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[2]*Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité, Paris, France and Centre National de la Recherche Scientifique, Unité Mixte de Recherche 8158, Paris, France;* [3]*Department of Psychology, New York University, New York, New York; and* [4]*Laboratoire de Psychologie Cognitive, Université Aix-Marseille and Centre National de la Recherche Scientifique, Marseille, France*

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Jonikaitis D, Szinte M, Rolfs M, Cavanagh P. Allocation of attention across saccades. *J Neurophysiol* 109: 1425–1434, 2013. First published December 5, 2012; doi:10.1152/jn.00656.2012.—Whenever the eyes move, spatial attention must keep track of the locations of targets as they shift on the retina. This study investigated transsaccadic updating of visual attention to cued targets. While observers prepared a saccade, we flashed an irrelevant, but salient, color cue in their visual periphery and measured the allocation of spatial attention before and after the saccade using a tilt discrimination task. We found that just before the saccade, attention was allocated to the cue's future retinal location, its predictively "remapped" location. Attention was sustained at the cue's location in the world across the saccade, despite the change of retinal position whereas it decayed quickly at the retinal location of the cue, after the eye landed. By extinguishing the color cue across the saccade, we further demonstrate that the visual system relies only on predictive allocation of spatial attention, as the presence of the cue after the saccade did not substantially affect attentional allocation. These behavioral results support and extend physiological evidence showing predictive activation of visual neurons when an attended stimulus will fall in their receptive field after a saccade. Our results show that tracking of spatial locations across saccades is a plausible consequence of physiological remapping.

remapping; saccades; spatial attention; visual stability

THE AVERAGE INTERSACCADIC interval is short, about one-third of a second, so in everyday situations, we view, study, recognize, and track objects across many fixations. Each object is therefore encoded from several locations on the retina and then processed at various times by several different sets of neurons in retinotopic visual processing areas (Sereno et al. 1995; Gardner et al. 2008). Clearly, every time we make an eye movement, the visual system needs to account for retinal image shifts to maintain object continuity as well as the stability of our visual world (Wurtz 2008).

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

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

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

Additionally, most remapping studies investigated updating of spatial locations, without respect to object features or identity (Duhamel et al. 1992; Nakamura and Colby 2002; Sommer and Wurtz 2002; Medendorp et al. 2003; Merriam et al. 2003; Parks and Corballis 2010; Hall and Colby 2011). Remapping provides a

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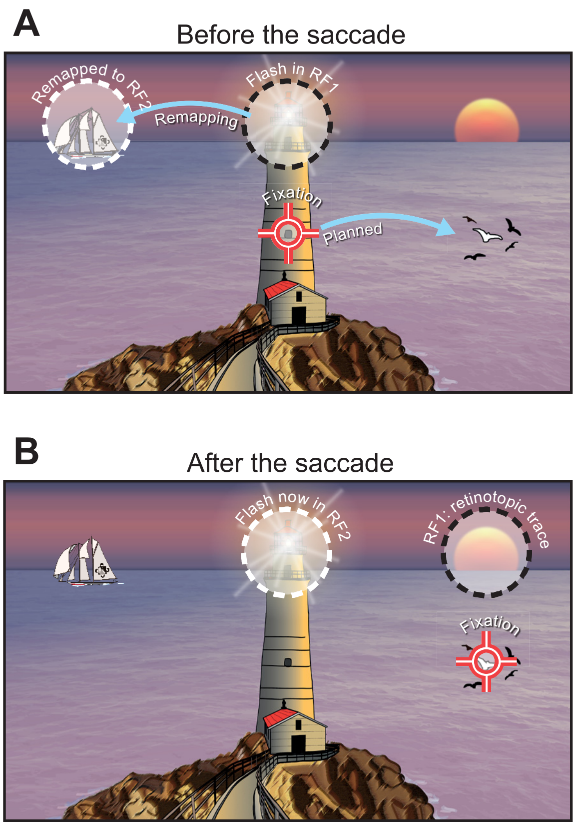

Fig. 1. Predictive remapping. While the observer is preparing a saccade from the lighthouse window to the white bird, a flash captures his or her attention. This flash is registered by a population of neurons with receptive fields at that location (RF1: black dashed circle in *A*). However, after the saccade, the receptive fields of those neurons are at an irrelevant location; corresponding to the retinotopic trace of the flash (RF1: black dashed circle in *B*). To keep track of this potentially relevant visual event, the visual system needs to relocalize, or remap, the attention captured by the flash to the retinotopic location the flash will have after the saccade. This remapping aids visual stability by preactivating, before and during the saccade, a population of neurons with receptive fields at the retinal location (RF2: white dashed circle in *A*) that will match the location of the flash after the saccade (RF2: white dashed circle in *B*).

predicted postsaccadic location for attended objects, but the prediction may have some error (Szinte and Cavanagh 2011; Szinte et al. 2012) and objects may move during a saccade. An auxiliary method to establish target locations can call on checking for whether postsaccadic object features match those stored in a transsaccadic memory (Deubel et al. 1996, 1998, 2010; Crapse and Sommer 2012). This process may take some time after the saccade (Zhou and Desimone 2011) but would be a viable strategy if spatial updating after the saccade takes some time to develop (Golomb et al. 2008). However, so far it is not known whether visual remapping is sufficient to elicit spatiotopic attention effects after the saccade or whether the visual system actively searches for particular cue features to realign attention to the cue following the saccade.

