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Pre-saccadic motion integration between current and future retinotopic locations of attended objects

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Pre-saccadic motion integration

Abstract

Object tracking across eye movements is thought to rely on pre-saccadic updating of attention between the object's current and its "remapped" location (i.e., the post-saccadic retinotopic location). Here we report evidence for a bi-focal, pre-saccadic sampling between these two positions. While preparing a saccade, participants viewed four spatially separated random dot kinematograms, one of which was cued by a colored flash. They reported the direction of a coherent motion signal at the cued location while a second signal occurred simultaneously either at the cue's remapped location or at one of several control locations. Motion integration between the signals occurred only when the two motion signals were congruent and were shown at the cue and at its remapped location. This shows that the visual system integrates features between both the current and the future retinotopic locations of an attended object, and that such pre-saccadic sampling is feature-specific.

New & noteworthy

We show behavioral evidence for motion integration between the current and the future retinotopic locations of a salient object just before a saccade. This pre-saccadic integration occurs only when the features at the two locations are congruent, in other words, only when the information from the target's future location matches the value it is expected to have once the target actually gets there. These results suggest the existence of a feature-gated integration occurring before saccades.

Keywords

Saccade, remapping, space constancy, motion integration

Introduction

Our visual system needs to integrate information about different features and locations in order to form a continuous and comprehensive experience of our surrounding world (Treisman and Gelade, 1980). Elements of the visual scene are represented by different feature-specific receptive fields in retinotopically organized visual areas (Essen and Zeki, 1978; Van Essen et al., 1981; Sereno et al., 1995; Gardner et al., 2008; Tanigawa et al., 2010). Therefore, every time the eyes move, the visual system has to update the locations of objects of interest in retinotopic coordinates to keep track of the objects' features. Earlier work has demonstrated that humans can track spatial (Deubel et al., 1998; Parks and Corballis, 2010; Pertzov et al., 2010; Boi et al., 2011; Szinte et al., 2012; Jonikaitis et al., 2013; Jonikaitis and Belopolsky, 2014) and feature-based information (Deubel, 1991; Verfaillie et al., 1994; Deubel et al., 2002; Hollingworth et al., 2008; Harrison and Bex, 2014) across eye movements. However, whether and how we integrate feature information from different locations across eye movements is debated (Melcher and Morrone, 2003; Melcher, 2007; Knapen et al., 2010; Morris et al., 2010; Mathôt and Theeuwes, 2013).

Mechanisms proposed to explain trans-saccadic feature integration rely on either pre-saccadic predictions (Cavanagh et al., 2010a) or top-down post-saccadic strategies (Deubel et al., 1998; Boi et al., 2011; Tatler and Land, 2011). Post-saccadic strategies can be thought of as a search for task relevant features or objects after each eye movement. Pre-saccadic predictions, on the other hand, propose that the visual system anticipates the consequences of impending saccades by predicting where task relevant targets will be after an eye movement (Duhamel et al., 1992; Wurtz, 2008; Cavanagh et al., 2010a). This prediction mechanism, called remapping, focuses on tracking the spatial location of targets across eye movements, but the extent to which feature information is carried over from the target's current to its remapped location is less clear. Some papers have suggested that this feature transfer may occur even before the saccade (Melcher, 2007; Harrison et al., 2013) and report an influence of the pre-saccadic target's features on post-saccadic probes presented at the target's predicted location (the remapped or spatiotopic location). Although these results are variable, they suggest that trans-saccadic memory for visual content is more abstract and limited (Pollatsek et al., 1984; Verfaillie et al., 1994; Carlson-Radvansky and Irwin, 1995; Melcher and Morrone, 2003). Moreover, others either have failed to report such feature-specific interactions (Knapen et al., 2010; Morris et al., 2010; Mathôt and Theeuwes, 2013) or show only limited feature-specific effects (for example, Subramanian and Colby, 2014; Yao et al., 2016).

In the current study, we measured the integration of feature-based information (motion direction) presented at two locations – the current and the remapped location of an attended target – before the execution of the

saccade (not across saccades as Melcher and Morrone, 2003). Integration refers here to the summation of visual signals across different retinotopic positions similar to the integration across sources modeled with Bayesian theories in cue combination (Landy et al., 1995) or multi-sensory integration studies (Ernst and Banks, 2001, Hillis et al., 2002). This contrasts with previous reports described above which consider integration as a transfer of feature information from the target's location to its remapped location. We report evidence for a bi-focal sampling of feature information by showing that an attended motion signal can be integrated pre-saccadically with another motion signal presented at its remapped location. Critically, this integration is both spatially specific and feature-specific, suggesting that the visual system activates a feature-specific integration process in anticipation of the retinal consequences induced by the impending saccade. This constitutes the first evidence of a mechanism simultaneously integrating features across different positions in space, provided they are expected to originate from the same object across the saccade.

Material and methods

— Figure 1 —

Participants

11 students (9 in the saccade task, 8 in the fixation task with 6 participating in both tasks) of the LMU München participated in the experiments (age 21-31, 6 females, 10 right-eye dominant, 2 authors), for a compensation of 9 Euros per hour of testing. All participants except two authors were naive as to the purpose of the study and all had normal or corrected-to-normal vision. The experiments were undertaken with the understanding and written informed consent of all participants and were carried out in accordance with the Declaration of Helsinki. Experiments were designed according to the ethical requirement specified by the LMU München and an institutional review board ethics approval for experiments involving eye tracking.

Setup

Participants sat in a quiet and dimly illuminated room, with their head positioned on a chin and fore-head rest. The experiment was controlled by an Apple iMac Intel Core i5 computer (Cupertino, CA, USA). Manual

responses were recorded via a standard keyboard. The dominant eye's gaze position was recorded and available online using an EyeLink 1000 Desktop Mounted (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. The experimental software controlling the display, the response collection as well as the eye tracking was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink toolboxes (Cornelissen et al., 2002). Stimuli were presented at a viewing distance of 60 cm, on a 21-in gamma-linearized SONY GDM-F500R CRT screen (Tokyo, Japan) with a spatial resolution of 1024 x 768 pixels and a vertical refresh rate of 120 Hz.

Procedure

The study was composed of a saccade and a fixation task tested in 4 to 5 experimental sessions (on different days) of about 60-90 minutes each (including breaks). These main tasks were preceded by their respective threshold tasks for each experimental session. Participants started with a training phase in which they were familiarized with the stimuli and the two different tasks. After the training phase, participants started each experimental session with 1 to 2 threshold blocks followed by 4 to 5 blocks of the saccade or fixation task. Participants ran a total of 3 blocks of the fixation task and 16 blocks of the saccade task. All participants who ran both tasks first completed the saccade task before starting the fixation task.

Saccade task

Each trial began with participants fixating a central fixation target (*ft*) forming a black (~0 cd/m^2) and white (60 cd/m^2) "bull's eye" (0.45° radius) on a gray background (30 cd/m^2). When the participant's gaze was detected within a 2.0° radius virtual circle centered on the *ft* for at least 200 ms, the trial began with a random fixation period (500-750 ms in steps of 50 ms) after which a black (~0 cd/m^2) circle replaced the *ft* and the bull's eye jumped to one of four possible saccade target positions (*st*) located 11° right, left, up or down from the *ft*. Participants were instructed to follow the bull's eye with their gaze as quickly and accurately as possible.

