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Predictive remapping of attention across eye movements

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Many cells in retinotopic brain areas increase their activity when saccades (rapid eye movements) are about to bring stimuli into their receptive fields. Although previous work has attempted to look at the functional correlates of such predictive remapping, no study has explicitly tested for better attentional performance at the future retinal locations of attended targets. We found that, briefly before the eyes start moving, attention drawn to the targets of upcoming saccades also shifted to those retinal locations that the targets would cover once the eyes had moved, facilitating future movements. This suggests that presaccadic visual attention shifts serve to both improve presaccadic perceptual processing at the target locations and speed subsequent eye movements to their new postsaccadic locations. Predictive remapping of attention provides a sparse, efficient mechanism for keeping track of relevant parts of the scene when frequent rapid eye movements provoke retinal smear and temporal masking.

The visual system has to deal with large displacements of the image on the retina every time the eyes move to bring potentially relevant target objects into high-acuity foveal vision. In stark contrast with what we see when a camera is quickly swept across a visual scene, these retinal image shifts escape conscious perception[1]. More importantly, we do not lose track of those parts of the scene that are of current interest and may be the targets of future eye movements. The inability to perceive changes in unattended parts of the scene, seen in inattentional blindness and change blindness procedures[2,3], indicates that attention restricts this displacement problem to a small number of locations[4]. Some hundred milliseconds before an eye movement[5,6], visual attention is focused at the upcoming target locations[7–11], shifting the activations in saccade and attention areas of the brain[12]. These activations can be considered to be pointers specifying the locations of currently attended objects, whether targets of upcoming saccades or not, enabling both the planning of actions toward them and enhanced processing at those locations[13]. We found that these attentional pointers to saccade targets are updated by a predictive remapping process briefly before the eyes start moving. This process shifts attention in the direction opposite the saccade to locations that correspond to the current targets neither in retinotopic nor in world-centered coordinates, anticipating, before the eyes arrive, the locations the targets will have on the retina after the saccade lands. Our results lend strong behavioral support to the proposal that predictive remapping[14,15], the fact that many cells in retinotopically organized brain areas show anticipatory responses if a pending saccade will bring a stimulus into its receptive field (**Fig. 1a**), is a critical and rapid mechanism for keeping track of the locations of attended targets as the eyes move[16].

The discovery of predictive remapping launched intense scientific activity exploring the different brain areas and pathways involved and revealing the requirements for this process[4,17]. Until now, however, only two studies have targeted behavioral correlates of remapping[18,19] and neither of these tested the appropriate locations to determine the functional correlates of remapping (**Fig. 1b** and **Supplementary Fig. 1**). To the best of our knowledge, this is the first study to directly investigate the consequences of remapping of eye movement targets on pre-saccadic perception and post-saccadic action. We adapted the classic double-step saccade task[20,21] that has been the central procedure of the physiological studies of remapping. In this task, observers make two consecutive eye movements to pre-specified target locations and, critically, the vector for the eye movement to the second target is not given by its current retinal location, but by its updated location when the first saccade has been executed (**Fig. 1a**). If this vector is pre-computed and attention is deployed to that retinal location before the first saccade, then the second saccade will be prepared even before the first lands. This procedure tests the appropriate locations for functional remapping (**Fig. 1b**) and our results provide strong evidence for two key roles of this predictive process: updating the retinal location of attended parts of the scene and facilitating subsequent movements to them.

RESULTS

We assessed the dynamics of perceptual performance in a difficult visual-discrimination task that examines the allocation of attention in a stimulus array (**Fig. 2a**) while subjects prepare a sequence of two saccades. We probed several locations in space at different times following the onset of the central movement cue, which indicated the locations of the two targets. The probe was a tilted Gabor grating, briefly presented for 20 ms at the end of a flickering stream of vertical gratings. This procedure allowed for high resolution of temporal probes of visual performance, a gold standard for the measurement

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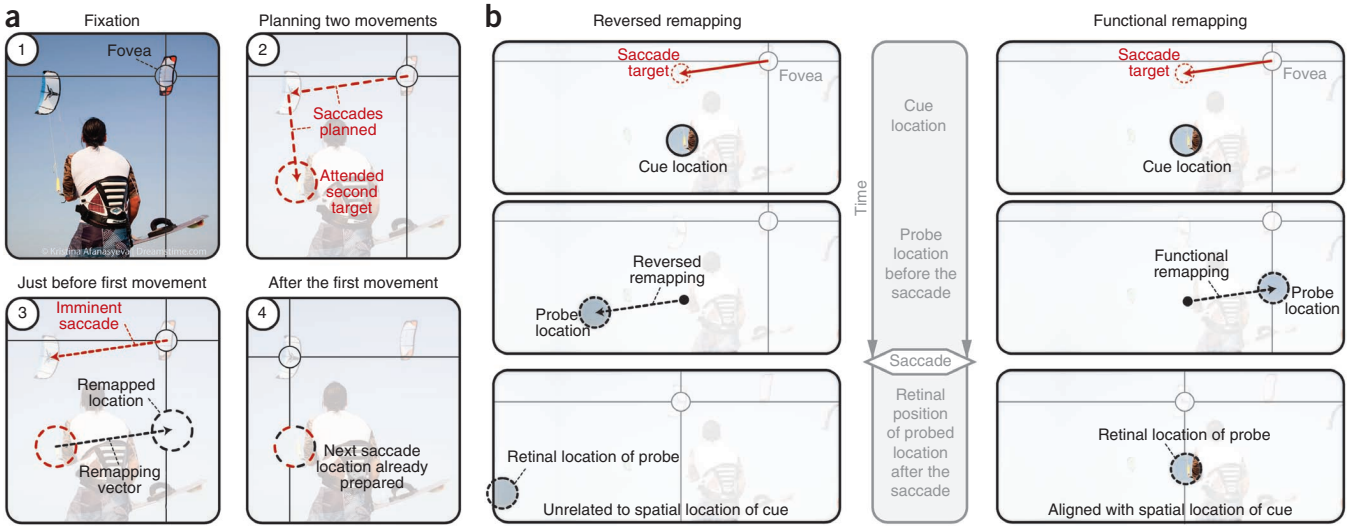