In the current study, we devised a task to investigate these two issues (Fig. 2). While participants planned a saccade, we induced attentional capture with the onset of an irrelevant color cue (Müller and Rabbitt 1989; Nakayama and Mackeben 1989; Carrasco and Yeshurun 2009; Schreij et al. 2010), as it is known that neural representations of attended objects are remapped across saccades (Gottlieb et al. 1998). We measured the allocation of spatial attention at different locations and at different times before and after the saccade by using a probe discrimination task in which participants had to report a Gabor orientation change. Indeed, improvements in probe discrimination can be used as a direct measure of attention allocation (Deubel and Schneider 1996; Ling and Carrasco 2006; Neggers et al. 2007; Gersch et al. 2009; Carrasco 2011; Jonikaitis and Deubel 2011; Rolfs and Carrasco 2012). With this novel design, we could determine whether spatial attention is predictively remapped before the saccade and whether, after the saccade, it is allocated to the spatial location of the cue, to the retinotopic location of the cue, or both. By varying the onset of the tilted Gabor test with respect to the saccade, we measured when those attentional benefits appeared or disappeared. In addition to examining the allocation of attention across saccades, we manipulated the status of the attention-capturing color cue, either keeping it onscreen after the saccade or removing it during the saccade. This manipulation allowed us to investigate whether the allocation of attention after the saccade depends on the continuing presence of the color cue. In particular, the presence of the color cue after the saccade could facilitate spatiotopic attentional benefits, as the visual system could use the cue to position attention after the saccade. If the presence of the color cue after the saccade facilitates attentional allocation, we should observe an increase of the attentional benefit following the saccade as information about the cue's location builds up.

MATERIALS AND METHODS

Participants

Fifteen participants (age between 21 and 29 yr, 5 females, normal or corrected-to-normal vision) took part in the experiment (11 participants completed the Transient-cue task, 14 completed the Sustained-cue task, and 0 completed both). All except for two of the authors (D. Jonikaitis and M. Szinte) were naive as to the purpose of the study. The experiments were undertaken with the understanding and written consent of each subject and were conducted in accordance with the Declaration of Helsinki. Experiments were carried out in Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians Universität München, Munich, Germany and Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité, Paris, France. Experiments were designed according to the ethical requirements specified by corresponding institutions even though no institutional review board (or corresponding institution) ethics approval was needed for experiments that do not involve invasive methods.

Setup

Participants sat in a quiet and dimly illuminated room. We recorded right-eye gaze position with an SR Research EyeLink 1000 desktop mounted eye-tracker, calibrated before each new block and whenever necessary. Participants' head movements were minimized using adjustable chin and forehead rests, allowing for an accuracy of recorded gaze position that is finer than 0.25° at a sampling rate of 1,000 Hz. Stimulus presentation and response collection was controlled by an Apple computer and implemented in Matlab (MathWorks, Natick, MA) using Psychophysics and Eyelink toolboxes (Watson and Pelli 1983; Brainard 1997; Cornelissen et al. 2002). Stimuli were presented at a viewing distance of 60 cm, on gamma-linearized screens, a 21-in. Sony GDM-F500R (1,280 × 1024 pixels, vertical refresh rate of 85 Hz) in Munich, or a 22-in. Compaq P1220 (1,024 × 768 pixels, vertical refresh rate of 120 Hz) in Paris.