In addition to the *ft* and *st*, the display contained four random dot kinematograms (*RDKs*) centered half way between the horizontal and vertical potential *st* locations (Figure 1, eccentricity of the *RDK* center: ~8.5°). Each *RDK* was composed of half black (~0 cd/m^2) and white (60 cd/m^2) dots (10' radius), restricted to 2.5° radius apertures. Dots moved in random directions at a constant speed of 5°/sec (limited life-time of 83 ms plus an exponentially distributed jitter with a mean of 67 ms). At different times following the appearance of the *st* (0-250 ms in steps of 50 ms), one or two of the *RDKs* became coherent for 100 ms, moving in one of the four cardinal

directions (right-0°, up-90°, left-180° or down-270°). The direction was selected randomly and independently, such that when two signals were presented, their directions were either congruent (1/4 of the trials) or incongruent (3/4 of the trials). We drew the motion direction of each dot from a circular normal distribution (von Mises) with a certain degree of concentration κ (inverse of the variance of a normal distribution), around the main motion direction (as in Williams and Sekuler, 1984, except for the limited life-time of our random dots). κ was 0 (uniform distribution across all directions) while the RDKs moved randomly, and two values were chosen for the coherent motion signals: a lower level, *s1*, and higher level, *s2*. These two κ values were determined in threshold tasks separately for the fixation and saccade conditions and individually for each participant. *s1* produced 50% correct discrimination when presented in isolation at the cued location, whereas *s2*, also at the cued location, produced 87.5% correct discrimination (see *saccade and fixation threshold task*). In the main tasks, *s1* was always presented at the cued location, and when there were two signals, *s1* was at the cued location and *s2* always at an uncued location. Finally, in additional control trials during the saccade and fixation tasks, either *s1* or *s2* was presented alone at the cued location to check that the signal levels from the threshold trials produced the expected performance.

100 ms before the onset of the motion signal(s), we cued one location with a green Gaussian blob (5° radius, σ=~1.7°, 80% contrast, mean luminance of 30 cd/m^2) presented in the background of one randomly selected *RDK* (i.e., the RDK partially occluded the blob). SOAs between the *st* and the onset of the motion signal(s) were selected in order to maximize trials in which signal(s) ended before saccade onset (mean saccade latency across participants ± SEM: 385.6 ms ± 9.8, median saccade latency: 367.3 ± 12.1 ms). All stimuli except *ft* and *st* were erased upon online saccade detection (which lagged the offline mean latency by 18.6 ms ± 0.5, with all RDKs disappearing from the screen 41.4 ms ± 2.0 before saccade offset). Note that in this task, saccade latencies were relatively long reflecting both the difficulty of our dual-task (motion discrimination during saccade preparation) and the experimental settings: 1) the *ft* did not jump to the *st* location but rather was replaced by a black dot; 2) the saccade target appeared at an unpredictable one out of four possible locations at a relatively large eccentricity (11°); 3) the RDKs were composed of limited life-time dots, increasing the number of transients on the screen and therefore reducing saliency of the *st* onset.

At the end of each trial, participants reported the main direction of the motion signal presented at the cued location using the keyboard (using the right, up, left, or down arrow key), followed by a positive-feedback sound in case of a correct response. They were told to ignore any motion signals they could detect in the uncued locations, but interestingly they consistently reported that they rarely or never experienced coherent motion

signals anywhere other than at the cued location.

Around 83% of the trials contained two signals. In these trials, *s1* was presented at the cue location and *s2* was presented (with equal probability) at the remapping, the remapping control, the future retinotopic trace, or the future retinotopic trace control location (in a single trial, only two positions could be tested depending on the saccade direction and the cue position, see Figure 1a. Signal *s2* never appeared at the mirrored location of the cue relative to the saccade direction, i.e. below the cue in Figure 1a). Around 17% of the trials contained one signal only (*s1 alone* at the cue location, *s2 alone* at the cue, remapping, remapping control, future retinotopic trace, or future retinotopic trace control location) with each of these having the same probability. We had more two-signal trials than single-signal trials as we were particularly interested in comparing two-signal trials to one another (e.g., *s1+s2* at Remapping vs. *s1+s2* at Remapping control, see Figure 2b), which we consider the fairest comparison (as it rules out effects of probability summation). However as some previous studies of motion integration (e.g., Melcher and Morrone, 2003) used the comparison of single to two-signals trials, we did include also a fair proportion of single-signal trials.

Participants completed between 3153 and 3727 trials of the saccade task. Correct fixation as well as correct saccade landing within a 2.0° radius virtual circle centered respectively on the *ft* and *st* were checked online. We also ensured that saccade trajectories did not cross the *RDK* locations. Trials with fixation breaks or incorrect saccades were immediately discarded and repeated at the end of each block in a random order (each participant repeated a total of 81 to 655 trials across all sessions).

Fixation task

In the fixation task, participants were instructed to continuously keep their eyes on the central *ft*. This task was identical to the saccade task except that the *st* never appeared. Then after a random period of fixation (400-650 ms) one randomly selected location was cued and followed 100 ms later by the presentation of 1 or 2 concurrent motion signals. Moreover, to match the saccade task, all stimuli except the *ft* were blanked between 0 and 150 ms after the motion signals offset (time that approximately matched to the offset occurring in the saccade task). As in the saccade task, participants reported the main direction of the motion signal presented at the cued location at the end of each trial.

Around 57% of the trials contained two signals. In these trials, *s1* was presented at the cued location and *s2* was equally likely to be presented at another location rotated by ±90° or 180° from the cued patch. Around 43% of the trials contained one signal only (*s1 alone* at the cue location or *s2 alone* at the cue, or at a location ±90° or

180° relative to the cued patch) with each of these having the same probability. In the fixation task we did not expect any interaction when the two signals were presented at separate locations and we therefore increased the proportion of trials with only a single signal to get a more stable baseline for the comparison of single-signal and two-signals trials.

Participants completed between 648 and 704 trials of the fixation task. Correct fixation within a 2.0° radius virtual circle centered on the *ft* was checked online. Trials with fixation breaks were immediately discarded and repeated at the end of each block in a random order (each participant repeated a total of 0 to 56 trials).

Saccade and fixation threshold tasks.

To avoid possible effects of task learning and to adjust across participants the baseline performance for the presentation of both *s1* and *s2*, threshold task blocks preceded the main tasks (including blocks of the saccade and the fixation tasks) at the beginning of each experimental session. The saccade and fixation threshold tasks matched their respective main tasks (same stimuli, timing, and instructions) with the exception that in all trials only one motion signal was presented and always at the cued location. As in the main tasks, participants reported the main direction of the cued motion patch. Following a procedure of constant stimuli, the motion dots' concentration κ varied randomly across trials around the main motion direction from 0.1 (very dispersed) to 10 (very coherent) in nine linearly spaced steps.