Figure 1 Predictive remapping across eye movements. (**a**) If two saccades are planned, first from the red to the blue kite and then to the kite handles visible near the surfer's left elbow, the second target (red circle) is attended in parallel to the first[9–11]. Remapping triggers a predictive activation of cells responding to the future retinotopic location of the second target, offset from its current location in the direction opposite the saccade vector (black circle)[16]. We found that this predictive activation was accompanied by an attention shift to that retinotopic location, specifying the location for the subsequent saccade. (**b**) The functional direction of remapping. Two previous studies have targeted behavioral correlates of remapping[18,19], but actually examined a reversal of remapping that has no functional correlate (see also **Supplementary Fig. 1**). In these studies, the effect of a spatial cue[18] (or, equivalently, an adaptor[19]) on subsequent pre-saccadic tests was assessed at a location offset from the cue location in the same direction as the saccade vector (middle left). This location is the opposite of the actual remapped location (middle right) and corresponds instead to the future world-centered location of the cue's current retinal location. After the saccade, this reversed remapped location covers retinotopic cortex that is far from the spatial location of the cue.

of attentional deployment. This fine-scale temporal structure was necessary to reveal the short-lived perceptual consequences of pre-saccadic remapping. After having executed the two successive eye movements, observers reported the direction of the tilt (clockwise or counterclockwise), regardless of its location. We ensured that the perceptual task could only be solved when observers deployed attention to a particular location by adjusting the stimulus tilt in a pre-test such that observers were 82% correct at the two target locations for probes presented 150 ms after the movement cue, ~100 ms before the saccade. On each trial (each observer ran a minimum of 3,000 trials), we probed one of four different locations (**Fig. 2a**): the first saccade target, the second saccade target, its remapped location or its opposite location, representing a neutral control location. Note that the remapped location of the second saccade target corresponds to the retinal position that the second saccade target will have only following the first saccade. It does not match either the spatial or retinal location of the second target before the saccade.

We plotted the average performance of nine observers as a function of the timing of the probe presentation relative to the first saccade, superimposed for all four probe locations tested (**Fig. 2b** and **Supplementary Fig. 2**). We found the expected advantage in discrimination performance at both the first and second saccade target locations[9–11] increasing from around 150 ms before the first saccade[5,6], with a somewhat more shallow slope for the advantage at the second saccade target. We also found a marked increase in performance at the remapped location for the second target, emerging

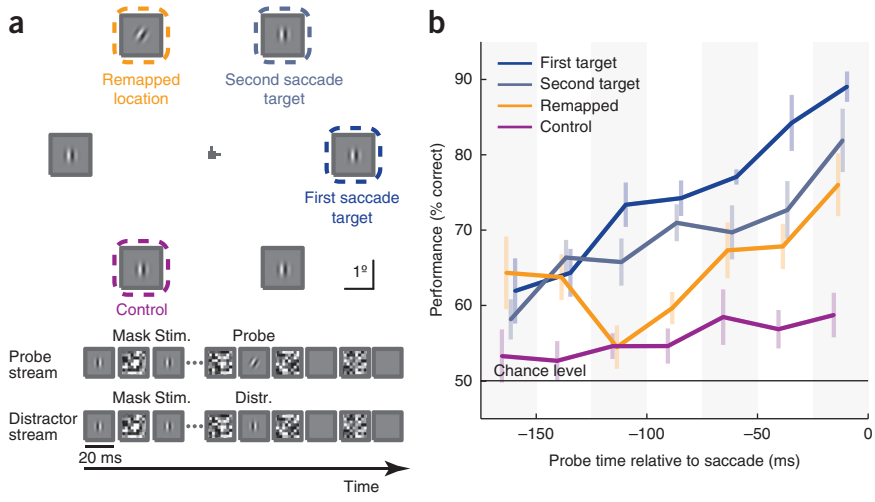

Figure 2 Predictive remapping of attention in the double-step task. (**a**) Stimulus layout. Six stimuli, arranged in a regular hexagon, displayed a flickering stream of grating-mask pairs. Following a central movement cue, subjects quickly made two eye movements, the first one left or right (here, right), the second one up or down (here, up). One of the six gratings changed orientation (probe stream; here at remapped location) 50–400 ms after the movement cue, whereas all others remained vertical (distractor streams). After the eye movements, subjects reported the direction of tilt that they had seen (\ or /), regardless of its location. Using performance in this task, we measured the deployment of attention at four locations (dashed frames) during the latency of the first saccade. (**b**) Performance as a function of probe offset relative to the saccade, superimposed for the probe locations tested. Error bars represent s.e.m.