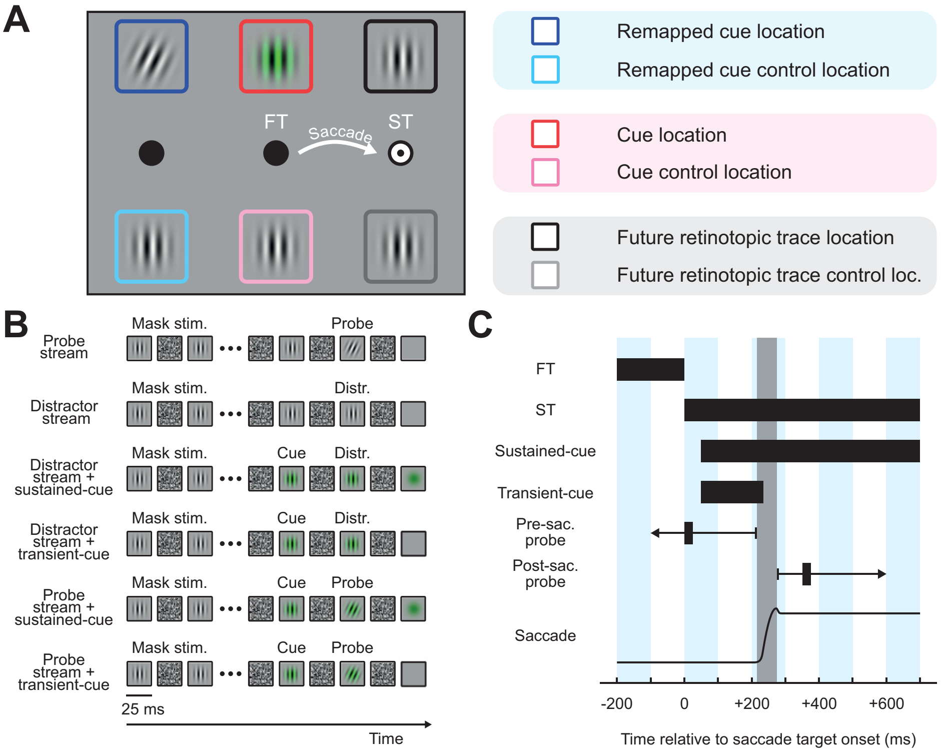

Fig. 2. Experimental procedure. *A*: Display setup. Participants were instructed to shift their gaze to the saccade target (ST), which could appear to the right or to the left of the fixation target (FT). We presented 6 visual streams composed of alternating Gabor and noise patches above and below the FT and ST. Shortly after the onset of the ST, an attentional cue (green) appeared directly above or below the FT. At different times relative to the saccadic eye movement, a probe (tilted Gabor) appeared within 1 of the 6 visual streams and participants reported its orientation. Relative to the position of the cue and to the saccade direction, the probe could appear at the "remapped cue location" (blue frame), the "cue location" (red frame), the "future retinotopic trace location" (black frame), or at their respective control locations mirrored across the horizontal meridian (respective light colors). Schematic is not to scale and the colored frames were not visible during the experiment. *B*: visual streams. As a function of the locations of the probe and of the cue, the visual streams could be 1 of 4 different streams. The "Distractor stream" was composed of vertical Gabors alternating with noise masks. The "Probe stream" was identical, except that at a random time one tilted Gabor appeared. The "Distractor stream + Sustained-cue," "Distractor stream + Transient-cue," "Probe stream + Sustained-cue," and "Probe stream + Transient-cue" streams were similar to the ones described above except that 70 ms after the ST onset all Gabors within these streams were green. Note that no Gabors were shown within any streams after the probe presentation, while the green color stayed on only in the Sustained-cue condition. *C*: stimulus timing. The FT disappeared first with the onset of the ST, followed 70 ms later by the cue. The saccade started with an average latency of 210 ms. The probe appeared either before the saccade (presaccadic probe) or after the saccade (post-saccadic probe). Horizontal arrows denote the time interval during which the probe could appear.

Procedure

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

In addition, six discrimination-task-related objects (radius 2°) formed two rows composed of three objects each, 6° above and below the fixation and the two saccade target locations. The objects consisted of a stream of flickering stimuli, composed of vertical Gabor patches (frequency: 2.5 cpd; 100% contrast; random phase; standard deviation of Gaussian window: 1.1°; mean luminance: 40 cd/m^2) alternating with noise masks (each pixel's gray value from Gaussian distribution; M: 0.5; SD: 0.5; cut-off at 0, black, and 1, white; mean luminance: 40 cd/m^2), every 24–25 ms (3 frames at 120-Hz refresh rate or 2 frames at a 85-Hz refresh rate depending on the setup used). Between 100 ms before and 600 ms after saccade target onset (time selected randomly from a uniform distribution), a probe appeared randomly at one of the six locations, with equal probability. At that location and time, the Gabor changed orientation for one period of 24–25 ms followed again by a mask. We selected the probe orientation based on a threshold procedure explained below. Once the probe had appeared, no more Gabor patches followed at any of the locations and the noise masks now alternated with blanks. Seven-hundred milliseconds after saccade target onset, all objects disappeared and the participant reported the probe orientation (clockwise or counterclockwise from vertical) followed by a response feedback (a beep if incorrect). We stressed that the main task was to make accurate and fast saccades and told participants not to worry if they did not see the probe.

The probe discrimination task served as our measure of attention allocation. We summoned attention by presenting an attention-capturing cue (Müller and Rabbitt 1989; Nakayama and Mackeben 1989; Carrasco and Yeshurun 2009; Schreij et al. 2010), an abrupt color onset stimulus presented above or below central fixation. Specifically, 70 ms after saccade target appearance, the Gaussian envelope covering the cued Gabor patch changed color to green (mean luminance of Gabor + green Gaussian envelope 34 cd/m^2). Participants were asked to ignore this color onset, as the onset location did not predict the location of the probe. In the Transient-cue task, we removed the color cue during the saccade (i.e., the Gabor patch returned to gray); in the Sustained-cue task, the color cue remained onscreen after the saccade until the end of the trial.

Participants ran a minimum of five 1-h sessions for each of the tasks (if observers performed both tasks, the Sustained-cue condition preceded the Transient-cue condition), each session consisting of at least 480 trials. Before starting the experiment, each participant completed a training session (usually taking 15 min).

