Saccadic selection in visual working memory is robust across the visual field and linked to saccade metrics: Evidence from 9 experiments and more than 100,000 trials

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Running title: Saccadic selection in memory across the visual field.

Author note:

The data and code are available through the Open Science Framework at https://osf.io/6y9c5/?view_only=588388e4d3c2488d9cf035706b7e86bc.

Part of the analyses, results and conclusions have been presented in a talk at the European Conference on Eye Movements (ECEM) in 2022.

Acknowledgments:

This research was supported by a DFG research grant to S.O. and M.R. (OH 274/2-2 and RO 3579/6-2) as well as funding from the DFG's Heisenberg program (RO3579/8-1 and RO3579/12-1) and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant No 865715) to M.R.

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Abstract

Visual working memory and actions are closely intertwined. Memory can guide our actions, but actions also impact what we remember. Even during memory maintenance, actions such as saccadic eye movements select content in visual working memory, resulting in better memory at locations that are congruent with the action goal as compared to incongruent locations. Here, we further substantiate the claim that saccadic eye movements are fundamentally linked to visual working memory by analyzing a large data set (>100k trials) of nine experiments (eight of them previously published). Using Bayesian hierarchical models, we demonstrate robust saccadic selection across the full range of probed saccade directions, manifesting as better memory performance at the saccade goal irrespective of its location in the visual field. By inspecting individual differences in saccadic selection, we show that saccadic selection was highly prevalent in the population. Moreover, both saccade metrics and visual working memory performance varied considerably across the visual field. Crucially, however, both idiosyncratic and systematic visual field anisotropies were not correlated between visual working memory and the oculomotor system, suggesting that they resulted from different sources (e.g., rely on separate spatial maps). In stark contrast, trial-by-trial variations in saccade metrics were strongly associated with memory performance: At any given location, shorter saccade latencies and more accurate saccades were associated with better memory performance, undergirding a robust link between action selection and visual memory.

Keywords: visual working memory; eye movements; saccades; attention; selection

Public significance statement

When we try to memorize what we have just seen, the places we look at will determine what we will remember and what we will forget: whatever had been visible at the goal of your eye movement will most likely be stored in memory. Here, we demonstrate that this selection mechanism in visual memory is highly prevalent in healthy human observers and robust across eye movement directions. Moreover, fast and accurate saccades as opposed to slow inaccurate ones are associated with an improved ability to remember a visual stimulus on a single trial, underscoring the immediate and intertwined relationship between actions and visual memory.

Introduction

Perception and action often rely on information that has already disappeared from view. For example, a chef who is cooking an elaborate meal consisting of several courses must keep track of a lot of information at once. While standing in front of pots and pans containing the ingredients for different courses, the chef can draw on their visual memory to determine which pot contains which dish and can thereby decide which lid to lift when more ingredients are needed. To keep this information in mind, the chef uses a capacity-limited visual working memory (Cowan, 2001; Luck & Vogel, 1997, 2013; Marois & Ivanoff, 2005; Pashler, 1988). Recent conceptual frameworks emphasize the bidirectional links between visual working memory and actions (Heuer et al., 2020; Myers et al., 2017; Olivers & Roelfsema, 2020; Van der Stigchel & Hollingworth, 2018; van Ede, 2020; van Ede & Nobre, 2023). From this perspective, visual working memory is more than a passive sensory storage system—visual memory provides relevant information for future actions and actions in turn determine what is maintained in memory.

Saccadic eye movements constitute an ideal testbed for studying the interactions of memory and actions in the human mind. With about 200,000 saccades per day, they are the most frequent action that humans generate. Indeed, there are multifaceted reciprocal influences of eye movements and visual memory (for review see Aagten-Murphy & Bays, 2018; Van der Stigchel & Hollingworth, 2018). Memory informs saccadic motor control (Bahle et al., 2018; Beck et al., 2012; Foerster & Schneider, 2020; Hollingworth et al., 2008; Hollingworth & Luck, 2009; Ohl et al., 2013; Olivers et al., 2006; for fixational eye movements as markers of visual memory see Draschkow et al., 2022; van Ede et al., 2019, 2020; van Loon et al., 2017) and saccades substantially influence what we remember (Bays & Husain, 2008; Henderson & Hollingworth, 2003; Irwin, 1991; Ohl & Rolfs, 2017, 2018, 2020; Schut et al., 2017; Shao et al., 2010; Tas et al., 2016; Udale et al., 2022).

In the present study, we determined how closely visual working memory and actions are intertwined by inspecting saccade-based selection of content currently maintained in visual working memory (Ohl & Rolfs, 2017, 2018, 2020). Previous studies have demonstrated that saccades constitute an effective selection mechanism during memory maintenance by prioritizing memory representations at locations congruent with saccade goals (Hanning et al., 2016; Hanning & Deubel, 2018; Ohl & Rolfs, 2017, 2018, 2020; for review see Heuer et al., 2020). Employing a dual-task protocol, observers in these studies had to maintain a stimulus feature in memory while programming an eye movement during memory maintenance (**Figure 1a**). Although the motor task was independent of the memory task, saccade programming resulted in better memory performance for stimuli presented at the saccade goal location. Based on this finding and the prevalence of saccades in natural vision, we have argued that saccadic eye movements constitute an ecologically valid and fundamental selection mechanism in visual working memory (Ohl & Rolfs, 2017). This saccadic selection occurred even when only little information had to be maintained (e.g., for a set size as small as two stimuli; Ohl & Rolfs, 2020). Most strikingly, saccades automatically selected content in memory even when the saccade target location is least likely to be probed in the memory test (Ohl & Rolfs, 2017, 2020).

Here, we set out to assess four predictions that will allow us to determine the robustness, the generalizability, and the level of coupling between visual memory and actions. First, we predict that saccadic selection in visual working memory should be evident on an individual-observer level. More specifically, saccadic selection should not only be present in a subgroup of observers but instead manifest across the entire population of healthy observers in varying degrees.

Second, saccades should select memory representations at their target irrespective of the direction of the saccade, that is, the location of the eye movement target with respect to the current fixation location. The generalizability of saccadic selection across saccade directions is critical for the assumption that saccades indeed play a major role for prioritizing content in visual working memory—particularly in the absence of other cues that may guide top-down selection. If saccadic selection is only observed for a particular saccade direction (e.g., horizontal saccades), this would constitute a major challenge for the postulated fundamental role of eye movements as a selection mechanism in memory. Indeed, the observation that saccades enhance contrast sensitivity across the visual field apart from the upper vertical meridian (Hanning et al., 2022) already provides such a challenge for perceptual processes. For instance, such findings call the assumed pivotal role of pre-saccadic attention shifts in establishing visual continuity across saccades into question or at least emphasize the need to provide a more nuanced account that addresses these variations across the visual field. Here, we will assess whether similar constraints need to be considered for saccadic selection in visual working memory.

Third, and complementary to the first two predictions regarding the robustness and generalizability of saccadic selection, we will inspect whether spatial variations in visual memory performance (i.e., differences in memory performance across the visual field) are associated with spatial variations in oculomotor behavior. Assessing how spatial asymmetries underlying visual memory and saccade generation relate to each other allows us to determine whether the interaction of visual memory and saccades occurs in a shared topology (i.e., a common map) or between separate maps. In its most extreme form, a shared topology could be implemented as a spatial map with neurons that are involved in both saccade programming and the maintenance of visual features in memory. In this scenario, the same spatial distortions of that map should be present in both visual memory performance and the generation of saccadic eye movements. Alternatively, the links between memory and saccades could be established through communication between separate maps underlying visual memory on the one side and eye movements on the other. These maps could either be independent from each other or attuned to each other (e.g., one map is adapting the constraints set by the other map). Taking the perspective of a strong coupling between actions and memory, we predict that spatial variations in visual working memory and the oculomotor system covary. Our analyses will test this critical question regarding the architecture of active visual memory. Previous investigations of spatial variations in visual crowding and variations in the landing position of saccadic eye movements, for instance, identified a common topology of vision and the oculomotor system (Greenwood et al., 2017). Here, we predict that oculomotor-related variations across the visual field are also associated with variations in visual working memory performance across the visual field.