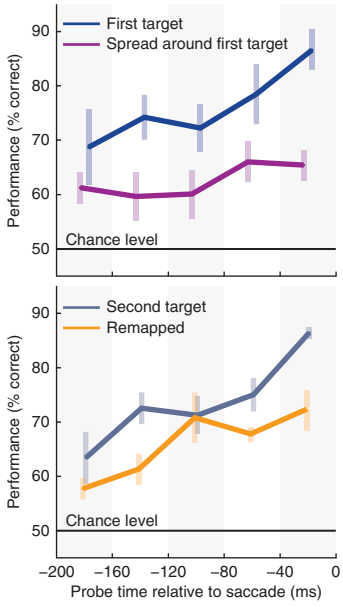

Figure 3 Controlling for the spread of attention in the double-step task. We repeated the double-step task in a new set of subjects, probing the location adjacent to the first saccade target to test whether attentional benefits extend around saccade targets, an alternative interpretation of the effect at the remapped location. Performance is shown as a function of probe offset relative to the saccade. Attention did not spread around saccade targets. Instead, it shifted specifically to the remapped location of the second saccade target. Error bars represent s.e.m.

just 75 ms before the saccade. This benefit reached a magnitude comparable to that observed at the second saccade target itself and all nine observers showed it consistently (analyzed at a resolution of 75 ms to counteract the additional noise). In fact, across observers, the performance at the remapped location in the last 75 ms preceding the saccade correlated significantly with the performance at the second saccade target in the same time window ($r = 0.91$, $P < 0.001$), suggesting that the two allocations are strongly linked: an observer who successfully allocates attention to the second target also allocates substantial attention to its predicted post-saccadic location. Note that before the saccade, when this benefit is seen, the remapped location does not correspond to the second saccade target location in either retinotopic or world-centered coordinates. Contrary to the time course of perceptual facilitation at the second saccade target, performance at the remapped location revealed a drop almost to chance level in the time between 125 to 100 ms before the saccade (while attention is allocated to the saccade targets), excluding the possibility that the pre-saccadic enhancement is a general attentional cuing effect resulting from the movement cue. The stable performance at the control location indicates that the observed benefits do not represent a spatially nonspecific increase in performance.

The remapped location for the second target corresponds to the position this target will have on the retina following the first saccade. Activity in the saccade control regions of the brain is required at this location to send the second saccade to its target once the first saccade has landed. In the absence of this remapped activity, the second target could be rediscovered following the first saccade (assuming it is still present); however, if its location has been successfully remapped to the appropriate location, the second saccade should be ready to execute as soon as the first saccade lands. Indeed, we estimated that the second saccade had a minimum latency benefit of 19.2 ± 14.8 ms (corresponding to a 9.2 ± 7.1% difference in second saccade latency; mean ± 95% confidence interval) when there was evidence that an observer had successfully shifted his or her attention to the remapped location (for example, correctly identified the probe stimulus orientation at that location; see Online Methods). This effect was most pronounced just before the saccade; taking only trials when observers correctly identified a probe presented in the last 25 ms before the saccade (rather than the whole pre-saccadic period as in the main analysis), the conditional benefit was 28.3 ± 23.0 ms. Thus, an attention shift to the remapped location before the first saccade was associated with a speeded execution of the second saccade or, equivalently, the preprogramming of the second saccade was associated with a deployment of attention to the remapped location before the eyes moved to the first target. A similar speeding of the second saccade was also seen for trials in which observers successfully identified the target at the pre-saccadic location of the second target (9.9 ± 6.6 ms), but not at all seen contingent on performance at other locations (first target, −10.3 ± 7.1 ms; control location, −29.2 ± 32.7 ms). As previously mentioned, attention must be allocated first to the target before it can be transferred to the remapped location. The remapped location cannot be computed without first localizing its current location.

Although the specificity of these effects is marked and consistent with the remapping of attention to the future location of targets on the retina, we have to rule out two alternative explanations. The benefit at the remapped location may have arisen simply from an attentional spread to locations adjacent to the saccade targets or a strategic deployment of attention to the cued side of the display. In two separate control experiments, we ruled out both. To test for the spatial extent of attentional benefits around saccade targets, we repeated the double-step experiment, but, in addition to testing the saccade target locations as well as the remapped location of the second saccade target, we also examined visual performance at a new control location, the one adjacent to the first saccade target that was not the target of the second saccade. If attentional benefits extend around saccade targets, this control location should also show a change in performance across time, as it is next to the first saccade goal. We found that it did not. Performance at the first saccade target increased strongly across time (**Fig. 3** and **Supplementary Fig. 3**), starting more than 150 ms before the first saccade, while it remained consistently low across that whole interval at the adjacent location controlling for attentional spread. Performance at the second saccade target location also showed a strong increase (**Fig. 3**) and we again found a strong performance increase occurring about 100 ms before the first saccade is executed at the remapped location of the second target.