Threshold procedure. BASELINE. Before each session, we evaluated the probe tilt angles that gave a criterion 82% correct performance for each probe locations when cued with a 100% valid color cue and these baseline probe angles were determined for the various eccentricities (pre- and postsaccade) and presentation times needed to cover the possible probe conditions during the main experiment. The purpose of this baseline was to establish the performance level that is achieved with attention allocated to the probe location as much as possible (100% valid cue) so that in the main experiment performance that reached this level for the baseline probe orientation indicates a strong engagement of attention. We used interleaved QUEST staircases (Watson and Pelli 1983), varying the probe orientation at different locations until participants reached a desired 82% correct discrimination performance. Just like in the main experiment, we asked participants to make a saccade, and 70 ms after the saccade target onset, a cue (abrupt color change) appeared. The cue location could be any of the six object locations and probes appeared always at the cued location. In the threshold procedure, therefore, the cue was 100% valid, instructing participants where to shift attention. Three staircases were evaluated for probes presented 100 ms after the cue onset, corresponding to the presaccadic period (~50 ms before the saccade started). A first staircase was for probes above and below the fixation target (eccentricity 6°, average tilt angle across participants: 17°); a second for the probes above and below the saccade target (eccentricity 10° and tilt ~ 20°); and a third for the probes presented opposite of the saccade target (eccentricity 10° and tilt ~20°). We also measured three other staircases for probes presented 450 ms after cue onset, corresponding to the postsaccadic period. Postsaccadic probes had different eccentricities and thus different orientation thresholds (eccentricities 6°, 10°, and 17.1°; tilt ~14°, ~20°, and ~24°). Only trials in which a correct saccade occurred were used for the threshold procedure.

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

Data Analysis

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

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

The performance in the probe discrimination task is expressed as the percentage of correct orientation discriminations. As the probe appeared at a random time, we binned probe presentation times into 100-ms time bins before and after the saccade for further analysis. In presaccadic analyses, each bin contained all probes whose presentation ended in a given 100-ms interval; in postsaccadic analyses, each bin contained all probes whose presentation started in a given 100-ms interval. This analysis thus excluded all probes overlapping with the saccade in time. On average for each participant, a bin contained ~60 trials (for distributions of trials for different conditions, see Figs. 5 and 6). Since there were two response alternatives, the chance level of probe discrimination was at 50%. For the analysis of probe discrimination performance, we pooled data across saccade directions. Statistical analyses included repeated-measure ANOVA, and direct comparisons between different time bins were done with paired *t*-tests. Transient-cue and Sustained-cue tasks were compared with each other using a mixed effects ANOVA, which allows for comparisons of conditions containing partly overlapping participant pools.

RESULTS

The average saccade latency was 210 ± 32 ms (means ± SE) in the Sustained-cue task and 228 ± 56 ms in the Transient-cue task. These latencies match those observed in other studies inves-

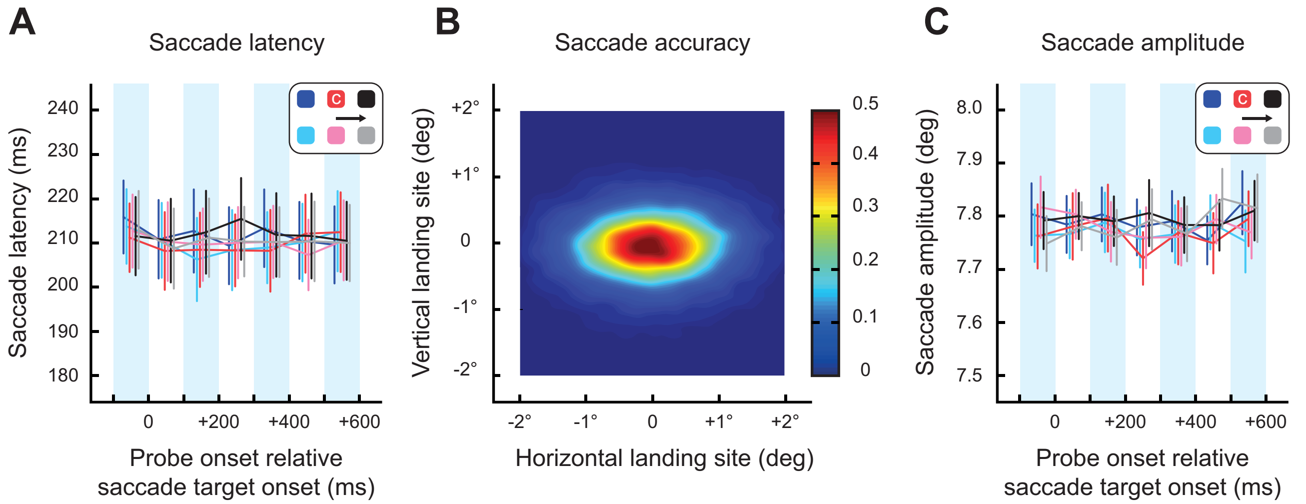

Fig. 3. *A*: Saccade latency as a function of probe presentation time and probe locations. Colors indicate the probe locations with respect to saccade target and onset cue, as described in the small legend icon. Error bars indicate SE. *B*: saccade accuracy for all saccade directions and probe locations. Redder colors represent higher incidence of saccades to that location. *C*: saccade amplitude as a function of probe presentation time and probe location. Same conventions as in *A*. *A*–*C* show data from the Sustained-cue condition. Data from the Transient-cue (not displayed) condition were not statistically different.