Fourth, if action execution and memory performance are closely intertwined, then the way we produce a particular action should be associated with memory performance on a single-trial level. Saccade metrics (i.e., saccade latency, saccade amplitude, saccade landing error, and saccadic peak velocity) characterize the specific characteristics of a saccade generated in a trial. Specifically, saccade latency reflects the time between onset of a go signal (in our tasks, the movement cue) and the onset of the saccade. The inspection of saccade latency is a sensitive tool to study the visuomotor processing underlying saccadic decisions including movement preparation and movement initiation (Stanford et al., 2010). Moreover, while saccades consistently shift gaze to a given target location in the visual field, the underlying vector of the saccade will vary from trial to trial, resulting in a distribution of saccadic end points near the target location. We will quantify this variability of saccade vectors using two metrics, the saccade amplitude (i.e., the Euclidean distance between the starting and end point of the saccade) and the saccadic error (i.e., the Euclidean distance between the end point of the saccade and the center of the target location). Although, saccadic eye movements follow stereotypical kinematics, there is considerable variation in the velocity profile (and, hence, the duration) of the movement. We capture this aspect of movement execution using the peak velocity of a saccade. Note that the four different saccade metrics used for our analyses are not orthogonal dimensions. Indeed, the peak velocity and amplitude of the eye movement are lawfully related (i.e., the main sequence; Bahill et al., 1975) such that larger eye movements result in higher peak velocities. Moreover, saccade amplitude and landing error both capture information about the saccadic landing site relative to the saccade target location. Nevertheless, the inspection of saccade metrics captures single-trial eye movement characteristics and allows us to quantify which metric in particular is associated with memory performance. Identifying the consequences of actions for visual memory maintenance on a single-trial level is informative about the degree of coupling between visual memory and actions. Based on a recently developed taxonomy (Rolfs & Schweitzer, 2022), we distinguish three types of sensory consequences of actions — intended, intrinsic, and incidental — for the first two of which we have specific predictions.

Directing the eyes (and hence the retina) to a new location in the external world constitutes an intended consequence of eye movements (Rolfs & Schweitzer, 2022). Any deviation from the intended consequence (e.g., an inaccurate action as captured by the saccade's amplitude and the saccade's landing error) may therefore affect subsequent visual (memory) processing. Consequently, we predict better memory performance for trials in which the eyes land close to the location of the remembered item (i.e., saccades with a small landing error) as compared to memory performance for trials with less accurate saccades.

Intrinsic consequences of actions represent internal routines that affect visual processing during the preparation and execution of a movement (e.g., the automatic shifts of attention before saccades). Thus, any variations in the action-based internal process that also affect memory performance would demonstrate how visual memory is coupled to action through the action's intrinsic consequences (Rolfs & Schweitzer, 2022). Indeed, visual performance for stimuli presented at the saccade target location shortly before saccade onset is better before short-latency as compared to long-latency saccades (Jonikaitis & Deubel, 2011; Jonikaitis & Theeuwes, 2013; Jonikaitis, Klapetek, & Deubel, 2017; Yan, Zhaoping & Li, 2018). These short-latency saccades appear to reflect instances of optimal target selection and minimal noise during visuomotor processing with concurrent benefits for processing of the visual information at the saccade target location. A similar argument can be made for saccadic peak velocity, which together with saccade latency determines an action's movement vigor (Shadmehr & Ahmed, 2020). While peak velocity constitutes an important parameter for characterizing an action, it remains to be explored how it relates to memory performance. If vigorous (short-latency and high-speed) movements reflect optimal movement preparation, they may also entail more efficient visual processing of pre-saccadic information (Rolfs & Ohl, 2021). Accordingly, we predict that saccades with shorter latencies and higher peak velocities are associated with better memory performance than saccades with longer latencies and lower peak velocities. In summary, investigations of covariations between visual memory performance and saccade metrics, both across trials and on a single-trial level, speak to the degree of coupling between perception and action by linking an action's intended and intrinsic consequences for visual processing (Rolfs & Schweitzer, 2022). We hope to glean such insights into the architecture of visual memory and saccadic eye movements.

All of these predictions are testable but require a large number of observers and a large number of trials per observer in order to obtain robust individual estimates. Moreover, many trials are required to establish the degree to which variations in visual working memory and saccade metrics are linked. We aimed to accomplish these objectives by compiling a large data set with more than 100k trials obtained from eight previously published and one unpublished experiment. In all experiments, observers memorized a configuration of orientations and generated a saccade to one of eight identically marked locations during memory maintenance. In the unpublished experiment, we asked observers to generate an additional, second saccade back to the initial fixation location (i.e., a return saccade). This allowed us to control whether gaze location during the presentation of the memory probe would affect saccadic selection in memory.

Although we predict that saccadic selection in visual working memory is a robust mechanism, it will certainly vary between observers. Moreover, there are differences between the nine experiments: while involving highly similar tasks, instructions, and spatial layouts, they do vary in the specific experimental conditions (e.g., memory load, movement cue delay, masking; **Figure 1b**). We accounted for these differences in observers and experiments by using Bayesian hierarchical models (for a tutorial see Rouder & Lu, 2005) that included observers and experiments as group-level effects (i.e., as random effects), allowing us to determine the variance components and correlations for all variables of interest that tested our hypotheses of robust saccadic selection in memory (i.e., congruency between saccade target and memory probe location, as well as across the visual field).

Using Bayesian hierarchical models—accounting for both the variance across observers and experiments—we were able to quantify new predictions from a link between visual working memory and saccadic eye movements. We revealed that saccadic selection in visual working memory is a robust behavior that was present in a large portion of the observers and across the entire visual field. While general spatial asymmetries in memory and saccade parameters were independent, trial-by-trial variations in memory and saccade metrics were tightly linked.

Method

Participants. The compiled data set included data obtained from 74 observers (ages 19–39 years; gender: 52 female and 22 male), combined from nine different experiments. Several observers participated in multiple versions of the experiment over the years (i.e., 38 observers participated exactly once, four observers participated in two experiments, three observers in three experiment, one observer in four experiments, two observers in five experiments, and one observer in seven experiments) resulting in a total of 49 unique observers. In all experiments, we dedicated an entire session to the training of the dual-task protocol before starting data collection in the multiple session experiments. Results from eight out of these experiments have been reported previously (for details see **Figure 1**; Ohl & Rolfs, 2017, 2018, 2020). In the additional experiment, 8 observers (ages 19–36 years; gender: 6 female and 2 male; 8 right-handed; 5 right-eye dominant) were tested in two sessions (1 training and 1 test session). We compensated observers for participation with 7€ per session. Observers gave their written informed consent before the first session. All observers had normal or corrected-to-normal vision. The study was approved by the ethics committee of the Psychology Department of the Humboldt-Universität zu Berlin and it followed the guidelines of the Declaration of Helsinki (2008).

Material and procedure. All included experiments exhibit a common trial structure (identical event order, stimulus material and spatial configuration). Each experiment varied in an experimental dimension of interest (e.g., set size, delays).

In the unpublished experiment (referred to as Return_saccade_e1 in **Figure 1b**), we aimed to control for the eccentricity of the memory probe. To this end, we asked observers to generate two successive saccades in response to a movement cue (i.e., a saccade to the cued location and subsequent return saccade back to the central fixation point), such that all possible memory probe locations were equidistant from the fixation location. The experiment was conducted in a dimly lit room. Observers put their head on a chin and forehead rest to remove artefacts resulting from head movements. We tracked observers' dominant eye positions using an Eyelink 1000 Desktop Mount eye tracker (SR Research, Ottawa, ON, Canada) with a sampling rate of 1 kHz. We displayed visual stimuli on a gamma-corrected VIEWPixx /3D monitor (VPixx Technologies Inc., Saint Bruno, QC, Canada) in scanning backlight mode (luminance in a range of 0 – 100 cd/m^2) at a spatial resolution of 1920 x 1080 pixels and a refresh rate of 120 Hz. The screen was positioned at 57 cm distance away from the observers' eyes. The experiment was run on a DELL Precision T3600 (Debian GNU Linux 8) and implemented in Matlab (Mathworks, Natick, MA, USA) using the Psychophysics toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) for stimulus presentation and the Eyelink toolbox (Cornelissen et al., 2002) for control of the eye tracker.