Participants completed 2 blocks of 192 trials each during the saccade threshold task and 1 block of 192 trials each during the fixation threshold task. As in the main tasks, correct fixation and saccade execution (in saccade threshold task) were checked online and incorrect trials were repeated at the end of each threshold block in a random order.

For each participant and experimental session individually, we determined two threshold values: the κ leading to correct main motion direction discrimination in 50% (*s1*) and in 87.5% (*s2*) of the trials. To do so, we fitted cumulative Gaussian functions to performance gathered in the threshold blocks. The two threshold levels were used in the main tasks. The *s1* threshold level (50%) was chosen in order to allow both an increase or decrease of discrimination performance without reaching ceiling levels too easily. The second threshold level (87.5%) was chosen to be higher as it would be used in *s1+s2* trials at uncued locations where performance would be worse by definition. Moreover, in the saccade threshold task, thresholds were defined separately for the two possible cue locations—in between the *ft* and *st* or in the opposite direction of the saccade. We used these values in the corresponding conditions of the saccade task.

Data pre-processing

Before proceeding to the analysis of the behavioral results we scanned offline the recorded eye-position data. Saccades were detected based on their velocity distribution (Engbert and Mergenthaler, 2006) using a moving average over twenty subsequent eye position samples. Saccade onset was detected when the velocity exceeded the median of the moving average by 3 SDs for at least 20 ms. We included trials if a correct fixation was maintained within an 2.0° radius centered on *ft* (all tasks), if a correct saccade started at *ft* and landed within an 2.0° radius centered on *st* (saccade and saccade threshold tasks only) and if no blink occurred during the trial (all tasks).

In total, we included 22958 trials (88.4% of the online selected trials, 74.9% of all trials played) in the saccade task and 5178 trials (97.1% of the online selected trials, 97.0% of all trials played) in the fixation task.

Behavioral data analysis

For each participant, we computed performance (percentage of correct discrimination of the cued motion signal), across trials in which the coherent motion signals ended in the last 150 ms before the saccade onset in the saccade task and across all trials in the fixation task. We next transformed performance to sensitivity (d'): *d'* = *z*(hit rate) - *z*(false alarm rate), where hits were trials in which observers reported the correct signal direction (e.g., rightward response for rightward stimulus) and false alarms were trials in which observers reported that direction for any other signal direction (e.g., rightward response for leftward, upward, or downward stimulus). From these values we determined d'-ratios by dividing sensitivity in two conditions (e.g. with d'_{s1+s2} / $d'_{s1\ alone}$ for the comparison of sensitivity in two motion signal trials to sensitivity in single-signal trials and $d'_{s1+s2\ \text{"remapping"}}$ / $d'_{s1+s2\ \text{"remapping control"}}$ for the comparison of sensitivity between two motion signal trials at the remapping location). Figures 2, 3 and 5b show averages across participants of individual d'-ratios computed as explained above. Figure 5a shows the average across participants of individual sensitivity (d').

Next, we drew (with replacement) 10,000 bootstrap samples from the original d'-ratios and computed 10,000 samples. We determined the significance of d'-ratios by comparing the bootstrapped samples with a parity value (d'-ratio =1). To do so, we subtracted the means of the bootstrap distribution to the parity value and derived two-tailed p-values from the distribution of these differences. An equivalent procedure was used to test sensitivity (d') against chance level (d' = 0) for different control conditions (see Results and Figure 5a).

For incongruent *s1+s2* trials, we tested whether the observed proportion of incorrect reports of the cued direction differed from the expected number, assuming that the incorrect reports were randomly distributed across the different possible options. To do this we first computed the expected frequencies for each combination of incorrect report directions and *s2* directions (right-0°, up-90°, left-180° or down-270°). The expected frequency for choosing the *s2* direction was ~8.33% (e.g., reporting 'right' if *s2* was right) while it was ~5.56% for all other combinations (see Saarela and Landy, 2015, for the probability equations). We next tested the observed frequencies against these expected frequencies for the different directions of *s2* signals using the bootstrapping procedure as described above (see Results and Figure 4).

Results

— Figure 2 —

Our goal was to determine if pre-saccadic motion integration occurred between an attended location and its remapped location (i.e., the location on the retina that the cued location will occupy after an imminent saccade). To this end, we presented four random dot kinematograms (*RDKs*) and cued one of them with a salient attention-capturing color cue during saccade preparation (Figure 1). Following the onset of the cue and preceding the saccade, we presented a coherent motion signal (*s1*) for 100 ms at the cued location. In the *s1 alone* condition, we presented this signal alone. In the *s1+s2* condition, we presented *s1* simultaneously with a second coherent motion signal, *s2*, at one of four locations relative to the *s1*: at the remapped location of the cue (dark blue arrows in Figure 1a), at a remapping control location (light blue arrows), at the retinotopic location where the pre-saccadic cue will be after the saccade (i.e., in the direction of the saccade) which we call the future retinotopic trace of the cue (Golomb et al., 2008; Jonikaitis et al., 2013; Golomb et al., 2014), or at the future retinotopic trace control (light gray arrows). Furthermore, the motion direction of *s2* was either congruent or incongruent (respectively left and right panels in Figure 1a) with the direction of *s1*. At the end of each trial, participants reported the cardinal direction of the cued location (*s1*: up, down, left, or right). We measured the influence of *s2* on participants' ability to discriminate the direction of the cued motion signal, *s1*. We quantified motion integration as a motion sensitivity ratio (d'-ratio), by dividing a participant's sensitivity (d') to discriminate the cued signal *s1* in *s1+s2* trials by their sensitivity to *s1 alone* trials. A d'-ratio of 1 indicates the absence of

integration, whereas a d'-ratio larger than or smaller than 1 indicates respectively an increase or decrease in motion sensitivity in *s1+s2* trials.

We observed that motion sensitivity at the cue location *s1* increased by 32% (1.32 ± 0.14, $p = 0.008$, mean ± SEM) if a congruent motion signal *s2* was presented at the remapping location (Figure 2a). Interestingly, motion sensitivity remained unaffected when motion signals at the cue and remapping locations were incongruent (0.99 ± 0.11, $p = 0.89$). Moreover, the pre-saccadic integration of the motion signals was specific to the remapping location. It did not occur when a second signal *s2* was presented at the remapping control location (congruent: 1.12 ± 0.12, $p = 0.32$; incongruent: 0.96 ± 0.11, $p = 0.66$), the future retinotopic trace location (congruent: 1.07 ± 0.09, $p = 0.39$; incongruent: 1.00 ± 0.08, $p = 0.97$), or the future retinotopic trace control location (congruent: 1.12 ± 0.08, $p = 0.09$; incongruent: 1.00 ± 0.10, $p = 0.93$).