tigating attentional allocation and saccade planning (Deubel and Schneider 1996; Golomb et al. 2008; Jonikaitis and Deubel 2011; Rolfs et al. 2011; Rolfs and Carrasco 2012), suggesting that the appearance of the color cue did not have a major impact on saccade latencies. Additionally, as our display consisted of several flickering stimulus streams starting well before the appearance of the saccade target, the probe onset itself did not stand out from these background events and so did not disrupt saccade planning. Figure 3*A* shows that average saccade latencies for probes presented at different locations and at different times after the saccade target onset are largely similar. Repeated-measures ANOVAs did not show an effect of either probe position with respect to the saccade target or probe presentation time and this for both tasks (all $P > 0.05$). Figure 3*B* shows saccade accuracy. Average saccadic errors (as measured in distance from the saccade target center at 8° eccentricity) across participants was 0.23 ± 0.03° in the Sustained-cue task and 0.25 ± 0.05° in the Transient-cue task. Finally, as observed in Fig. 3*C*, saccade landing position did not vary as a function of the probe presentation time, or probe position for either of the tasks (all $P > 0.05$).

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

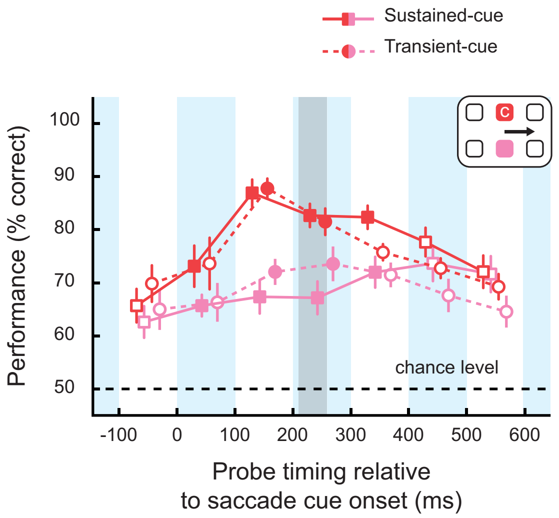

Fig. 4. Probe discrimination performance at the cue location before and after the color cue onset for Sustained-cue and Transient-cue conditions. Colors indicate the probe locations as described in the small legend icons for each panel. We computed performance in temporal bins separated by 100 ms. For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

Next, we analyzed discrimination performance over time before and after the saccade, first for the Sustained-cue (see Fig. 5) and then for the Transient-cue conditions (see Fig. 6). Figure 5, *top*, shows probe discrimination performance, whereas Fig. 5, *bottom*, shows the total number of trials used in each time bin by dividing them with respect to whether the color cue was already shown (postcue trials, plotted upwards) or not (precue trials, plotted downwards). The earliest presaccadic time bin (300–200 ms before the saccade) contains mostly precue trials; the latest time bin (100–0 ms before the saccade) contains mostly postcue trials; the intermediate time bin (200–100 ms before the saccade) contains a mix of both. Figure 5*B* shows that in the Sustained-cue condition, before the saccade began, probe discrimination improved markedly at the cue location with respect to its control location. A repeated-measures ANOVA (with probe time and its location as main factors), showed that probe discrimination performance before saccade onset was affected by time [$F(2,26) = 15.40$, $P < 0.001$], probe location [$F(1,13) = 34.36$, $P < 0.001$], and the interaction between the two factors [$F(2,26) = 12.75$, $P < 0.001$]. Probe discrimination performance increased strongly at the cue location compared with control location for probes presented up to 200 ms before the saccade [200–100 ms before saccade, $t(13) = 2.62$, $P < 0.05$; 100–0 ms before saccade, $t(13) = 9.78$, $P < 0.001$, filled squares in Fig. 5*B* mark statistically significant comparisons].

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

Next, we analyzed probe discrimination performance at other locations in the visual field. The first set of locations we analyzed was the locations above and below the saccade target (Fig. 2*A*). Before the saccade starts, these two locations are not directly relevant for the saccade task nor are they related to the cue location, even though it has been suggested that one of those locations is the location to which predictive remapping is directed (Mathôt and Theeuwes 2010), a view that is no longer maintained (remapping is directed in the opposite direction see Fig. 1*A*; Krauzlis and Nummela 2011; Mathôt and Theeuwes 2011; Rolfs et al. 2011). After the saccade ends, this location on the display now corresponds to the retinotopic trace location for attentional benefits, i.e., the retinal location the cue had previously occupied (Golomb et al. 2008, 2010a, 2010b, 2011). A retinotopic trace