As in all previous experiments of this series, we instructed observers to remember oriented stimuli (i.e., Gabors) for a memory test at the end of the trial in which a *response cue* highlighted the stimulus the orientation of which had to be reported (**Figure 1a**). The trial sequence was also identical in all conducted experiments, and we will specifically highlight the experimental manipulation that differed in the new as compared to the previous experiments. At the beginning of the trial, we asked observers to direct their gaze to a central fixation point (i.e., a white disk with 0.17 dva diameter on top of a black disk with a diameter of 0.68 dva) displayed on uniform gray background (luminance of 77 cd/m^2). We presented this fixation symbol simultaneously with eight task-relevant circular placeholders (black; 1.95 dva diameter), at an eccentricity of 6 dva from the center of a placeholder to the center of the screen. The eight placeholders were positioned on an imaginary circle with equal distance between two adjacent placeholders. Four placeholders were displayed on the vertical and horizontal meridians, and the remaining four placeholders at equidistant oblique locations. The locations of the placeholders were fixed across the entire experiment and identical across all experiments, therefore allowing us to analyze the influence of visual field location in a large data set. 500 ms after successful fixation of the central fixation point, we presented the memory set consisting of four oriented Gabors (±45° from vertical, 50% contrast, randomly assigned spatial frequency of either 1.5 or 2.25 cycles per degree, random phase, and a 0.65° SD Gaussian envelope) for 100 ms at randomly assigned placeholder locations. At the remaining four locations, we presented unoriented noise patches (pixel noise, band-pass filtered from half to twice the spatial frequency of the Gabors, 50% contrast, 0.65° SD Gaussian envelope) simultaneously with the memory array. Following a short delay of 400 ms after memory array offset, we presented a *movement cue* (black line with a length of 0.26 dva that we attached to the outline of the fixation symbol). This endogenous movement cue randomly pointed to one of the eight placeholders, prompting observers to move their eyes quickly (i.e., within 400 ms following movement cue onset) to the indicated location and then immediately back to the center of the screen. Following a delay of 1200 ms after the movement cue, a response cue (the linewidth of one placeholder changed from 0.05 dva to 0.085 dva) highlighted one location. Please note that the response cue delay in the other published experiments was 800 ms except for experiment O&R_2017_e3 in which we systematically varied the response cue delay from 500 – 3600 ms. We asked observers to report the orientation of the Gabor that had been presented inside of that placeholder. Observers generated their report by pressing one of two possible keys on the keyboard, indicating whether the remembered orientation had been clockwise or counterclockwise relative to vertical. Observers did not receive feedback on their performance in the test sessions.

Importantly, in our dual-task protocol, the movement cue was uninformative about which location would be highlighted by the response cue in the later memory test. The location an eye movement was executed to was therefore uninformative about the location of the memory test. Note that we varied movement cue validities (i.e., rendered the saccade target location least likely to be probed in the memory test) in two experiments (*O&R2017_e4* and *O&R2020_e3, cf.* **Figure 1b**).

Observers initiated the beginning of a new block by pressing a key. The experiment consisted of 20 blocks composed of 24 trials each. Each observer therefore completed a total of 480 trials in the experimental session including 120 trials in which movement cue and response cue indicated the same location (i.e., congruent trials), and 360 trials in which the location of the movement cue and response cue were incongruent.

We aligned eye and screen coordinates using standard nine-point calibration and validation routines at the beginning of the experiment, after breaks, and whenever necessary. Before a trial started, we ensured that observers' gaze position was no further than 1.5 dva away from the fixation point for a minimum of 200 ms. We stopped a trial when observers' gaze position exceeded that maximum distance before the movement cue instructed them to move their eyes. Moreover, we aborted trials with blinks in that interval, and trials in which no saccade was generated within 400 ms following movement cue onset. Observers repeated all aborted trials which were presented in randomized order at the end of a given block.

Data analysis. We conducted parameter estimation using a Bayesian framework in R (R Core Team, 2022) that computed the posterior probability for our models using the R package *brms* (Bürkner, 2017), interfacing the STAN environment with *rstan* (Stan Development Team, 2021). We modelled visual memory performance (i.e., the binary variable coding incorrect answers as 0 and correct answers as 1) using the Bernoulli distribution and logit link function. We modelled saccade metrics using an exGaussian distribution for saccade latencies accounting for the observed skewed latency distribution and Gaussian distributions for the saccade amplitude, saccade peak velocity and saccade landing error. In all models, we contrast-coded predictors that were factors and explicitly stated which factor level we chose as the baseline condition. Importantly, to account for the nested random factor structure in our data set (i.e., observers were nested in experiments), we defined *observers* and *experiments* as group-level effects. We then additionally estimated each population-level effect (i.e., each fixed effect) as a group-level effect both for the observer group-level as well as the experiment group-level. We report the estimates for the population-level effects from the various models in the respective Tables but refrain from including the huge number of group-level effects in the Tables (apart for Table 1 in which we also report the group-level estimates to provide an exemplary illustration of the obtained group-level parameters in the Bayesian hierarchical models). All model estimates (including the detailed group-level effects for all other models) can be accessed through the open science framework repository (see below).

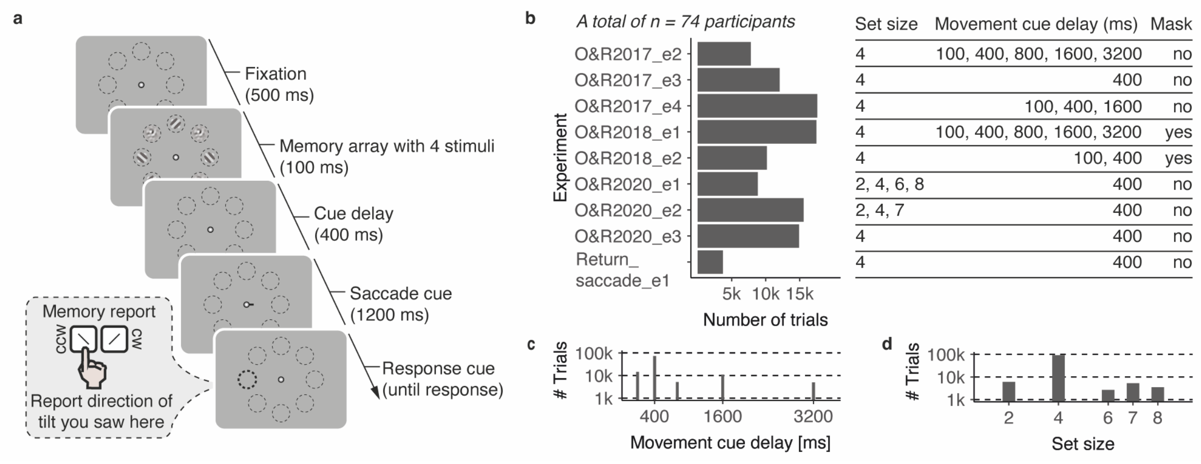
In our Bayesian hierarchical models, we used standard weakly informative priors for all population- and group-level effects. More specifically, for modeling visual memory performance, we used a normal distribution as the prior for the intercept and all population-level effects (M = 0, SD = 10). For the group-level effects, we specified a weakly informative t-student distribution (degrees of freedom = 3, M = 0, SD = 10). We followed the same strategy for modelling saccade metrics with a small number of exceptions. For instance, we modelled the intercept of saccade latency using a normal distribution (M = 200, SD = 100), and the intercept of saccade amplitude using a normal distribution (M = 6, SD = 10) to account for the different range of values in these dependent variables. For modelling saccadic peak velocity, we specified a normal distribution as the prior for intercept (M = 300, SD = 100) and population-level effects (M = 0, SD = 100) and a t-student distribution (degrees of freedom = 3, M = 0, SD = 100) for the group-level effect.

The fitting procedure was as follows: Each Markov chain included a total of 4,000 samples (i.e., 2,000 warmup, and 2,000 post-warmup samples). We aimed at posterior distributions consisting of 8,000 post-warmup samples and thus fitted the Bayesian hierarchical models using four chains with 4,000 iterations each. None of the final models included divergent transitions. The potential scale reduction factor (Gelman & Rubin, 1992) for the parameter estimate was 1.00 in almost all cases and never exceeded 1.01, suggesting convergence for the Markov Chain Monte Carlo sampling.