To exclude the possibility that the local performance increase at the remapped location resulted from a strategic deployment of attention to the pre-cued side of the display, we ran a second control experiment. In this single-cue version of the double-step experiment (**Fig. 4a**), a central cue indicated the target of the first saccade (any of the six locations in the display), whereas the second target was always the next location in the clockwise direction. Otherwise, the experiment was identical to the control experiment described above. Again, performance at the first saccade target increased strongly across time (**Fig. 4b** and **Supplementary Fig. 4**), starting ~150 ms before the first saccade, whereas it remained constantly low throughout that whole period at the adjacent location controlling for attentional spread. Performance at the second saccade target location also showed a strong increase (**Fig. 4b**). At the remapped location of the second target, we again found a substantial performance increase, occurring just 50 ms before the first saccade is executed. The spatiotemporal

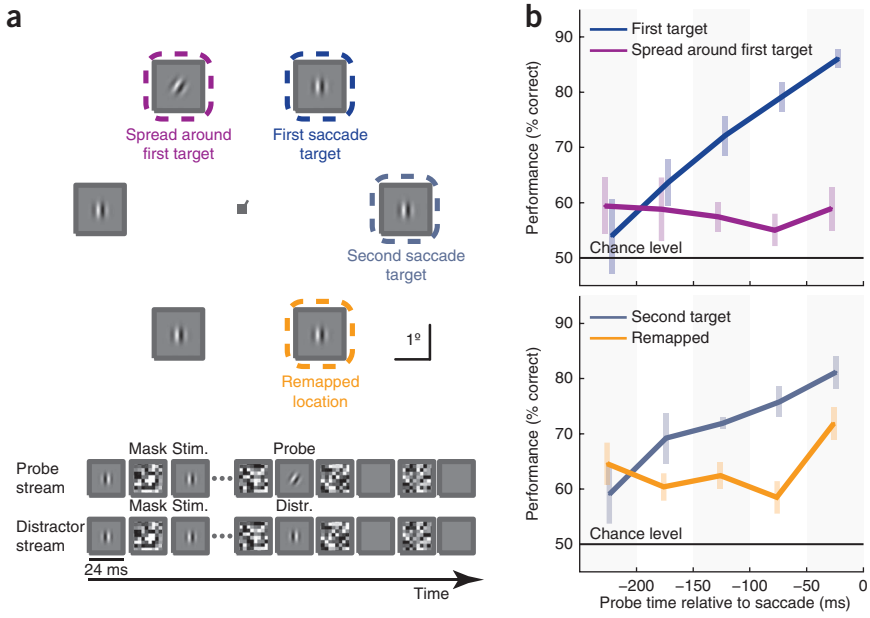

Figure 4 Controlling for cue-based facilitation in the double-step task. (**a**) In this version of the double-step task, we used only one cue, excluding the possibility of a cue-based attentional facilitation at the remapped location. The single cue indicated the first saccade target (any of the six; here upper right); the second saccade target was always the next stimulus in the clockwise direction (here, right). We measured the deployment of attention at four locations (dashed frames) during the latency of the first saccade. Testing the location adjacent to the first saccade target, this experiment also again tested whether attentional benefits extend around saccade targets, an alternative interpretation of the effect at the remapped location (see also **Fig. 3**). (**b**) Performance as a function of probe offset relative to the saccade. Again, briefly before the saccade, attention shifted specifically to the remapped location of the second saccade target. Error bars represent s.e.m.

specificity of this effect indicates that it is not a result of attentional spread around the saccade target locations. Moreover, as probe locations were balanced around the saccade targets and the movement cue pointed nowhere near the remapped location, our results can neither be explained by strategic nor cue-based deployment of attention, which in any case may occur only early during the preparation of a saccade[6].

In our first three experiments, we found that, before a saccade, attention to a second saccade target is updated in a retinotopic frame of reference. Using the same general procedure, we next studied the dynamics of attention at the remapped location for a single saccade target; this remapped location is at (or near) the fovea[22], where the target will land after the saccade. Although this situation is maximally ecologically valid (the fovea is the future retinotopic location of every imminent saccade target), it has not yet been tested in neurophysiological studies of remapping. Probing attention at the fovea is difficult, as the presentation of a probe stimulus at the fovea is likely to interfere with the preparation of an eye movement. Using constantly flickering stimuli, our procedure avoids this issue by masking the transient caused by the probe (**Supplementary Figs. 2–5**). The display contained three horizontally aligned and equally spaced object locations (**Fig. 5a**): fixation, saccade target (denoted by a line pointing away from fixation) and a control location at the opposite side. We plotted the average performance of nine observers as a function of probe time before the saccade (**Fig. 5b** and **Supplementary Fig. 5**). Performance strongly increased at the saccade target as the eye movement neared. Although performance was always very high at fixation, allowing for less variation across time, it showed the same time course as the benefit for the remapped location in the double-step task, with a continuous increase starting around 75 ms before the saccade. We observed no variation of performance at the control location, again excluding the possibility of a nonspecific pre-saccadic performance increase.