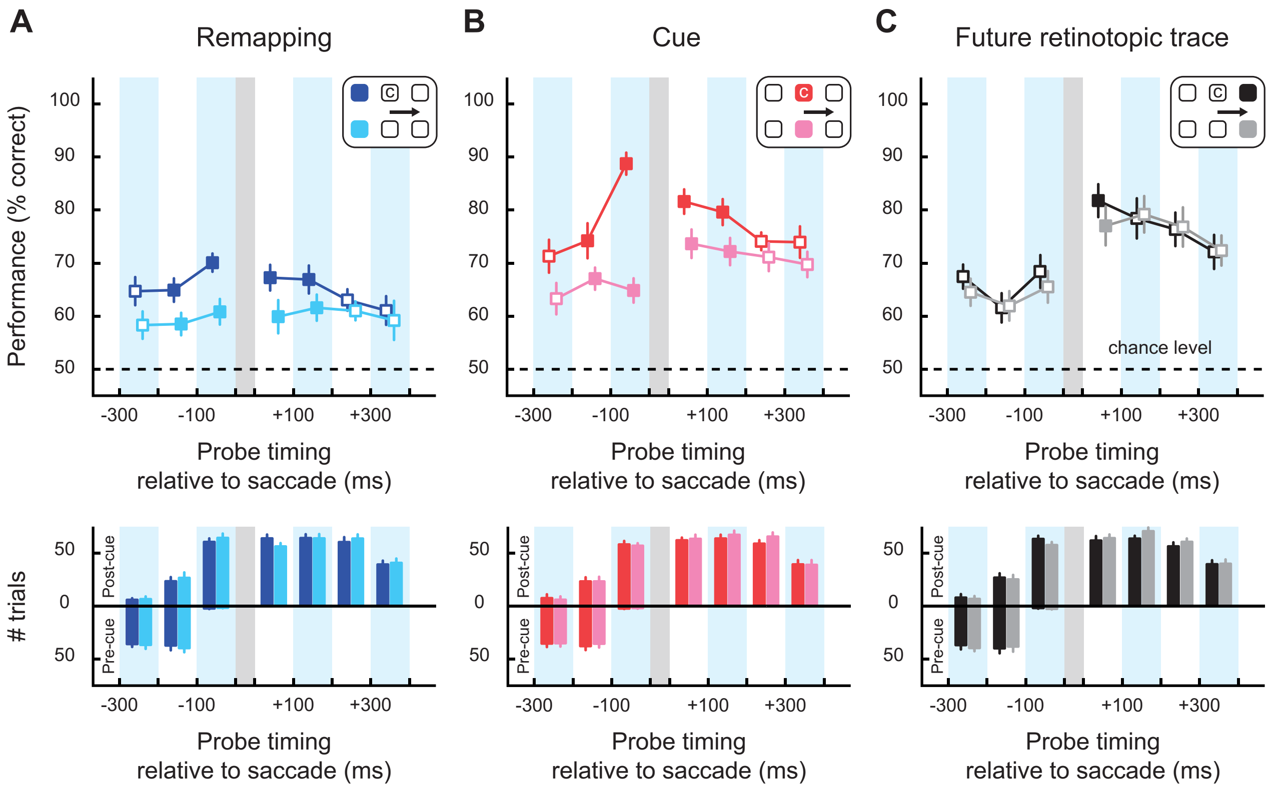

Fig. 5. Probe discrimination performance before and after saccades for the Sustained-cue condition is shown at *top*: Performance for probes presented at the remapped location and its control (*A*), at the cue location and its control (*B*), and at the future retinotopic trace location and its control (*C*). Colors indicate the probe locations as described in the small legend icons for *A–C*. We computed performance in temporal bins separated by 100 ms both for probes appearing before the saccade started and for probes appearing after the saccade finished. For a given temporal bin, filled symbols indicate significant differences between a location of interest and its control, based on repeated-measures *t*-tests. Numbers of trials when probe was shown either before the color cue (precue trials, plotted downwards) or after the color cue (postcue trials, plotted upwards) are shown at *bottom*. Same color conventions as in the upper panels. The number of precue and postcue trials for each bin sums up to the total number of trials available for that time bin. Error bars are SE.

exists only after the saccade; thus in the presaccadic period we refer to that location as the "future retinotopic trace location." Probe discrimination performance increased at both the future retinotopic trace location and at its control location [Fig. 5*C*; effect of time was significant $F(2,26) = 5.54$, $P < 0.01$], but there was no significant difference between the two locations [$F(1,13) = 0.93$, $P = 0.35$] nor an interaction between the two factors [$F(2,26) = 0.44$, $P = 0.65$]. Paired *t*-tests showed no significant differences between the two locations at any time point before the saccade (all $P > 0.05$). Thus probe discrimination increased at both locations with a similar time course and magnitude, probably due to their proximity to the saccade target (Gersch et al. 2009). This discrimination performance before the saccade therefore fails to show the advantage reported by Mathôt and Theeuwes (Mathôt and Theeuwes 2010). A possible explanation for this discrepancy is that Mathôt and Theeuwes's stimulus created a strong perception of apparent motion between the presaccadic cue and the attentional probe. A recent replication of their experiment revealed general reaction time benefits along the path connecting the cue and target (as compared with eccentricity-matched control locations) strengthening this conjecture (Harrison et al. 2012).