Next, we quantified the spatial specificity of motion integration by comparing *s1+s2* trials when *s2* was presented at the remapping versus the remapping control location. In this analysis, we compare two *s1+s2* conditions to each other, thus ruling out spatially unspecific probability summation effects (i.e., where participants could respond on the basis of two independent decisions made on each signal irrespective of its position, Watson, 1979; Meese and Williams, 2000). We found motion integration of 22% when *s2* was presented at the remapped location of the cue compared to when it was presented at its control location (Figure 2b, 1.22 ± 0.10, $p = 0.014$). Again, motion integration was limited to congruent motion directions and we did not observe motion integration when comparing future retinotopic trace location versus future retinotopic trace control location (0.97 > d'-ratios > 1.04; 0.67 > *p*s > 0.52).

We also computed motion integration with trials binned as a function of the motion offset relative to the saccade onset in a 100 ms wide moving window (corresponding to the motion signal duration) stepping in 50 ms steps for signal offset of -100 ms to 0 ms before the saccade onset (Figure 3). Most notably, in the last 50 ms preceding a saccade, a congruent motion signal (*s2*) at the remapped location of the cue was significantly integrated with the cued (*s1*) motion signal both when compared with discrimination of a single signal at the cued location (Figure 3a, signal ending between -150 ms and -50 ms before saccade: 1.33 ± 0.14, $p = 0.013$; signal ending between -100 ms and 0 ms before saccade: 1.38 ± 0.16, $p = 0.001$) and when compared with two signals at the cued and at the remapping control location (Figure 3b, signal ending between -150 ms and -50 ms before saccade: 1.30 ± 0.16, $p = 0.028$; signal ending between -100 ms and 0 ms before saccade: 1.32 ± 0.14, $p = 0.009$). These effects follow the typical time course of remapping; we only found significant motion integration if the motion signals ended within 50 ms of the saccade onset (Kusunoki and Goldberg, 2003; Rolfs et al., 2011;

Jonikaitis et al., 2013; Szinte et al., 2015) and not for motion signals presented earlier during saccade preparation (all *ps* > 0.08). Nevertheless, we decided to collapse trials in which motion signals ended in the last 150 ms before the saccade onset in all main analyses, to profit from the maximum power of our data set. Note that all conclusions presented above were confirmed when we restricted analyses to the last 50 ms preceding the saccade.

Together these results indicate that pre-saccadic motion integration is robust and highly spatially specific, because the cued motion signal *s1* was only integrated with a second motion signal *s2* presented at the location on the retina that the cue will occupy after the saccade (i.e., the cue's remapped location). Moreover, they suggest that motion integration before the saccade is feature-specific as we found enhancement of motion sensitivity only when we presented matching motion directions at the cued and remapped locations. Interestingly, when motion signal directions did not match, one might have expected that sensitivity would drop, as both directions would be integrated into a third one. Instead, we found that the presentation of an incongruent motion signal at the remapped location of the cue had no effect on the discrimination of the cued motion signal.

— Figure 3 —

Next, we verified that our observedmotion integration effects for congruent trials were not due to participants simply reporting the second signal's direction. To do this, we evaluated the trials in which participants did not correctly report the direction of the cued signal. Figure 4 shows the difference between the expected (assuming random report) and the observed number of incorrect direction reports for the four possible directions of *s2* for incongruent *s1+s2* trials. If participants simply reported the *s2* directions, the right diagonal would systematically show a lot higher-than-expected number of trials (Saarela and Landy, 2015). This did not happen (Figure 4a). Instead, we found that when an *s2* incongruent signal was presented at the remapped location of the cue, incorrect reports were randomly distributed across the different possible options (all *ps* > 0.06). Moreover, *s2* rarely influenced any of the responses (see colored boxes in Figure 4) suggesting that participants tended to ignore the *s2* signal when its direction was incongruent with the cued signal.

— Figure 4 —

We also presented *s2* alone at uncued locations in a fraction of the trials, without *s1* at the cued location (*s2 alone* condition). We found that motion discrimination was at chance level (Figure 5a) for *s2* presented alone at any uncued location: at the remapped location (d' = 0.15 ± 0.11, $p = 0.14$), at the future retinotopic trace location (d' = 0.09 ± 0.11; $p = 0.40$), and at their respective control locations (remapping control: d' = 0.06 ± 0.08, $p = 0.38$; future retinotopic trace control: d' = 0.16 ± 0.12, $p = 0.16$). The fact that the direction of *s2 alone* at the uncued location was not reportable at better than chance levels indicates that the contribution of *s2* when both signals are present must reflect pre-decision integration of the two signals.

Finally, we investigated whether our effects were contingent on saccade preparation or reflected motion integration biases present even in fixation conditions. In a control task, participants maintained fixation while judging the direction of motion in the cued patch. We did not find any significant motion integration (d'-ratio) between the cued signal and a signal presented at any other location (*s1+s2* compared to *s1 alone*), either for congruent or for incongruent trials (Figure 5b, all *ps* > 0.12). In particular and in contrast with the saccade task, we did not find any marked increase of sensitivity when we presented a congruent *s2* at a position which would have corresponded to the remapping location in the saccade task (location 90 degrees counter-clockwise from *s1*: 1.00 ± 0.14, $p = 1.00$).

Importantly, for both the fixation and the saccade tasks reported above, we presented the signal(s) when participants' gaze was resting in the center of the display. Although the execution of the saccades introduced a small additional delay between the presentation of the motion signals and the participants' report of the cued direction, the crucial difference between the two tasks was the saccade preparation and execution.

— Figure 5 —

Discussion

We demonstrated that two motion signals are partially integrated when they are presented before a saccade and occur at two specific retinotopic locations: the location of an attended object and the location that the same object will occupy after the saccade (remapping location). This pre-saccadic motion integration was spatially specific (it occurred only between these two locations), feature-specific (it occurred only for matching features), and contingent on the preparation and execution of a saccade (it was not found for the fixation task). As described below, these effects cannot be explained by probability summation or by visual priming. They

constitute the first evidence of a mechanism that integrates matching visual features across different positions in space, when these features are located at the two retinotopic locations that an attended object occupies across a saccade. While others showed previously that some visual features can be integrated over different positions in space either after (Golomb et al., 2014) or across a saccade (Melcher and Morrone, 2003; but see Morris et al., 2010; Oostwoud Wijdenes et al., 2015; Ganmor et al., 2015; Wolf and Schütz, 2015), our study is the first to show motion integration over two spatially and retinotopically distinct positions implicated in the pre-saccadic predictions of remapping.

We suggest that the motion direction at the cued location, which is detectable on its own at significantly above-chance levels, acts as a filter or prior, selecting the signal from the remapped location when it matches the signal at the cued location and integrating the two, improving detection in this context only. The signal at the remapped location on its own cannot be detected above chance levels and it is only in combination with the cued signal, when the two match, that it has an influence. This bi-local, feature-gated integration is functionally plausible since the same object will fill these two locations with matching features before and after an eye movement. Given the imperfect timing in switching selection from the pre- to the post-saccadic location (Kusunoki and Goldberg, 2003, Nummela and Krauzlis, 2011; Jonikaitis et al., 2013; Rolfs, 2015), it is reasonable that the sampling from the two may overlap in time. It would then be useful to limit the concurrent sampling to matching features as this avoids picking up features from irrelevant (i.e., incongruent) items that happen to be at the remapped location.