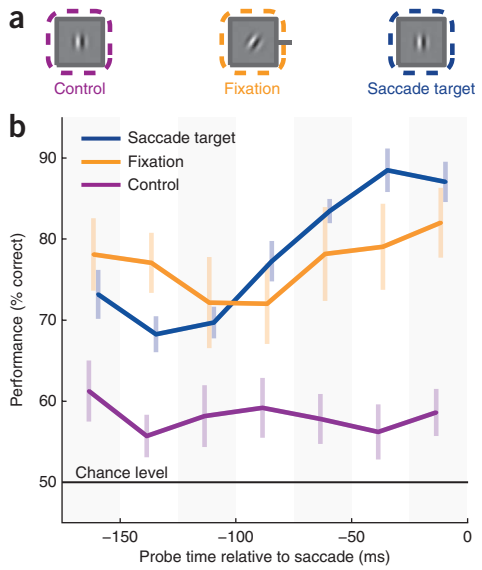

Figure 5 Predictive remapping of attention to the fovea. (**a**) Stimulus layout in the single-step task. We presented three stimuli, arranged at equal distances in a line. Otherwise the procedure was identical to that in the double-step task (**Fig. 2a**). Following a movement cue (here, right), subjects quickly made an eye movement to the indicated target and reported the direction of the tilted stimulus, regardless of its location. (**b**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars represent s.e.m.

DISCUSSION

We studied the functional correlates of predictive remapping of targets of saccadic eye movements[16]. Using a sensitive perceptual probe, we assessed the dynamics of spatial attention before a saccade without interrupting saccade programming. The probe revealed a robust increase in visual performance at the remapped, future retinal locations of a sequence of movement goals, occurring less than 100 ms before the eye started moving. This benefit was short-lived and spatially constrained to the remapped locations and is explained by a local attentional facilitation (rather than other well-established changes in visual performance such as perceptual learning[23], lateral or temporal facilitation[24,25]). Moreover, it did not result from a general spread of attention deployed to the saccade targets themselves. In fact, the perceptual benefit at the remapped location was associated with a decrease of saccade latencies to subsequent targets, emphasizing the functional consequences of remapping of attention.

Predictive remapping has often been associated with phenomenal, visual stability across saccades[4,13,17,26]. Although the proposal that

remapping helps maintain feature information in world-centered coordinates[19] has been challenged recently[13,27], our data suggest that pre-saccadic shifts of activations that index only the locations of attended targets may be sufficient for visual stability. In fact, our data provide immediate behavioral evidence for the recent proposal that these shifting attentional pointers are the essence of trans-saccadic remapping[13], providing an efficient and sparse mechanism to keep track of relevant locations in space as the eyes explore the visual scene[4]. Based on efference copy (or corollary discharge) of the upcoming saccade[22,28,29], neurons in the retinotopic areas controlling saccades and attention pre-activate in anticipation of a soon-to-arrive stimulus[14,15]. This activation projects to the corresponding locations in lower level visual areas[30,31], alerting those parts of the retinotopic visual cortex that will analyze targets of interest after the saccade. The results presented here reveal two functional consequences of the predictive remapping process, the attentional benefits at the remapped location just before the saccade (subserving attentional facilitation of world locations once the saccade has landed[18,32]) and preprogramming of future action.

METHODS

Methods and any associated references are available in the online version of the paper at http://www.nature.com/natureneuroscience/.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

M.R., D.J., H.D. and P.C. designed the experiments. M.R. and D.J. conducted the experiments and analyzed the data. M.R. and P.C. wrote the manuscript. P.C. and H.D. supervised the project. All of the authors discussed the results and commented on the manuscript.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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ONLINE METHODS

Participants. We tested nine observers (age 19–32, 2 female, 7 right-eye dominant, 7 right-handed, 2 authors) in Paris for the two main experiments and nine observers (age 22–28, 2 female, all right-eye dominant, 8 right-handed, 1 author) in Munich for the two double-step control experiments (7 in the single-cue and 6 in the two-cue control). Observers had normal or corrected-to-normal vision and gave informed consent before study participation. We conducted the experiments in accordance with the Declaration of Helsinki.

Setup. Observers sat in a silent and dimly lit room with the head positioned on a chin rest. We presented stimuli at a distance of 63 cm on a 22-inch Sony GDM-F520 screen (1,050 × 1,400 pixels, 100-Hz vertical refresh rate) and recorded the dominant eye's gaze position using an EyeLink 2000 Desktop Mount (SR Research). An Apple MacPro computer running MATLAB (MathWorks) with standard toolboxes[33–35] controlled stimulus presentation and response collection.