The inferential statistics were based on 95% credible intervals by sampling from the posterior distribution and determining the 2.5 and 97.5 percentiles. In the Results section, we report the medians and credible intervals after converting the logits to probabilities, while the tables contain the original logit estimates from the Bayesian hierarchical models. Moreover, we report the probability of an effect's direction (e.g., the proportion of samples from the posterior distribution that is larger than zero, or the proportion of samples that is larger in one vs. another condition).

During pre-processing, we detected saccades from the eye tracking data using a velocity-based algorithm with noise-dependent velocity (Engbert & Mergenthaler, 2006). Using this algorithm, we transformed the raw eye positions of the dominant eye into a 2D velocity space and classified saccades as events in which successive eye positions exceeded the median velocity by 5 SDs for at least 8 ms. If two saccadic events were separated by less than 20 ms, we combined them into a single saccade. From the set of detected saccades in a trial, we defined the response saccade as the first saccadic eye movement that landed within a maximum distance of 3.6° from the center of the saccade target (corresponding to 60% of the target's eccentricity from initial fixation). The reported saccade metrics are based on these response saccades, using the following definitions: Saccade latency is the time between cue onset and the first sample exceeding the velocity threshold. Saccade amplitude is the Euclidean distance between screen positions of the first and the last sample that were part of the saccade. Landing error is the Euclidean distance between the position of the last sample that was part of the saccade and the center of the target location. Peak velocity is the maximum value of any sample that was part of the saccade. Trials including additional saccades with an amplitude larger than 1 dva in a time window between trial onset and movement cue onset were excluded from final analyses. For the unpublished experiment, a total of 3,710 trials (97%) entered the final data analysis. The entire data set including all nine experiments comprised 108,088 trials.

Transparency and openness. The data (https://osf.io/scq6w), analysis code in R, as well as the fitted models are available through the Open Science Framework at https://osf.io/6y9c5/. The analyses were based on a compiled data set of eight already existing experiments and, thus, we did not specifically determine the sample size for our current set of analyses, and we did not preregister this study. However, given the large number of participants and trials per participant, the Bayesian hierarchical mixed models explicitly aimed for testing the generalizability and robustness of the interplay between visual working memory and saccadic eye movements.



Set size	Movement cue delay (ms)	Mask
4	100, 400, 800, 1600, 3200	no
4	400	no
4	100, 400, 1600	no
4	100, 400, 800, 1600, 3200	yes
4	100, 400	yes
2, 4, 6, 8	400	no
2, 4, 7	400	no
4	400	no
4	400	no

Fig. 1. Trial design and summary of included experiments. **a** Trial sequence in the experiment *Return_saccade_e1. The trial sequence of the experiment was identical to the eight other experiments except for the response cue delay (i.e., delay between saccade cue onset and response cue onset). The response cue delay in the experiment Return_saccade_e1 was extended to 1200 ms to provide sufficient time for generating both saccades. In previous experiments it was fixed at 800 ms or was varied in a range from 500 – 3600 ms in experiment O&R2017_e3.* **b** Overview of experiments included in the present data set, displaying the number of the experiment in a publication, as well as the number of trials collected in that experiment. **c** Number of trials testing the different movement cue delays (either

100, 400, 800, 1600 or 3200 ms). **d** Number of trials testing the different load conditions (either 2, 4, 6, 7, or 8 oriented stimuli).

Results

Whether and how saccadic eye movements affect the maintenance of representations in visual working memory is informative with respect to the cognitive architecture in active observers. Here, we analyze nine experiments—comprising more than 100k trials that we obtained from a total of 74 observers (including 49 unique observers)—pursuing two main objectives. First, we aimed to determine whether saccadic selection in visual working memory is evident in all observers and at all locations in the visual field. Second, we aimed to uncover whether variations in visual memory performance are associated with saccade metrics across the visual field.

Saccadic selection is highly prevalent in the tested population.

We predicted memory performance as a function of spatial congruency between the memory probe and saccade target location using a Bayesian hierarchical model which considered that both different observers and different experiments contribute to the variance in the observed memory performance (**Table 1**). In addition to estimating how the congruency between the location of the memory probe and saccade target affects memory performance at the population-level, we allowed congruency to vary for observers and experiments at the group-level as well. This mixed-model architecture therefore enabled us to determine how saccadic selection varies between observers *and* between experiments. In line with our previous findings (Ohl & Rolfs, 2017, 2018, 2020), the model (*bhm1*; **Table 1**) showed better memory performance for memory items displayed at a location congruent with the saccade target than at incongruent locations (Δpc 0.083; 95% CI [0.06, 0.106]; probability of being positive pd > 99.9%; **Figure 2a**). Indeed, our analyses revealed a memory advantage at congruent as compared to incongruent locations for each individual experiment (**Figure 2b**). The results from the unpublished experiment—in which a second saccade brought the gaze back to the central fixation point before the appearance of the response cue—also showed this saccadic selection effect (Δpc 0.07; 95% CI [0.012, 0.133]; probability of being positive pd > 98%). At the level of individual observers, the model estimated a positive saccadic selection effect in every single observer (see black points in **Figure 2c**). Moreover, the magnitude of saccadic selection (average difference of proportion correct between congruent and incongruent locations) was positive in 69 of 74 observers, attesting to better memory performance at the saccade target (gray points in **Figure 2c**). The small discrepancy between the results of the Bayesian hierarchical model and averaging across observers is a consequence of hierarchical shrinkage (Efron & Morris, 1977). Participants varied strongly in their overall memory performance. Importantly, we observed better memory performance at locations congruent with the saccade target location as compared to incongruent locations across all different levels of performance. This generalization provides further support that saccades are a fundamental selection mechanism in visual working memory irrespective of how well a person can remember the stimuli in the task.

Noteworthy, a memory benefit on an individual-observer level was to be expected, as we combined the data obtained in multiple small n-designs that already provided evidence for better memory performance at the saccade target on a group level. The previous analysis only provides a descriptive assessment of saccadic selection at the observer level that ignores the detection of a significant effect within observers. As a consequence, we complemented the hierarchical modeling with determining the Bayesian prevalence of the saccadic selection effect in the population through a two-step analysis approach (Ince et al., 2021). First, we classified the presence of a saccadic selection effect in each individual observer into the two categories *effect present* vs. *effect absent* (using separately a conservative and a more liberal criterion; see below). Thus, the Bayesian prevalence is based on the detection of an effect within individual observers. In a second step, we used Bayesian inference to estimate the population prevalence and its uncertainty for a true positive effect in the population. For both criteria, we observed that a large proportion of the population showed saccadic selection in visual working memory: Using a conservative criterion—in which observers were classified as showing saccadic selection only when performance in congruent trials was significantly better than in incongruent trials—yielded a population prevalence of 48.8% (95% HPDI 37.0–60.0%). Notably, none of the observers had significantly better memory performance in incongruent as compared to congruent trials. In contrast, using a more liberal criterion—in which the average performance in congruent trials simply had to exceed the average performance in incongruent trials—showed a prevalence of saccadic selection in 92.9% (95% HPDI 85.3–97.4%) of the population.

Saccadic selection is spatially specific.

The more fine-grained analysis relating memory performance to angular distance between the saccade target and the memory probe location further corroborated the influence of saccades on visual working memory (**Figure 2d**). Memory performance at the saccade target location was better than memory performance at the neighboring location ($\Delta pc_{0\text{-}1}$ 0.080; 95% CI [0.057, 0.103]; probability of being positive pd > 99.9%). Memory performance was on a similar level (i.e., not significantly different) for probes presented at non-target locations with a distance of one, two, three, or four locations away from the saccade target ($\Delta pc_{1\text{-}2}$ 0.008; 95% CI [–0.004, 0.021]; probability of being positive pd = 92%; $\Delta pc_{1\text{-}3}$ 0.006; 95% CI [–0.005, 0.017]; probability of being positive pd = 86%; $\Delta pc_{1\text{-}4}$ –0.011; 95% CI [–0.025, 0.003]; probability of being positive pd = 7%). Interestingly, memory performance was slightly better at the location opposite from the saccade target as compared to locations that were three items away from the saccade target ($\Delta pc_{4\text{-}3}$ 0.016; 95% CI [0.001, 0.032]; probability of being positive pd = 98%). Crucially though, memory performance at the saccade target location significantly exceeded memory performance at the location opposite from the saccade target ($\Delta pc_{0\text{-}4}$ 0.069; 95% CI [0.045, 0.095]; probability of being positive pd > 99%).