Our observation that, prior to a saccade, the visual system samples the retinotopic location an attended object will occupy after a saccade is in line with earlier work reporting remapping of spatial attention (Rolfs et al., 2011; Jonikaitis et al., 2013; Szinte et al., 2015). In particular, it has been proposed that spatial attention shifts towards retinotopic post-saccadic target locations even before the onset of an eye movement (Cavanagh et al., 2010a). These findings can be linked to electrophysiological studies (see Rolfs & Szinte, 2016, for potential mechanisms) showing that neurons activate predictively if a saccade will bring a target into their receptive fields (Goldberg and Bruce, 1990; Duhamel et al., 1992; Walker et al., 1995; Umeno and Goldberg, 1997; Sommer and Wurtz, 2006). These studies proposed that the visual system uses an efference copy of the forthcoming saccade (Holst and Mittelstaedt, 1950; Sperry, 1950; Sommer and Wurtz, 2002) to predict the future locations of stimuli of interest. This "remapping" occurs for salient and behaviorally relevant objects (Gottlieb et al., 1998; Kusunoki et al., 2000; Berman and Colby, 2009) and is well-suited to contribute to the trans-saccadic processing

of attended object locations (Wurtz, 2008; Cavanagh et al., 2010a; Jonikaitis et al., 2013; Rolfs, 2015; Yao et al., 2016). Our current findings constitute further evidence for the existence of processes sampling information at attended and remapped locations.

Although the remapping process is consistent with our results, we must also consider the possible effects of other consequences of saccade preparation, specifically, the biased spatial processing surrounding the saccade target itself (Moore et al., 1998; Tolias et al., 2001; Zirnsak et al., 2014). Indeed, large biases in sensory processing at the saccade target location are evident during saccade preparation resulting in improved detection of visual information (Deubel and Schneider, 1996; Baldauf and Deubel, 2008; Rolfs et al., 2011), increased perceived contrast (Rolfs and Carrasco, 2012), and reduced visual crowding (Harrison and Bex, 2014). If our observed motion integration were due to such biased processing around the target of the saccade, or due to the allocation of attention towards locations close to the saccade target (Zirnsak and Moore, 2014), we might have observed motion integration effects at those two locations ("future retinotopic trace" and its control, Figure 1A). Instead, we observed integration with signals at the location furthest away from the saccade target ("remapping", Figure 1A), consistent with a recent physiological report (Neupane et al., 2016).

The link between remapping and the pre-saccadic shift of attention we observe here and in previous studies (Rolfs et al., 2011; Jonikaitis et al., 2013; Szinte et al., 2015) relies on the similarities in both the timing and spatial characteristics. Nevertheless, a debate exists on whether single-cell receptive field shifts could really support the remapping of attention we found. In particular, different authors have pointed out that the size of the RFs in remapping areas is too big to account for the precision of observed attentional shifts (Mayo and Sommer, 2010; Zirnsak and Moore, 2014). In a previous response to this point, it was suggested that localization cannot be a function of individual receptive fields but rather of populations (Cavanagh et al., 2010b). Here we show spatially specific effects that again could only be explained by a profile of activity across many responding units, given the large size of RFs in areas known to be involved in remapping.

We observed integration of motion signals presented at the attended and its remapped location only if they had congruent directions. Although these effects are feature-specific, they differ markedly from earlier reports of feature-based attention that operates throughout the whole visual field (Martinez-Trujillo and Treue, 2004; Melcher et al., 2005; Maunsell and Treue, 2006; Wegener et al., 2008; Liu and Mance, 2011; White and Carrasco, 2011; Jonikaitis and Theeuwes, 2013). Our effects instead rely on a feature-specific mechanism that is also spatially localized. One earlier study found that motion signals are integrated across eye movements,

when they occurred at the same spatial but different retinotopic locations, separated in time (Melcher and Morrone, 2003). In contrast to this earlier report, we investigated the integration that occurs between two locations presented *simultaneously* and *before* the onset of the saccade. In addition, we addressed two issues concerning integration that may have been problematic in the Melcher and Morrone (2003) study. First, Morris et al. (2010) showed that when comparing single- and two-signal trials to evaluate integration in the two-signal case, temporal uncertainty of the motion signal onsets can cause the sensitivity to the single motion signal to be underestimated. This, in turn, leads to an overestimation of signal integration when the single and two-signal trials are compared. To deal with this in our study, the spatial cue exactly predicted the onset time of the simultaneously presented motion signals, greatly reducing temporal uncertainty. Second, as Morris et al. (2010) noted, a performance improvement with two signals that may appear to be evidence of integration can often be explained by the probability summation of two independent detection events (Watson, 1979; Meese and Williams, 2000). To determine how probability summation might explain our results, consider first that we found a performance improvement only when the same signal was present at the cue and its remapped location just before the execution of a saccade. In order to consider a probability summation stage that pools independent detections, we would therefore have to limit this pooling to only the cued and remapped locations and only in the saccade task. But in this case, detections would be pooled from the cue and its remapped location before a saccade, when either congruent or incongruent signals were shown. This would improve (congruent) and degrade (incongruent) the performance, respectively. Instead, we found significant improvement only for congruent signals presented at these locations, while incongruent signals were simply ignored as shown both by the analysis of incorrect trials (Figure 4) and of trials in which a signal was presented alone at the remapped location of the cue (Figure 5). These results argue against probability summation as a possible mechanism for our observed spatially and feature specific integration effects. Moreover, as the two signals were presented simultaneously, we can also rule out priming and serial dependence as possible contributors to our effects (Maljkovic and Nakayama, 1994; 1996; Fischer and Whitney, 2014).

Previous studies have shown pre-saccadic interactions for visual features other than motion. First, strong interference effects on an attended target were reported if its remapped location was either filled with a mask or flanked by distractors prior to the saccade (Hunt and Cavanagh, 2011; Harrison et al., 2013). Interestingly, we did not observe such masking effects here (no decrease of performance when incongruent signals were at the remapped location), probably because we used faint and below threshold stimuli at the remapping location (the

direction of *s2* alone was un-reportable) rather than the high contrast stimuli used in the previous studies at or around the remapped location. Second, studies of another form of pre-saccadic feature transfer found that orientation adaptation transferred from the fixation to the saccade target location prior to the execution of the eye movement (Melcher, 2007; Zirnsak et al., 2011). These positions are analogous to the "cue" and “future retinotopic trace” locations in our stimulus layout (ours were offset into the periphery) where we never found any significant integration. Additionally, as the location tested in that study was the saccade target location, these results are hard to interpret given that saccade preparation strongly biases saccade target processing (Deubel and Schneider, 1996; Baldauf and Deubel, 2008; Rolfs and Carrasco, 2012; Harrison and Bex, 2014). Finally, a recent single cell recording study shows shape selectivity in remapping LIP neurons units which remap both spatial and shape information (Subramanian and Colby, 2014). The spatial and feature specificity of the motion integration that we show here suggests that our effects may rely on such cells.