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

Finally, we analyzed the two locations on the other side of the saccade goal. These two locations were related neither to the saccade target nor to the cue and were in the opposite visual hemifield from the saccade target. However, before the saccade starts, the location at the same vertical position as the cue is the location on the retina that the cue will occupy after the saccade (see Fig. 2*A*) and is therefore the remapped location of the cue (Duhamel et al. 1992; Kusunoki and Goldberg 2003; Hall and Colby 2011; Krauzlis and Nummela 2011; Rolfs et al. 2011). Thus our presaccadic analysis was centered on finding whether the spatial attention captured by the color cue is predictively remapped to this location before the saccade (Fig. 5*A*). This would put in place the attention that would subsequently align with the cued location after the saccade supporting the postsaccadic perceptual benefits that we found there (postsaccadic cue location). A repeated-measures ANOVA showed a significant effect of probe position [$F(1,13) = 20.17$, $P < 0.001$]; the probe presentation time effect was marginally significant [$F(3,39) = 3.18$, $P = 0.06$]; and the interaction between the two factors was not significant [$F(3,39) = 0.68$, $P = 0.51$]. Paired *t*-tests revealed that probe discrimination was

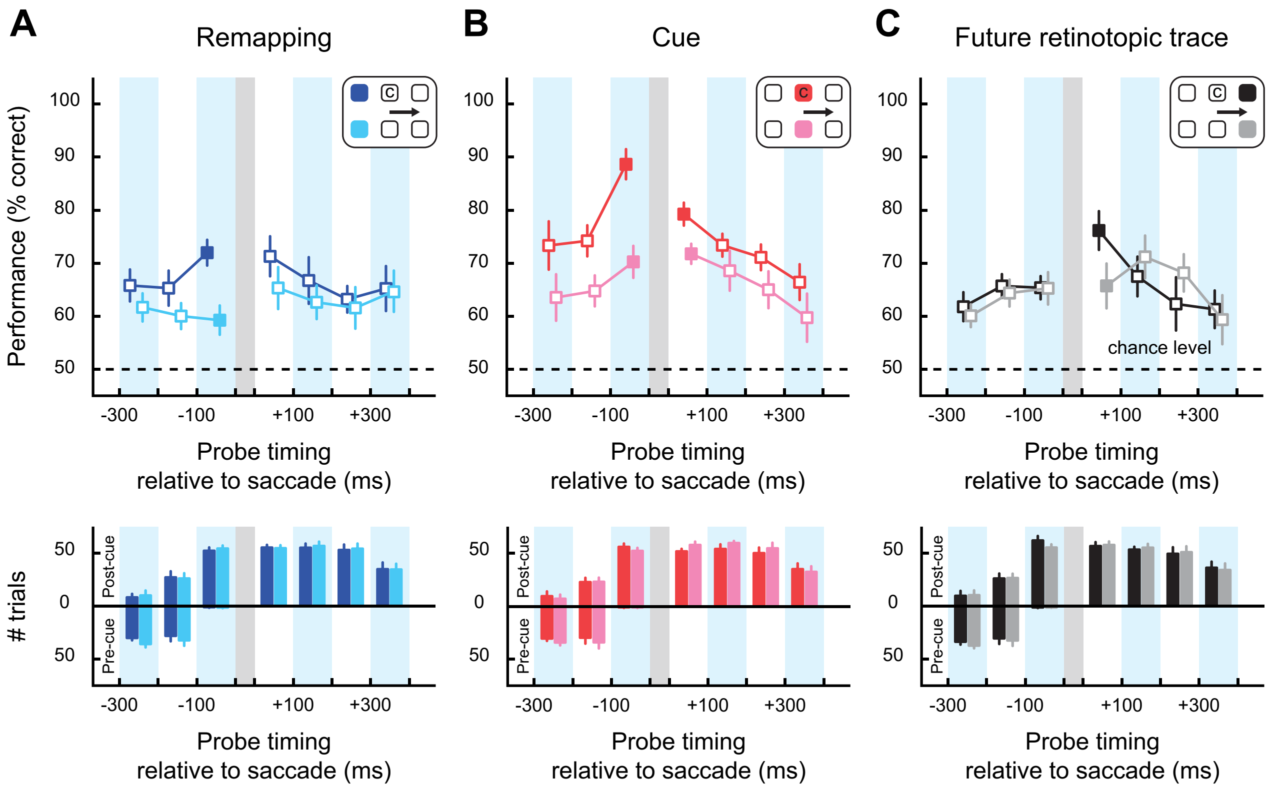

Fig. 6. Probe discrimination performance before and after saccades for the Transient-cue condition. All conventions are the same as in Fig. 5.

better at the remapped location than at the control location in time intervals 200–100 ms before saccade onset [$t(13) = 3.12$, $P < 0.01$] and 100 to 0 ms before saccade onset [$t(13) = 5.45$, $P < 0.001$].