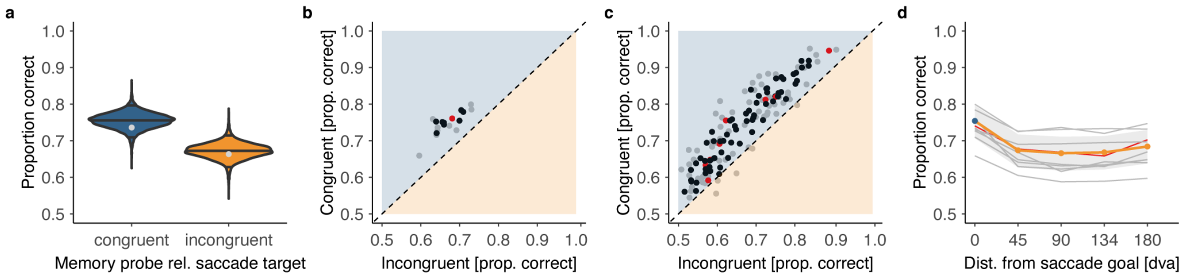


Fig. 2. Saccadic selection in visual working memory. **a** Posterior distributions of memory performance for items displayed at locations that were congruent (in blue) or incongruent (in orange) with the saccade target. Gray points display the mean performance across observers. **b** Memory performance in congruent and incongruent trials in the nine different experiments reported as median performance extracted from the posterior distribution of model *bhm1* (in black; performance in the unpublished experiment depicted in red) and reported as mean performance for each experiment (in gray). **c** Individual observers' (n = 74) memory performance in congruent vs. incongruent trials reported as median posterior probability extracted from the model *bhm1* (in black; performance in the unpublished experiment depicted in red) and reported as mean performance for each observer (in gray). **d** Memory performance extracted from the posterior distribution as a function of the distance between saccade target location and memory probe (congruent trials in blue, incongruent trials in orange). Shaded area (in gray) depicts the 95% credible interval. Gray lines show mean performance in each experiment.

Memory performance varies across the visual field.

Collapsing data from nine experiments with identical spatial configurations allowed us to address whether memory performance in the active observer varied across the visual field. The observed memory profiles in congruent and incongruent trials (**Figure 3A**) were consistent with well-documented perceptual visual field anisotropies (e.g., Abrams et al., 2012; Anderson et al., 2014; Baldwin et al., 2012; Barbot et al., 2021; Benson et al., 2021; Corbett & Carrasco, 2011; Edgar & Smith, 1990; Fuller et al., 2008; Fuller & Carrasco, 2009; Greenwood et al., 2017; Himmelberg et al., 2020; Kupers et al., 2019, 2022; Lestrange-Anginieur & Kee, 2020; Levine & McAnany, 2005; Liu et al., 2006; McAnany & Levine, 2007; Nazir, 1992; Pointer & Hess, 1989; Rosén et al., 2014; Rubin et al., 1996; Schmidtmann et al., 2015; Silva et al., 2018; Song et al., 2011; Thomas & Elias, 2011; Tootell et al., 1988; Von Grünau & Dubé, 1994; see Himmelberg et al., 2023 for a review), including a horizontal-vertical anisotropy (performance is superior on the horizontal as compared to the vertical meridian), better performance in the lower as compared to the upper visual field, and a vertical-meridian asymmetry (performance is superior at the lower as compared to the upper vertical meridian). Interestingly, perceptual anisotropies are apparent and even partially exacerbated during saccade preparation (Hanning et al., 2022). We quantified the horizontal-vertical anisotropy in our data by inspecting whether memory performance varied between the horizontal (i.e., collapsing across West and East locations) and vertical (i.e., collapsing across North and South locations) meridian. The Bayesian hierarchical model (*bhm2*, **Table 2**) revealed that memory performance was poorest at the vertical meridian in incongruent trials (pc 0.65; 95% CI [0.61, 0.68]; **Figure 3b**). Performance at the horizontal meridian was increased as compared to the vertical meridian (Δpc 0.06; 95% CI [0.03, 0.10]; probability of being positive pd > 99%). Memory performance was higher in congruent trials as compared to incongruent trials on the vertical meridian (Δpc 0.10; 95% CI [0.08, 0.13]; probability of being positive pd > 99.9%). Crucially, the magnitude of saccadic selection (i.e., the congruency effect) did not differ between the horizontal and vertical meridian (Δpc 0.00; 95% CI [-0.03, 0.03]; probability of being positive pd = 53%). Thus, saccades effectively increased memory performance at the saccade target for both meridians, and saccades neither mitigated nor enhanced the existing horizontal-vertical anisotropy. Second, we quantified upper vs. lower visual field differences by comparing memory performance in the upper (i.e., collapsing North, North-East, North-West) and the lower (i.e., collapsing locations South, South-East, South-West) visual field. The Bayesian hierarchical model (*bhm3*, **Table 3**) revealed worst memory performance at the upper visual field in incongruent trials (pc 0.66; 95% CI [0.61, 0.70]; **Figure 3c**). We did not observe a meaningful memory difference between the lower and upper visual field in incongruent trials (Δpc 0.01; 95% CI [-0.01, 0.03]; probability of being positive pd = 87%). Memory performance increased in congruent trials as compared to incongruent trials in the upper visual field (Δpc 0.07; 95% CI [0.04, 0.09]; probability of being positive pd > 99.9%). The same effect was apparent and more pronounced in the lower visual field (Δpc 0.03; 95% CI [0.01, 0.05]; probability of being positive pd > 99%). Thus, in contrast to the clear horizontal-vertical anisotropy, the difference between the upper and lower visual field was evident only in congruent trials. Third, we quantified the vertical-meridian asymmetry by comparing the visual memory performance at the upper and lower vertical meridian (see Bayesian hierarchical model bhm4 which provides estimates for memory performance as a function of congruency for each location; Table 4). Memory performance was better at the lower vertical meridian than at the upper vertical meridian in both congruent (Δpc 0.08; 95% CI [0.02, 0.12]; probability of being positive pd > 99%) and incongruent trials (Δpc 0.05; 95% CI [0.01, 0.08]; probability of being positive pd > 98%). The magnitude of the vertical meridian asymmetry did not differ between congruent and incongruent trials (Δpc 0.03; 95% CI [–0.01, 0.07]; probability of being positive pd = 92.3%).

Saccadic selection is effective at all tested locations.

Mean memory performance (i.e., proportion correct reports averaged across observers) as a function of congruency with the saccade target location suggests better performance at the saccade target location across the entire visual field (i.e., the orange performance profile is consistently inside the blue performance profile; **Figure 3a**). These observations were corroborated by a Bayesian hierarchical model (*bhm4*; **Table 4**) that predicted memory performance as a function of probe location and congruency with the saccade target, as well as their interaction. We observed considerable variations of memory performance across the visual field in incongruent trials, with memory performance at the upper location (North) being lowest (pc 0.643; 95% CI [0.600, 0.685]). Memory performance at three other locations (i.e., South, South-East, North-East) was on a similarly low level (**Table 4**); at the remaining locations performance was significantly higher ($\Delta pc_{N\text{-}E}$ –0.045; 95% CI [–0.081, –0.008]; probability of being negative pd > 97%; $\Delta pc_{N\text{-}SW}$ –0.058; 95% CI [–0.087, –0.029]; probability of being negative pd > 99%; $\Delta pc_{N\text{-}W}$ –0.104; 95% CI [–0.138, –0.067]; probability of being negative pd > 99.9%; $\Delta pc_{N\text{-}Nw}$ –0.043; 95% CI [–0.070, -0.0–6]; probability of being negative pd > 99%). Importantly, however, we observed better memory performance in congruent as compared to incongruent trials at each tested location (Δpc_{E} 0.116; 95% CI [0.073, 0.157]; Δpc_{SE} 0.078; 95% CI [0.038, 0.119]; Δpc_{S} 0.129; 95% CI [0.096, 0.162]; Δpc_{SW} 0.83; 95% CI [0.047, 0.120]; Δpc_{W} 0.084; 95% CI [0.051, 0.116]; Δpc_{NW} 0.060; 95% CI [0.024, 0.096]; Δpc_{N} 0.086; 95% CI [0.055, 0.117]; Δpc_{NE} 0.055; 95% CI [0.018, 0.092]; all probabilities of being positive pd > 99%: **Figure 3d**). Finally, the memory advantage at the saccade target was higher at the South as compared to the North location. In summary, our analyses revealed both general asymmetries in performance and robust saccadic selection in visual working memory across the entire visual field.