Physiological studies have also reported that when a target is presented just before a saccade, it activates cells with receptive fields at both the current retinal location and the remapped location of the target before the saccade (Kusunoki and Goldberg, 2003). Our results suggest that these two populations of cells are linked together to feed information into a single, object-specific representation. However, the integration only occurs when the remapped location has the same features as the target location as they would if they originated from the same object across the saccade. This suggests that the features sampled from the target location serve as strong priors for evaluation of signals from the remapped location (e.g., a Bayesian biased integration). Such a mechanism could explain the fact that incongruent signals presented at the cue and its remapped location were largely ignored (Figure 4). This predictive spatial and feature-based selection may also be related to the earlier observations that the visual system constructs object-centered, spatial representations across eye movements (Boi et al., 2011) as these would be facilitated by the pre-saccadic selection of object features from their expected post-saccadic location (Cavanagh et al., 2010a; Lisi et al., 2015).

We consider that the occurrence of these effects even before the saccade reflects the imperfect timing of the predictions that keep track of attended object across saccades (see also Nummela and Krauzlis, 2011; Jonikaitis et al., 2013; Rolfs, 2015). In addition, given the inevitable delays and slow speed in implementing the remapping, it is plausible that it has to begin before the saccade for it to be in place when it is needed, as the saccade lands. In any case, our results show that the effect of this premature selection would not be detrimental to every-day vision as the integration that occurs would be limited to situations in which the two locations contain the same

features.

Altogether, our results show that before saccades, motion information is sampled and integrated from both the current location and the predicted post-saccadic retinotopic location of a salient and behaviorally relevant object. These results provide the first evidence for a mechanism integrating features across non-overlapping locations in space, provided they are expected to come from the same object before and after an eye movement.

Authors contributions

M.S., D.J., M.R., P.C. and H.D designed the experiment. M.S. performed the experiments and analyzed the data. M.S., D.J., M.R., P.C. and H.D discussed the results and wrote the paper.

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Disclosures

The authors declare no competing financial interests.

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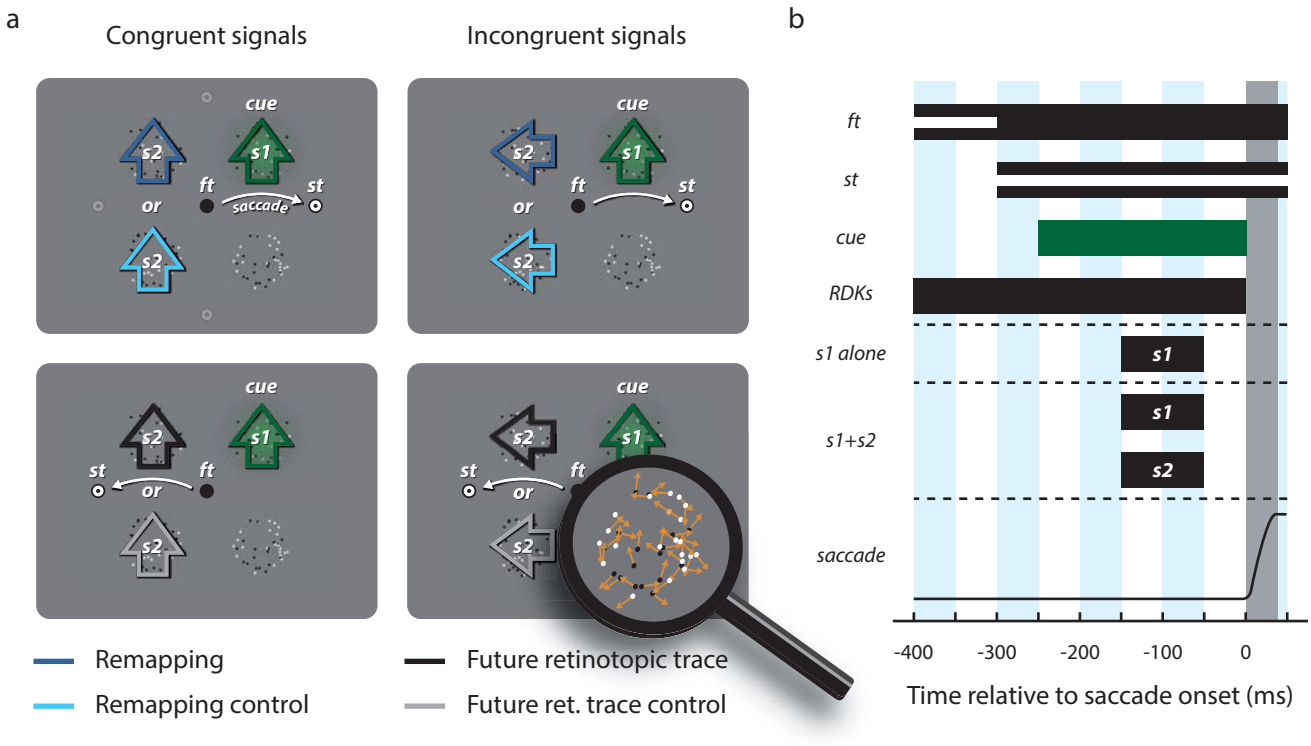
Figure 1. Experimental procedure. **a.** Display setup and main conditions. Participants were instructed to saccade from the fixation target (*ft*) to the saccade target (*st*) that appeared at one of four possible cardinal directions (during a trial a single *st* was shown, light-grey targets are here for illustration). At four locations, equidistant from *ft* and the potential saccade targets, we presented four random dot kinematograms (RDKs) showing incoherent motion (see zoom). At different times before saccade onset, motion briefly became coherent either at the cued location only (using signal level *s1*), or simultaneously at the cued location (*s1*) and another location (using signal level *s2*). 100 ms before the onset of the motion signal(s), one of the *RDKs* was cued by a green blob (*cue*). At the end of each trial, participants reported the motion direction at the cued location. Relative to the location of the cue and to the saccade direction, *s2* appeared either at the remapping location of the cue (dark blue arrow), the future retinotopic trace location of the cue (black arrow) or at their respective control locations mirrored relative to the saccade vector (light blue and grey arrows). Moreover, as directions of signals were selected randomly and independently, *s1* and *s2* could either have congruent (left panels) or incongruent (right panels) directions. **b.** Stimulus timing. At different times after a random fixation duration, the bull's eye at *ft* (see white lines) was replaced by a black dot together with the onset of the bull's eye at the *st*. At different times following the appearance of the *st* (0-250 ms in steps of 50 ms), one (*s1 alone*) or two (*s1 + s2*) *RDKs* became coherent simultaneously for 100 ms. 100 ms before the motion signal(s) one location was cued by a green blob. Everything except *ft* and *st* was erased upon online saccade detection.