Double-step experiment. During each trial, we presented a green fixation dot (0.3 × 0.3°) at the center of a uniform gray display. Six object locations, highlighted by green square outlines (1.5 × 1.5°), were arranged 5° from central fixation to form the corners of a regular hexagon. In each of these boxes, a stream of stimuli flickered, alternating between vertical Gabor patches (2.5 cpd, 100% contrast, random phase on each presentation) and white noise, each presented for 20 ms. After a normally distributed random interval (M = 1,000 ms, s.d. = 300 ms, cutoff at 3.3 s.d.), a saccade cue appeared consisting of two lines (0.2° long, one left or right, one up or down) pointing away from the fixation dot. Participants performed this saccade task as quickly and accurately as possible. One of the Gabors changed orientation 50–400 ms after the onset of the saccade cue. After this probe presentation, all Gabor patches disappeared and noise patches flickered on and off at 25 Hz. After finishing the saccade task, participants reported by a button press whether the probe was tilted clockwise or counterclockwise, regardless of its location (that is, we never asked for the probe location itself). In each trial, the probe appeared randomly at either the first saccade goal, the second saccade goal, the remapped location of the second saccade goal (left or right to the second saccade goal) or at an irrelevant location (same distance from the first saccade goal as remapped location, but in the other direction). If participants failed to look at both target locations within 1,500 ms, we gave a visual feedback and the trial was repeated later in the block. There was no feedback for the perceptual task.

Participants ran a minimum of 3,000 trials in 6 1-h sessions. Before each session, we obtained three 82% orientation-discrimination thresholds for probe patches presented in the upper (25.1 ± 8.8°, M ± s.d. of tilt at threshold, across participants), middle (16.7 ± 5.3°) and lower (25.0 ± 6.8°) parts of the visual field using interleaved QUEST staircases[36] in the same task. We presented probes only at the saccade target locations and in a time window of 150–200 ms after saccade cue onset and provided auditory feedback on performance in the perceptual task.

Double-step control experiments. Designed to control for attentional spread around saccade targets as an explanation of our remapping effect, both the two-cue and the single-cue control experiments were identical to the double-step experiment except for the following differences. We presented stimuli at a distance of 70 cm on a 22-inch Lacie Electron 22 Blue screen (1,024 × 1,280 pixels, 85-Hz vertical refresh rate) and recorded eye movements using an EyeLink 1000 tower mount. We presented probes either at the first saccade target, the second saccade target, the remapped location of the second target or at a control location, the location adjacent to the first saccade target, but opposite the second target. As a result of the different refresh rate, stimuli in the flickering streams changed at 21.5 Hz; hence, the probe duration was 23.5 ms. In addition, in the single-cue control, a single cue indicated the first saccade goal (any of the six stimulus locations) and the second saccade goal was always the next target in the clockwise direction.

Participants ran a minimum of 1,920 trials in 4 1-h sessions in the single-cue control and a minimum of 3,000 trials in 6 1-h sessions in the two-cue control. In the two-cue control, orientation discrimination thresholds for probe patches presented in the upper, middle and lower parts of the visual field were 14.6 ± 5.4°, 13.5 ± 5.1° and 14.5 ± 5.5°, respectively. In the single-cue control, we obtained separate orientation discrimination thresholds for the first and the second saccade target and for each of them separately for the upper (12.5 ± 7.5° at first and 18.0 ± 9.5° at second saccade target), the middle (11.9 ± 3.7° at first and 23.2 ± 5.4° at second target) and the lower (8.0 ± 2.1° at first and 19.3 ± 5.9° at second target) visual field. We used discrimination thresholds obtained for the first and second saccade targets for the control location (adjacent to first saccade target) and the remapped location (adjacent to second saccade target), respectively.

Single-step experiment. The single-step task was different from the double-step task only in the following ways. We used three object locations, one at the center of the screen (fixated at trial start) and two at a horizontal distance of 6°. The saccade cue was a 0.5° line pointing away from either the left or the right side of the central square, denoting the saccade target. Failure to look at the target within 1,000 ms triggered a feedback and the trial was repeated later in the block.

Participants ran a minimum of 2,000 trials in 4 1-h sessions. In the pre-test, we obtained two separate orientation discrimination thresholds, one for probes at fixation (17.0 ± 5.7°) and one for the saccade target (13.3 ± 7.6°). We presented the probes at fixation 150–200 ms before saccade cue onset, while this location was still attended.

Data pre-processing. We detected saccades with a velocity-based algorithm[37] and defined a response saccade as the first saccade that left a circular fixation region and landed inside a target-centered circular region (radii of 2°). We rejected trials with blinks, no response saccades starting 100–400 ms after saccade cue onset, saccades larger than 1° before a response saccade, or saccades to the remapped location (circular region with radius of 2°) by 500 ms after the response saccades. We included a total of 23,318 trials (or 86.4%) in the double-step experiment, a total of 16,136 trials (or 89.6%) in the two-cue control experiment, a total of 10,532 trials (or 78.4%) in the single-cue control experiment, and a total of 15,409 trials (or 85.6%) in the single-step experiment in data analyses.