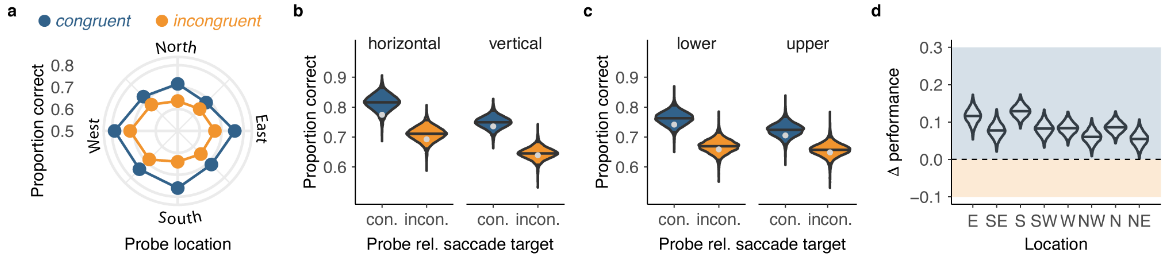


Fig. 3. Visual memory performance across the visual field. **a** Mean memory performance averaged across observers in congruent (blue) and incongruent trials (orange). **b** Memory asymmetries along the horizontal vs. vertical meridian (i.e., horizontal-vertical anisotropy) comparing congruent (in blue) and incongruent (in orange) trials as derived from model *bhm2*. Gray dots represent the mean proportion correct obtained by averaging across observers. **c** Memory asymmetries in the lower vs. upper visual field comparing congruent (in blue) and incongruent (in orange) trials as derived from model *bhm3.* Gray dots represent the mean proportion correct obtained by averaging across observers. **d** Saccadic selection in visual working memory as a function of memory test location. Effect size is expressed as difference performance between congruent and incongruent trials derived from the posterior distribution of model *bhm4*. Violin plots represent 99% of the posterior distribution. Blue background depicts benefits at the saccade target location.

Saccade metrics vary across the visual field.

Importantly, saccadic eye movements are also known to display asymmetries across the visual field (Bhidayasiri et al., 2001; Greene et al., 2014; Greenwood et al., 2017; Hanning et al., 2022; Irving & Lillakas, 2019). In our data, saccade metrics (i.e., saccade latency, amplitude, landing error, and peak velocity) were consistent across observers and experiments. At the same time, they featured sufficient variance to determine whether variations in saccade metrics and visual working memory across the field were associated (**Figure 4**). In line with previous observations, the four Bayesian hierarchical models revealed a particularly strong difference between the upper and lower visual field (*bhm5* to *bhm8* in **Table 5**): Saccade latency at all locations was similar to that at the North location (reference condition in model *bhm5*; latency 209 ms; 95% CI [196, 220]; **Figure 4e**) with the exception of longer latencies in the lower visual field ($\Delta\text{latency}_{SW}$ 3.7 ms; 95% CI [0.6, 6.8]; probability of being positive pd > 98%; $\Delta\text{latency}_{S}$ 11.1 ms; 95% CI [7.9, 14.3]; probability of being positive pd > 99.9%; $\Delta\text{latency}_{SE}$ 5.3 ms; 95% CI [2.3, 8.3]; probability of being positive pd > 99%). In line with predictions based on the experimental protocol, congruency had no influence on saccade latency, therefore excluding the possibility of a speed-accuracy tradeoff in our experiments.

Saccade amplitudes (*bhm6*) were larger for saccades directed to the lower visual field (South, South-East, South-West) than saccades directed to the North location (reference condition in model *bhm6*; amplitude 5.27 dva; 95% CI [5.12, 5.42]; **Figure 4f**). Saccade amplitude for the North and North-West location had a similar amplitude ($\Delta\text{amplitude}_{NW}$ 0.06 dva; 95% CI [-0.03, 0.14]; probability of being positive pd = 90%). It is worth noting that congruency of probe and saccade target location did not influence saccade amplitude at any visual-field location, suggesting that this experimental manipulation had no detrimental influence on saccade targeting.

The absolute saccade landing error (*bhm7*) to the North location (reference condition in model *bhm7*; error 1.34 dva; 95% CI [1.26, 1.41]) was comparable to other locations along the cardinal directions (**Figure 4g**). The landing error was larger, relative to the North location, only for three locations along the oblique axis (Δerror$_{NE}$ 0.09 dva; 95% CI [0.02, 0.17]; probability of being positive pd > 98%: Δerror$_{SE}$ 0.25 dva; 95% CI [0.07, 0.42]; probability of being positive pd > 99%: Δerror$_{SW}$ 0.25 dva; 95% CI [0.13, 0.38]; probability of being positive pd > 99). Again, congruency and its interactions with location had no influence on the saccade landing error.

Saccadic peak velocities (*bhm8*) were more heterogenous across locations than the other saccade metrics (**Figure 4h**). Saccades had the smallest peak velocity along the vertical meridian (the North location was the reference condition in model *bhm8*; velocity$_{N}$ 324 dva/s; 95% CI [305, 341]; Δvelocity$_{S}$ –1.6 dva/s; 95% CI [–16.6, 14.0]; Δvelocity$_{NW}$ 3.8 dva/s; 95% CI [–5.1, 12.2]; **Table 5**). Saccadic peak velocity at the other locations was higher as compared to the upper location. We observed the highest peak velocity at the South-East location (Δamplitude$_{SE}$ 39.2 dva/s; 95% CI [22.1, 56.5]).

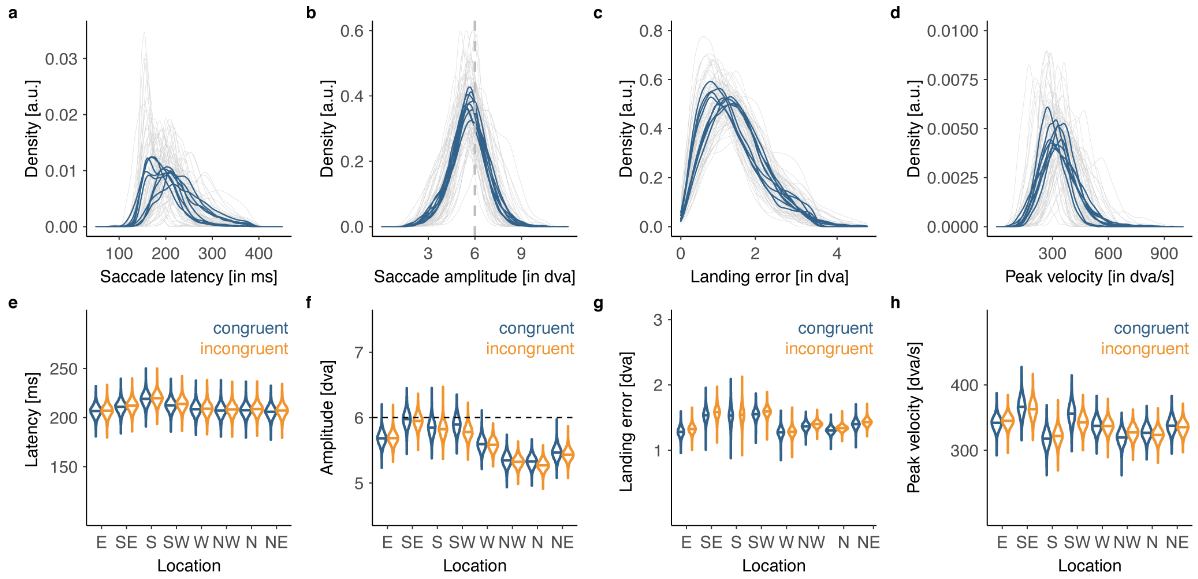


Fig. 4. Saccade metric variations as a function of saccade target location. **a-d** Density of saccade metrics (i.e., saccade latency, saccade amplitude, absolute landing error, and saccadic peak velocity) for each individual experiment (in blue) and each individual observer (in gray). **e** Saccade latency posterior distribution as a function of congruency (congruent in blue, incongruent in orange) and

saccade target location (obtained from model *bhm5*). **f** Saccade amplitude posterior distribution as a function of congruency (congruent in blue, incongruent in orange) and saccade target location (obtained from model *bhm6*). **g** Posterior distribution of the absolute landing error as a function of congruency (congruent in blue, incongruent in orange) and saccade target location (obtained from model *bhm7*). **h** Saccadic peak velocity posterior distribution as a function of congruency (congruent in blue, incongruent in orange) and saccade target location (obtained from model *bhm8*).