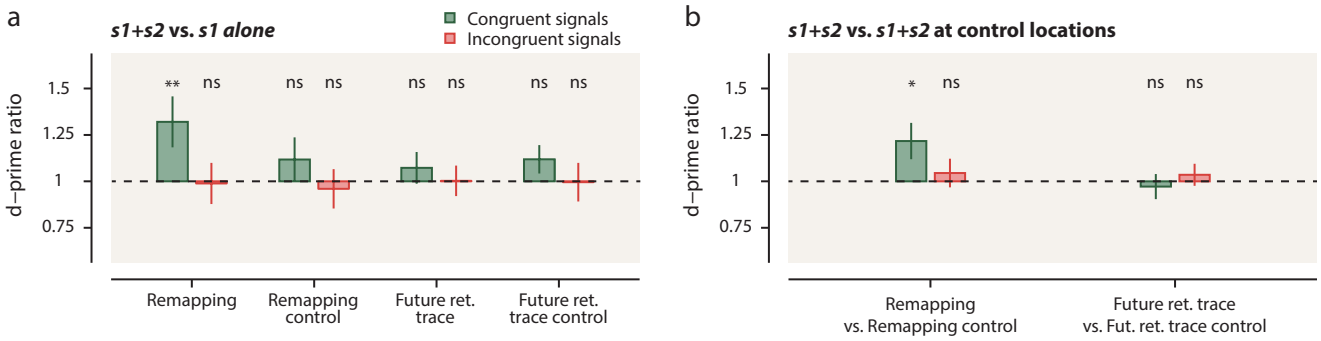
Figure 2. Motion integration. **a.** Motion sensitivity gain (d'-ratio) for congruent (green) and incongruent (red) signal directions. Ratios were computed for each participant by dividing sensitivity (d') in trials with two signals (e.g., *s1* at the cue and *s2* at remapping) by the sensitivity in single signal trials (see Material and methods). **b.** Motion sensitivity gain computed as ratio between trials with *s1* and *s2* presented together at the relevant location ('remapping' or 'future retinotopic trace' of the cue) and *s1* and *s2* at their control locations ('remapping control' or 'future retinotopic trace control'). Error bars show SEM, asterisks show statistical significance (*: $p < 0.05$; **: $p < 0.01$; ns: non significant).

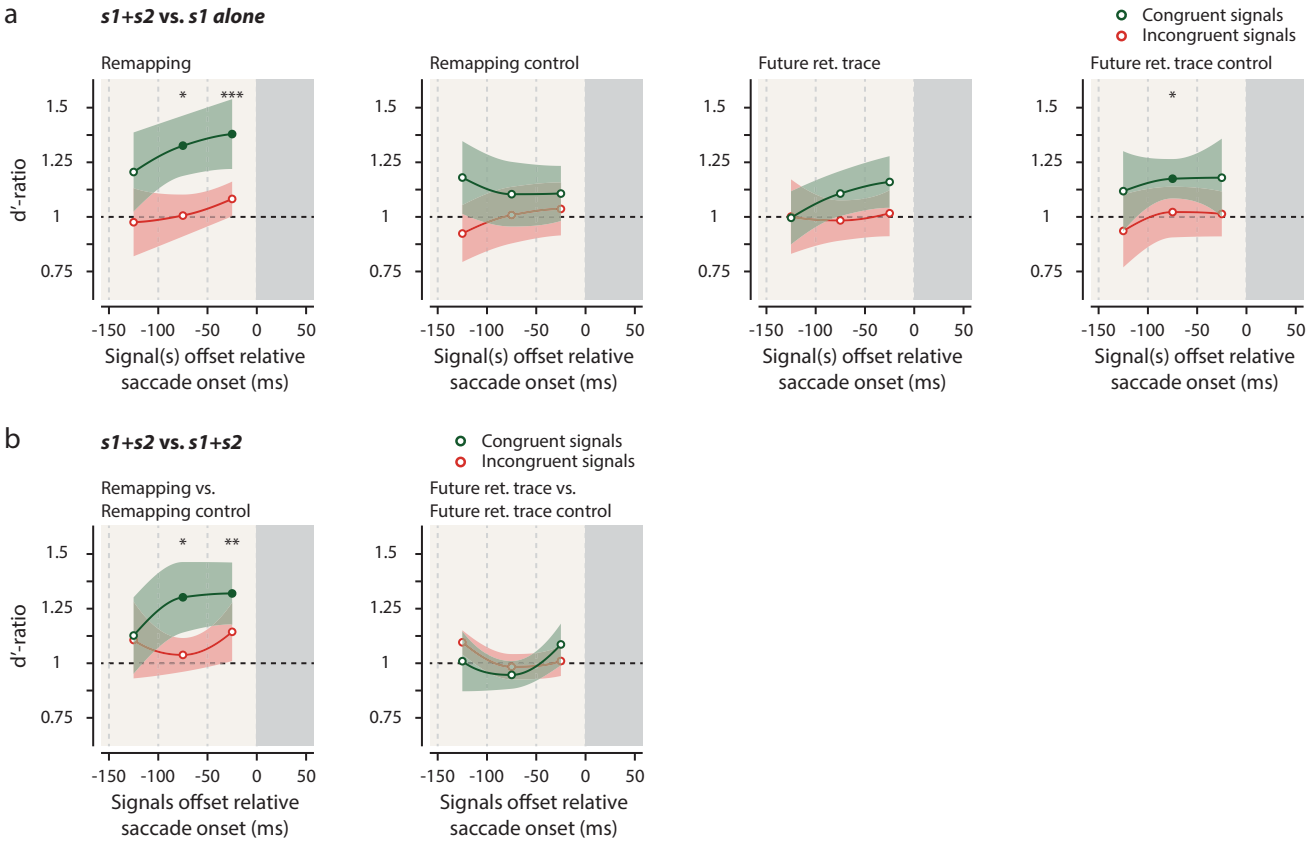
Figure 3. Motion integration relative to saccade onset **a.** Motion sensitivity gain (d'-ratio) computed by dividing sensitivity (d') in trials with two signals by the sensitivity in single signal trials for congruent (green) and incongruent (red) signal directions and for different signal offset times relative to the onset of the saccade (gray bar). **b.** Motion sensitivity gain computed as ratio between trials with *s1* and *s2* presented together at the relevant location ('remapping' or 'future retinotopic trace' of the cue) and *s1* and *s2* at their control locations ('remapping control' or 'future retinotopic trace control') for congruent (green) and incongruent (red) signal directions and for different signal offset times relative to the onset of the saccade. Error bands show SEM, lines show cubic spline interpolation between the data points, filled dots and asterisks show statistical significance (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

