfer of activation from the initial location
830 of the cue to its future retinal position (Cavanagh et al., 2010).

831
832
833
834

a

Before the saccade

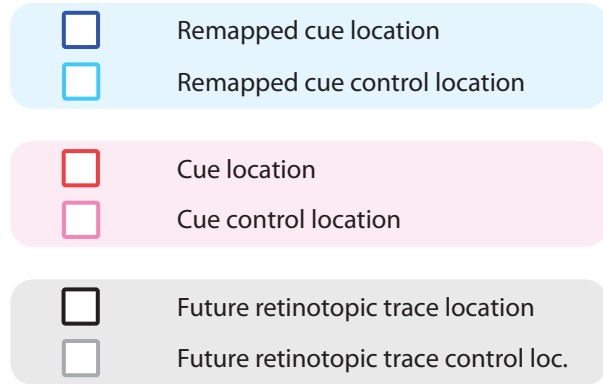
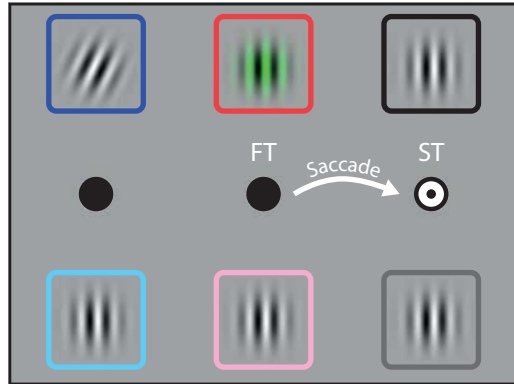


b

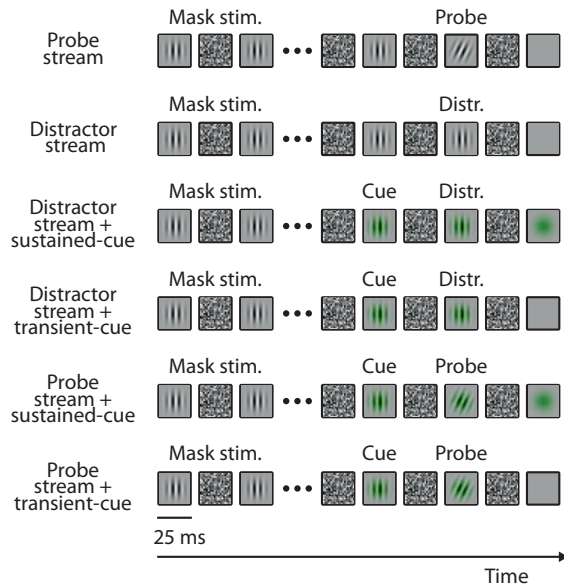
After the saccade



a



b



c