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

Discrimination performance in the Transient-cue condition (Fig. 6), where the cue was presented only before the saccade, showed largely similar effects. Discrimination at the cue and cue control locations before the saccade depended on probe presentation time [$F(2,20) = 12.37$, $P < 0.01$] and probe location [$F(1,10) = 15.51$, $P < 0.01$], but there was no interaction between these two factors [$F(2,20) = 2.36$, $P = 0.12$]. We obtained the same results after the saccade [probe presentation time, $F(3,30) = 12.01$, $P < 0.01$; probe position, $F(1,10) = 5.18$, $P < 0.05$; and interaction, $F(2,20) = 0.06$, $P = 0.97$]. Thus probe discrimination was better at the spatial cue position both, before and after the saccade. In particular, probe discrimination at the cue location was better than at the control location for the first 100 ms after the saccade [$t(10) = 2.06$, $P < 0.05$]. Again, we did not observe any benefits at the future retinotopic trace location before the saccade [probe position, $F(1,10) = 0.28$, $P = 0.60$; probe time, $F(2,20) = 3.22$, $P = 0.06$; and interaction, $F(2,20) = 0.14$, $P = 0.86$]. As in the Sustained-cue experiment, during the first 100 ms following the saccade, discrimination performance was better at the retinotopic trace location than at the control location [$t(10) = 3.36$, $P < 0.01$; probe position, $F(1,10) = 0.30$, $P = 0.59$; probe time, $F(3,30) = 8.68$, $P < 0.01$; and interaction, $F(3,30) = 4.37$, $P < 0.05$]. Thus, in the Transient-cue condition, we replicated the attentional retinotopic trace benefits observed in the Sustained-cue condition. Finally, we observed a benefit at the remapped location before the saccade [probe position, $F(1,10) = 21.32$, $P < 0.001$; time, $F(2,20) = 1.05$, $P = 0.36$; and interaction, $F(2,20) = 1.81$, $P = 0.18$] but not after (all P values >0.05).

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

DISCUSSION

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

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

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

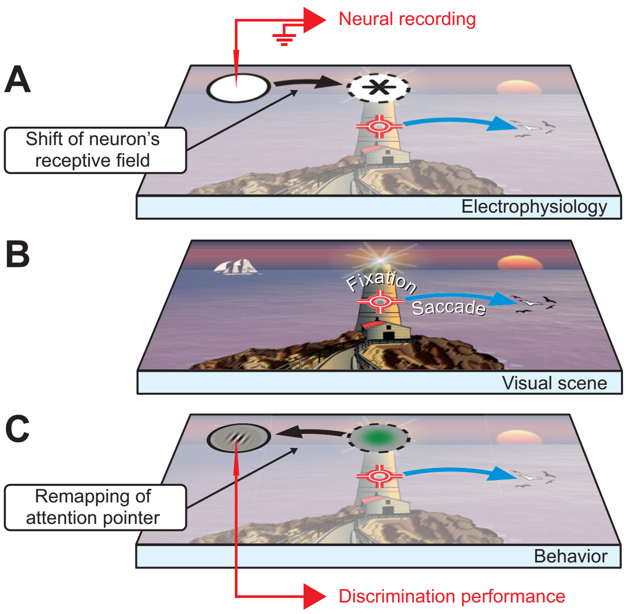

Fig. 7. Remapping in neurophysiology and behavior. While the observer is preparing a saccade from the lighthouse window to the white bird, a flash captures his or her attention (visual scene, *B*). Both electrophysiological (*A*) and behavioral (*C*) studies investigated how the visual system tracks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

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

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

Our findings address current controversies concerning the distribution of spatial attention after saccades. Golomb and colleagues have reported that after a saccade there is a strong attentional benefit at the retinotopic location that had been occupied by a memorized stimulus before the saccade (retinotopic trace location) and that in some cases it took up to a 100 ms for spatiotopic attention effects to occur (Golomb et al. 2008, 2010a; 2010b). Our results confirm the presence of the retinotopic trace after the saccade; however, we also observed clear spatiotopic effects immediately after the saccade. Contrary to our task, the studies of Golomb and colleagues used location memory to investigate spatiotopic and retinotopic processing benefits after the saccade. The time course of spatial updating across saccades for memorized locations might be different, as there is no urgency for the visual system to update information about the stimulus that has already disappeared from the visual field. Additionally, those studies did not measure attention allocation before the saccade, which leaves open the possibility that there is no presaccadic remapping of attention in a location memory task. This is in contrast to the presaccadic remapping of spatial attention in response to an attention-grabbing, currently visible stimulus. Future research would need to compare both situations directly.

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

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

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: D.J., M.S., M.R., and P.C. conception and design of research; D.J. and M.S. performed experiments; D.J. analyzed data; D.J., M.S., M.R., and P.C. interpreted results of experiments; D.J. and M.S. prepared figures; D.J. and P.C. drafted manuscript; D.J., M.S., M.R., and P.C. edited and revised manuscript; D.J., M.S., M.R., and P.C. approved final version of manuscript.

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