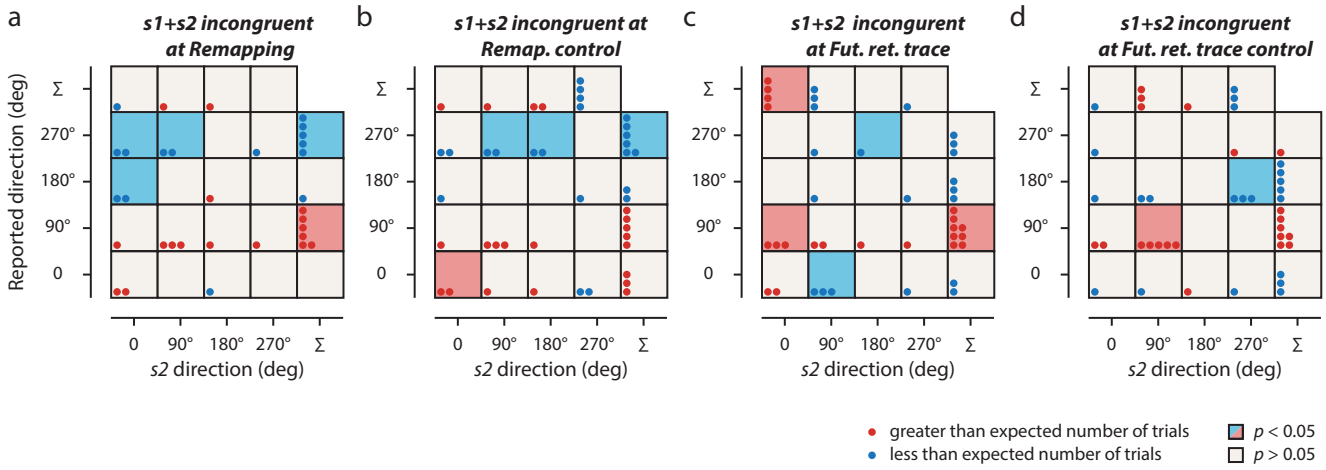
Figure 4. Analysis of incorrect report trials for incongruent trials. Cells display dots indicating the number of trials above (red) or below (blue) the expected number for each combination of reported direction and *s2* direction (assuming randomly allocated incorrect reports). These differences are computed across participants and rounded to the nearest integer for incongruent signals presented at the remapping (a), the future retinotopic trace location (c) and their respective control locations (b and d). The top row and the right column show the marginal distributions. Colored boxes highlight statistical significance (red or blue boxes: $p < 0.05$, beige boxes: $p > 0.05$).

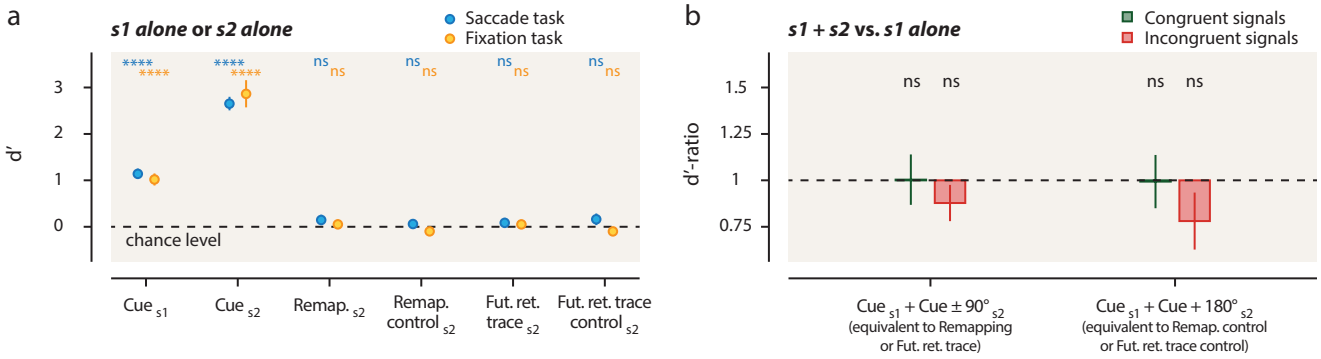
Figure 5. Single-signal and fixation control trials. **a.** Motion sensitivity (d') for the presentation of a single signal (*s1* alone or *s2 alone*) at either the cue, the remapping, the remapping control, the future retinotopic trace and the future retinotopic trace control locations in both the saccade (blue dots) and the fixation task (orange dots). Note that *s2* was presented at a higher signal level to compensate for reduced performance at the uncued locations in the *s1+s2* trials of the main tasks (see Material and methods) but it was also tested again at the cued location to verify the threshold settings. For the fixation task, results are displayed for signals presented at spatial positions equivalent to those in the saccade task, now defined relative to the cue location as without the saccade there is no true "Remapping" or "Future retinotopic trace" locations. Under these conditions, these remapping and the future retinotopic trace locations correspond to signal presented at ±90° of rotation from the cue location, the remapping control and future retinotopic trace control locations then correspond to signal presented at 180° of rotation from the cue location. **b.** Motion sensitivity gain (d'-ratio) in the fixation task with two against one signal trials, computed for congruent (green) and incongruent (red) signal directions. Ratios are computed by dividing sensitivity (d') in trials with two signals (e.g., *s1* at the cue and *s2* presented at ±90° from the cue location) by the sensitivity in single signal trials. Error bars show SEM, asterisks show statistical significance (****: $p < 0.0001$; ns: non significant).


a
Congruent signals
Incongruent signals
cue
s1
s2
ft
st
or
saccade
Remapping
Remapping control
Future retinotopic trace
Future ret. trace control
b
ft
st
cue
RDKs
s1 alone
s1
s1+s2
s1
s2
saccade
-400
-300
-200
-100
0
Time relative to saccade onset (ms)


a
s1+s2 vs. s1 alone
Congruent signals
Incongruent signals
d−prime ratio
1.5
1.25
1
0.75
** ns ns ns ns ns ns ns
Remapping
Remapping control
Future ret. trace
Future ret. trace control
b
s1+s2 vs. s1+s2 at control locations
d−prime ratio
1.5
1.25
1
0.75
* ns ns ns
Remapping vs. Remapping control
Future ret. trace vs. Fut. ret. trace control


a
s1+s2 vs. s1 alone
Congruent signals
Incongruent signals
Remapping
Remapping control
Future ret. trace
Future ret. trace control
d'-ratio
1.5
1.25
1
0.75
*
***
*
-150 -100 -50 0 50
Signal(s) offset relative saccade onset (ms)
b
s1+s2 vs. s1+s2
Congruent signals
Incongruent signals
Remapping vs. Remapping control
Future ret. trace vs. Future ret. trace control
*
**
Signals offset relative saccade onset (ms)


a
s1+s2 incongruent at Remapping
b
s1+s2 incongruent at Remap. control
c
s1+s2 incongurent at Fut. ret. trace
d
s1+s2 incongruent at Fut. ret. trace control
Reported direction (deg)
Σ
270°
180°
90°
0
0
90°
180°
270°
Σ
s2 direction (deg)
greater than expected number of trials
less than expected number of trials
p < 0.05
p > 0.05


a
s1 alone or s2 alone
Saccade task
Fixation task
d'
3
2
1
0
chance level
**** ****
**** ****
ns ns
ns ns
ns ns
ns ns
Cue s1
Cue s2
Remap. s2
Remap. control s2
Fut. ret. trace s2
Fut. ret. trace control s2
b
s1 + s2 vs. s1 alone
Congruent signals
Incongruent signals
d'-ratio
1.5
1.25
1
0.75
ns ns
ns ns
Cue s1 + Cue ± 90° s2
(equivalent to Remapping
or Fut. ret. trace)
Cue s1 + Cue + 180° s2
(equivalent to Remap. control
or Fut. ret. trace control)