Spatial asymmetries in memory and saccade metrics are independent.

Having established that both visual working memory and saccade metrics are prone to systematic variations across the visual field in the present set of experiments, we can test whether these variations are related to one another. A strong correlation between the asymmetries would indicate that both visual working memory and the oculomotor system share a common map of visual space, or alternatively, that they both inherit their asymmetries from a common source. The Bayesian hierarchical models revealed no meaningful associations between visual working memory performance and saccade metrics at the eight tested visual locations (*bhm9* to *bhm12*; **Table 6**). In all models, visual memory performance improved at the saccade target location, but variations in saccade metrics did not account for variations in memory performance across the visual field (**Figure 5**). Thus, the present analyses suggest that asymmetries in visual working memory performance and asymmetries in saccade metrics result from independent sources. These analyses suggest separate and independent topographies underlying visual working memory and saccade generation. This does not come as a surprise considering the marked discrepancies at the North location at which observers yielded the shortest saccade latencies and, at the same time, very low memory performance.

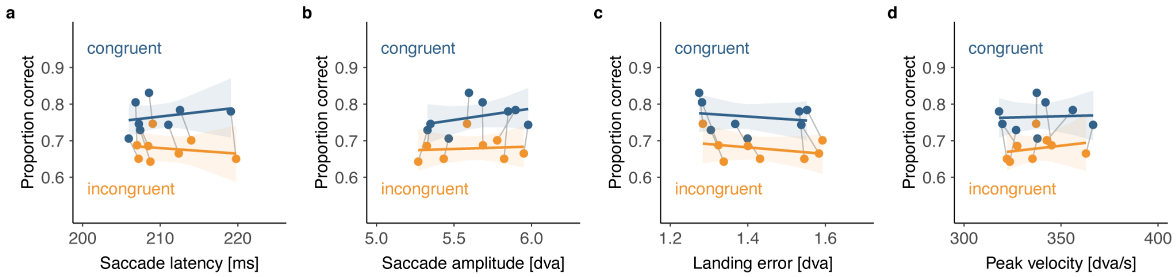


Fig. 5. Association of saccade metrics and memory performance across the eight locations. **a** Saccade latency and memory performance for congruent (in blue) and incongruent trials (in orange) depicted for the eight individual locations as obtained from the posterior distribution of model *bhm9*. **b** Saccade amplitude and memory performance for congruent (in blue) and incongruent trials (in orange) depicted for the eight individual locations as obtained from the posterior distribution of model *bhm10*. **c** Absolute landing error and memory performance for congruent (in blue) and incongruent trials (in orange) depicted for the eight individual locations as obtained from the posterior distribution of model *bhm11*. **d** Saccadic peak velocity and memory performance for congruent (in blue) and incongruent trials (in orange) depicted for the eight individual locations as obtained from the posterior distribution of model *bhm12*.

Trial-by-trial variations in memory and saccade metrics are associated.

In the next step, we determined whether trial-by-trial variations in saccade metrics and memory performance were associated (Greenwood et al., 2017). Based on the perspective of an active visual memory system, we predict a coupling of visual working memory to actions at the level of a saccadic eye movement's intrinsic (i.e., variations in selection with saccade latency and peak velocity) and intended (i.e., deviations from the saccade goal) consequences.

Importantly, this analysis requires a standardization of saccade metrics to account for a possible systematic relationship with memory on the experiment-, observer-, or location-level. For instance, saccade latencies are associated with memory performance on the experiment- and observer-level (**Figure 6**): Experiments and observers with shorter mean saccade latencies were associated with higher memory performance on average. By standardizing (i.e., z-transforming) the saccade metrics for each observer and location, we removed these systematic differences, which might otherwise have artificially increased the trial-by-trial association between memory performance and saccade metrics (**Figure 6**; note that this z-transformation also resulted in mean z-scores of zero for the different experiments).

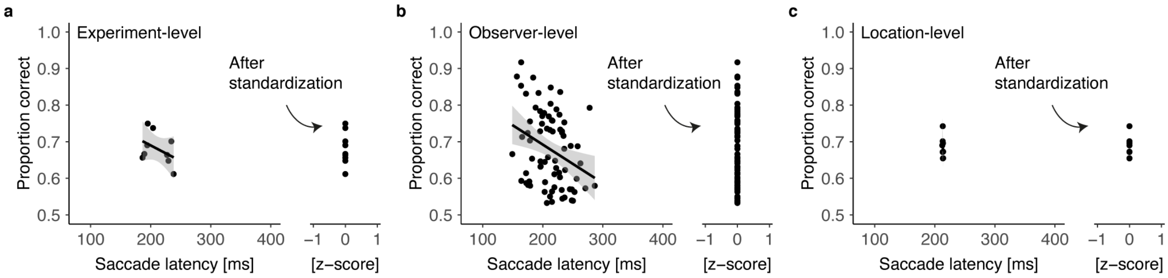


Fig. 6. Standardization of saccade latencies. **a** Association between mean memory performance per experiment and mean saccade latency per experiment (left panel). The right panel displays mean z-scores for the different experiments after standardization. **b** Association between mean memory performance and mean saccade latency per observer (left panel). Right panel displays the mean z-scores for the different observers after standardization. **c** Association between mean memory

performance and mean saccade latency per location (left panel). Right panel displays the mean z-scores for the different locations after standardization.

We then assessed whether the standardized saccade metrics could account for memory performance on a single-trial level. Again, the Bayesian hierarchical model (*bhm 13*) demonstrates how memory performance is increased in congruent trials (logit Congruency 0.41; 95% CI [0.29, 0.05]) as compared to baseline performance in incongruent trials (logit $\text{Intercept}_{\text{incongruent}}$ 0.72; 95% CI [0.51, 0.92]). In contrast to the analyses of independent spatial asymmetries, the Bayesian hierarchical model now suggests a clear association between visual memory performance and saccade metrics (**Figure 7**). The standardization of saccade metrics within location and observers revealed how in congruent trials, shorter saccade latencies (logit $\text{Latency}_{\text{congruent}}$ -0.10; 95% CI [-0.16, -0.05]; **Figure 7a**) and more accurate saccades (logit $\text{Error}_{\text{congruent}}$ -0.13; 95% CI [-0.22, -0.05]; **Figure 7c**) were associated with better memory performance while saccade amplitude (**Figure 7b**) and saccadic peak velocity (**Figure 7d**) did not explain further variance (**Table 7**). This association was limited to congruent trials: none of the saccade metrics in incongruent trials were associated with memory performance (i.e., all estimates inside the 95% credible interval; **Table 7**). In sum, the analysis of trial-by-trial variations revealed how saccade metrics and memory performance were associated, providing additional support for a strong link between saccade metrics and visual working memory.

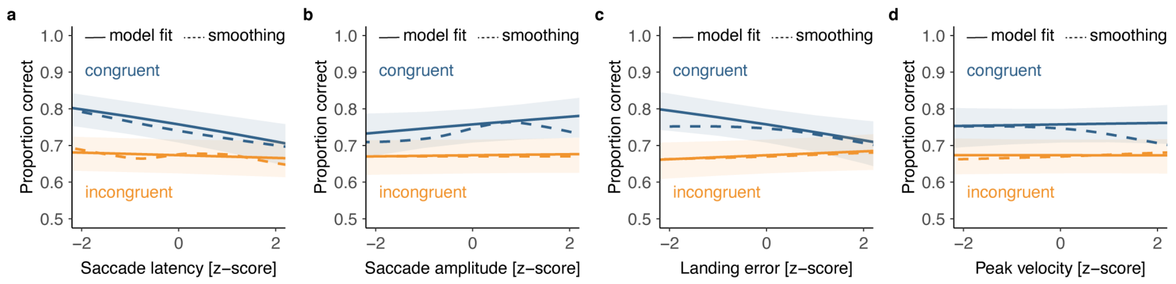


Fig. 7. Trial-by-trial association between memory performance and **a** saccade latency, **b** saccade amplitude, **c** landing error and **d** peak velocity. Solid lines display predictions of the model *bhm13*

determining how the linear, standardized (z-transformed) saccade metrics are associated with memory performance in congruent (in blue) and incongruent trials (in orange). Dashed lines visualize smoothing averages obtained from relating the z-scores of the saccade metrics to memory performance for congruent and incongruent trials. The smoothing is based on all trials, therefore ignoring that trials were obtained from different experiments and observers.