Data analysis. We used a permutation method[38] to generate confidence intervals, testing whether performance changed across time before a saccade (**Figs. 2b**, **3b**, **4b** and **5b**). The method is based on the idea that temporally invariant variables are indistinguishable from their random permutations across time. In an observer's original dataset, each response (correct or incorrect) is linked to a particular probe time. We randomly reassigned responses to the probe times (without replacement) for each observer separately and, subsequently, computed an average surrogate time course of performance as for the original data. We repeated that 1,000 times and computed means and 95% confidence intervals from these surrogate samples. If the average performance differed from the time course of the original data, we could be confident that performance varied as a function of time (**Supplementary Figs. 2a**, **3a**, **4a** and **5a**).

Estimating latency benefits contingent on high performance at a given location. We know the distribution of second saccade latencies for trials where an observer's perceptual report of a probe presented at a given location was correct, f_c, or incorrect, f_i. Neglecting lapses, f_i contains only trials with low perceptual performance (incorrect guesses), whereas f_c contains trials with high perceptual performance, $f_{c|high}$ and correct guesses $f_{c|low}$. To decompose f_c, we first fitted an ex-Gaussian distribution $F_i(t; \mu_i, \sigma_i, \tau_i)$ to fi. Because, by definition, $F_{c|low}(t; \mu_{c|low}, \sigma_{c|low}, \tau_{c|low}) = Fi(t; \mu_i, \sigma_i, \tau_i)$, we fitted f_c with a mixture of $p\, F_i(t; \mu_i, \sigma_i, \tau_i)$ and a second ex-Gaussian $(1 - p)\, F_{c|high}(t; \mu_{c|high}, \sigma_{c|high}, \tau_{c|high})$, where $p = p_i/p_c$, that is, the proportion of correct trials that were guesses. The reported latency differences between high and low performance at a given location represent the difference between the means of the distributions, $(\mu_{c|low} + \tau_{c|low}) - (\mu_{c|high} + \tau_{c|high})$. Because of relatively low performance, few trials were available for fitting $F_{c|high}$ for the control location and the procedure did not converge for four observers. We computed results for that condition over the remaining five observers. Note that the four remaining observers showed slightly longer latencies for correct trials at the control location, in agreement with the average data. These estimates imply that attending to a stimulus and correct performance go hand in hand, which is certainly not the case. That is, even if the probe location was attended, presumably decreasing saccade latency, observers were correct only on a proportion of trials. And, conversely, if the probe location was not attended (predicting longer saccade latencies), subjects may still have seen and correctly reported the probe. Therefore, this procedure results in a conservative estimate of the real latency difference between high and low performance trials.

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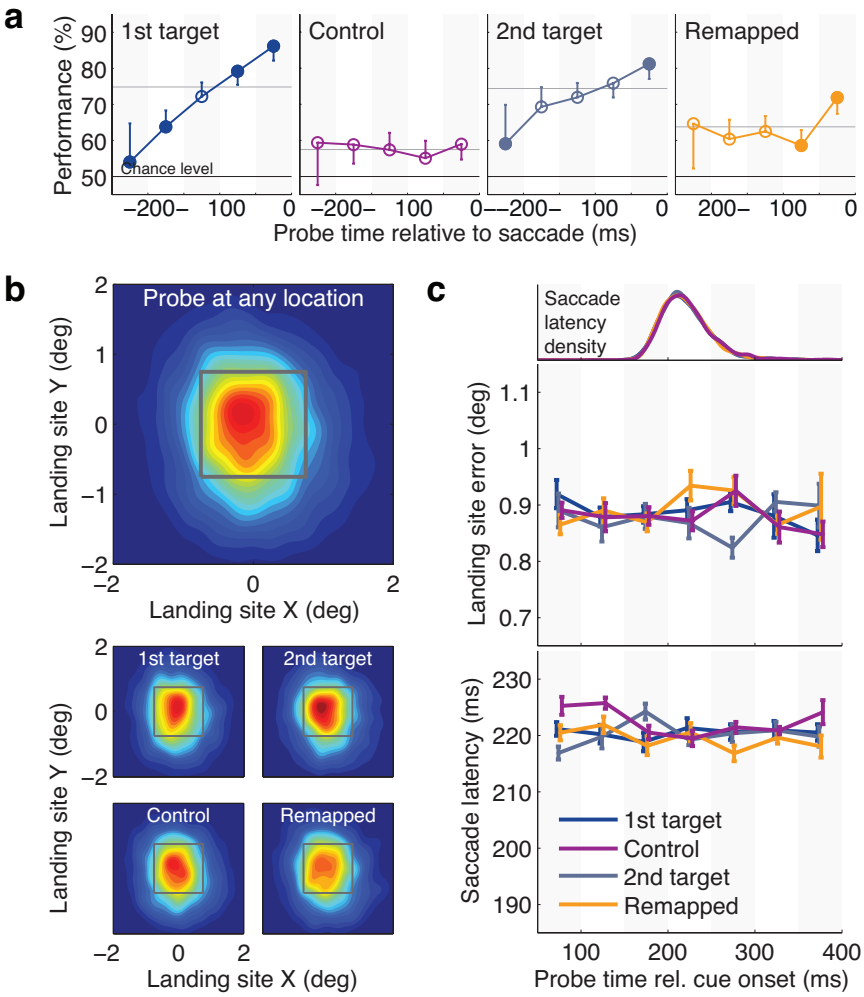
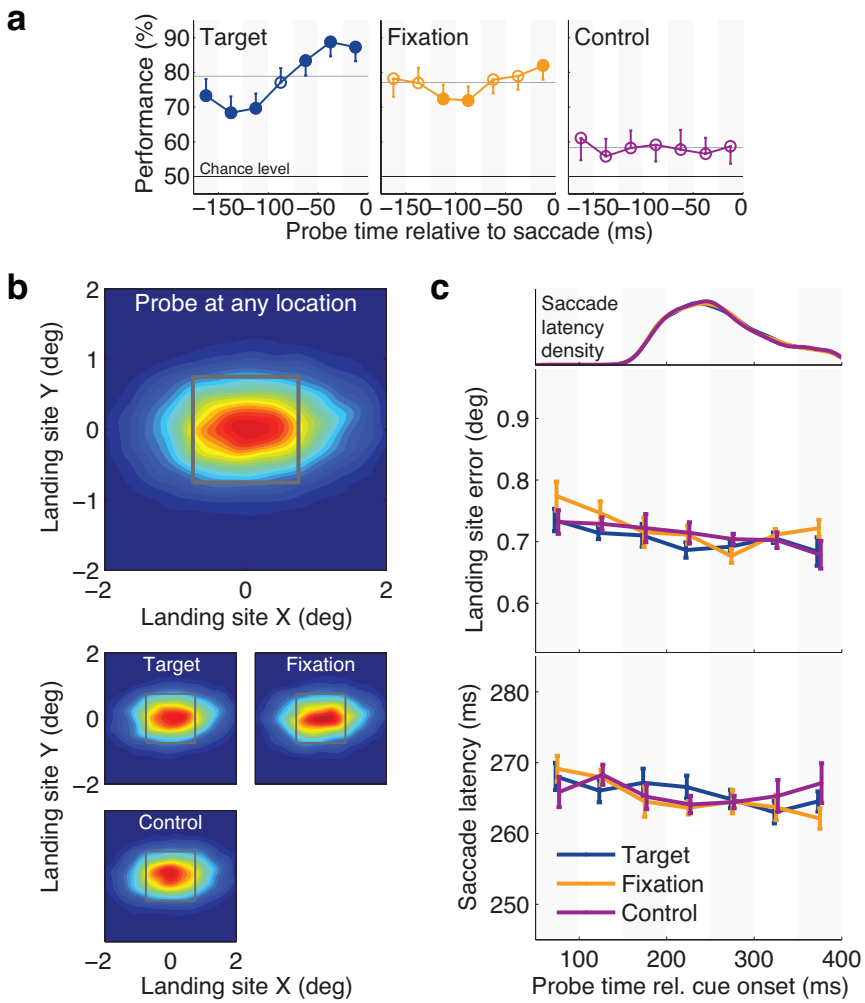


Supplementary Figure 4. Supplementary analyses for the single-cue double-step control experiment. We provide significance tests for the performance changes across time and show that the metrics and latency of the first saccade are largely independent of probe location and timing. (**a**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are 95% confidence intervals testing whether performance differed from the average (gray lines) (see **Online Methods**). Filled symbols highlight significant deviations. (**b**) Landing sites of the first saccade relative to the first saccade target (gray outline), plotted in 2D-density plots. The upper panel shows data from all conditions collapsed, the lower four panels show data for each probe location separately. (**c**) The upper panel shows the distribution of saccade onsets relative to the onset of the cue (i.e., saccade latencies). The four distributions overlap almost completely. The average overall saccade latency was 221±10 ms (*M*±*SD*, across observers) for first saccades and 222±34 ms for second saccades. The lower two panels show mean landing site error of the first saccade (Euclidian distance from the first target's center; middle) and its latency (bottom) as a function of probe location (different lines) and probe time relative to the onset of the saccade cue. Error bars are s.e.m.



Supplementary Figure 5. Supplementary analyses for the single-step experiment. We provide significance tests for the performance changes across time and show that the metrics and latency of the saccade are largely independent of probe location and timing. (**a**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are 95% confidence intervals testing whether performance differed from the average (gray lines) (see **Online Methods**). Filled symbols highlight significant deviations. (**b**) Landing sites of the saccade relative to the saccade target (gray outline), plotted in 2D-density plots. The upper panel shows data from all probe locations collapsed, the lower three panels show data for each probe location separately. (**c**) The upper panel shows the distribution of saccade onsets relative to the onset of the cue (i.e., saccade latencies). The four distributions overlap almost completely. The average overall saccade latency was 265±35 ms (*M*±*SD*, across observers). The lower two panels show mean landing site error of the first saccade (Euclidian distance from the first target's center; middle) and its latency (bottom) as a function of probe location (different lines) and probe time relative to the onset of the saccade cue. Error bars are s.e.m.