Discussion

We revealed robust saccadic selection in visual working memory and observed that variations in saccade metrics were associated with variations in memory performance on a trial-by-trial level. These findings rely on a large data set with more than 100k trials compiled from nine experiments that probed visual working memory after observers generated saccadic eye movements during memory maintenance. Saccadic selection of memory at the saccade target location was robust: selection was highly prevalent in the studied population and effective at all tested locations across the visual field. These findings confirmed our predictions derived from the perspective of an active visual memory system with a strong link between visual working memory and the oculomotor system. This robust behavior, together with our previous findings of effective saccadic selection even when the saccade target was least likely to be probed in the memory test (Ohl & Rolfs, 2017, 2020) and for set sizes as small as two stimuli (Ohl & Rolfs, 2020) emphasizes the impact of saccadic eye movements on the selection of internal memory representations.

Memory performance varied across the visual field.

We observed reliable asymmetries in memory performance across the visual field. Visual memory performance was better at the horizontal as compared to the vertical meridian, and better at the lower than the upper vertical meridian. Moreover, in congruent trials, memory was better in the lower as compared to the upper visual field. These findings are consistent with well-documented visual field asymmetries: at isoeccentric locations, visual performance is better along the horizontal as compared to the vertical meridian, better in the lower as compared to the upper visual field, and better at the lower vertical meridian than the upper vertical meridian (e.g., Abrams et al., 2012; Anderson et al., 2014; Baldwin et al., 2012; Barbot et al., 2021; Benson et al., 2021; Corbett & Carrasco, 2011; Edgar & Smith, 1990; Fuller et al., 2008; Fuller & Carrasco, 2009; Greenwood et al., 2017; Himmelberg et al., 2020; Kupers et al., 2019, 2022; Lestrange-Anginieur & Kee, 2020; Levine & McAnany, 2005; Liu et al., 2006; McAnany & Levine, 2007; Nazir, 1992; Pointer & Hess, 1989; Rosén et al., 2014; Rubin et al., 1996; Schmidtmann et al., 2015; Silva et al., 2018; Song et al., 2011; Thomas & Elias, 2011; Tootell et al., 1988; Von Grünau & Dubé, 1994, see Himmelberg et al., 2023 for a review). These anisotropies have been demonstrated in a variety of tasks such as orientation discrimination (Abrams et al., 2012; Barbot et al., 2021; Corbett & Carrasco, 2011; Himmelberg et al., 2020; Rosén et al., 2014), stimulus detection and localization (Baldwin et al., 2012; Lestrange-Anginieur & Kee, 2020; McAnany & Levine, 2007), spatial frequency (Edgar & Smith, 1990) and contrast (Fuller et al., 2008) estimation, crowding (Greenwood et al., 2017), detection of illusory contours (Rubin et al., 1996) and illusory motion direction discrimination (Fuller & Carrasco, 2009). Spatial anisotropies cannot be explained by asymmetries in attentional allocation: covert attention has been shown to improve performance uniformly across isoeccentric locations (e.g., Cameron et al., 2002; Carrasco et al., 2001, 2002; Purokayastha et al., 2020; Roberts et al., 2016, 2018; Talgar & Carrasco, 2002). Instead, visual field anisotropies are assumed to arise from low-level physiological factors such as variations in retinal ganglion cell density (Curcio et al., 1990; Curcio & Allen, 1990; Kupers et al., 2019, 2022; Silva et al., 2018; Song et al., 2011; Watson, 2014, see Himmelberg et al., 2023 for a review) and uneven pooling of neuronal inputs to early visual cortex (Baldwin et al., 2012; Benson et al., 2021; Kupers et al., 2019, 2022; Liu et al., 2006; Tootell et al., 1988; Van Essen et al., 1984). Interestingly, the upper vs. lower visual field asymmetry is reversed in the superior colliculus (SC; Hafed & Chen, 2016): SC neurons exhibit narrower tuning, higher firing rates and shorter firing latencies for stimuli presented in the upper as compared to the lower visual field. Recent findings suggest that the involvement of the SC in eye movement preparation leads to a brief peri-saccadic reversal of this asymmetry (Fracasso, Buonocore, & Hafed, 2022). Immediately before and during horizontal saccades, discrimination performance is transiently higher in the upper as compared to the lower visual field.

Importantly, perceptual visual field asymmetries persist in short-term memory: just like perceptual judgments, memory performance is better along the horizontal than along the vertical meridian (Montaser-Kouhsari & Carrasco, 2009; Smith, 2022). While these results were obtained during passive fixation, we extend them to an active visual framework. We furthermore demonstrate a vertical-meridian asymmetry in short-term memory, i.e., better memory performance for orientations presented at target-congruent locations at the lower as compared to the upper vertical meridian. Combined, our findings suggest that low-level perceptual asymmetries are preserved across temporal delays and intervening eye movements. Visual field asymmetries are markedly consistent across tasks, visual features and cognitive domains (i.e., perception, memory, saccadic selection) and may reflect tuning to statistics in our visual environment (Henderson & Serences, 2021; Schmidtmann et al., 2015; Von Grünau & Dubé, 1994). While primates routinely manipulate objects in their lower visual field—a task that requires high perceptual resolution—objects above the line of sight are most relevant for large-scale spatial orienting and navigation. In accordance with this, visual field asymmetries vary with stimulus properties: while contrast, hue and motion increments are more easily detected in the lower visual field, stimuli differing in their apparent distance from the observer are more readily discriminated in the upper visual field (Levine & McAnany, 2005). Moreover, the vertical-meridian asymmetry is absent in children who, due to their height, most often experience salient visual events above their line of sight (Carrasco et al., 2022).

Saccadic selection is spatially robust.

Despite general performance variations across the visual field, saccadic selection in visual working memory was independent of visual field location (and, hence, saccade direction): Memory performance at any tested location was better when that location was the saccade target than when it was not. Our findings complement previously reported asymmetries (or, the lack thereof) in the pre-saccadic selection of external visual information (Hanning et al.,

2022) where saccade preparation enhanced contrast sensitivity across the visual field apart from the upper vertical meridian. Note that in their study, enhancement was defined as a performance increase over a neutral baseline condition in which observers maintained fixation. When comparing valid and invalid (i.e., congruent and incongruent) trials, the authors observed a reliable pre-saccadic advantage at all locations, mirroring our results. Our studies did not involve a neutral fixation condition that would allow us to determine whether differences in memory performance between target-congruent and incongruent locations reflect memory benefits at the saccade target location, memory costs at non-target locations, or both (for a discussion see Heuer et al., 2020).

Saccade metrics vary across the visual field.

Beyond shaping perceptual processing, environmental regularities may impact the preparation and execution of visually guided actions: manual pointing movements are more accurate and exhibit higher peak velocities when directed towards the lower as compared to the upper visual field (Danckert & Goodale, 2001). By contrast, saccadic eye movements in our data set and in previous investigations (Honda & Findlay, 1992; Goldring & Fischer, 1997; Zhou & King, 2002; Tzelepi, Laskaris, Amditis, & Kapoula, 2010; Greene et al., 2014; Tiadi, Seassau, Bui-Quoc, Gerard, & Bucci, 2014; Greenwood et al., 2017; Hanning et al., 2022) show shorter latencies when directed towards the upper visual field. This pattern may indeed reflect the tendency to manually manipulate objects in the lower visual field and visually inspect the environment above the line of sight during navigation (Greene et al., 2014).

Spatial asymmetries in saccadic selection and saccade metrics are independent.

The large number of within- and across-observer repetitions as well as the wide range of memory probe and saccade target locations allowed us to gain further insight into the mutual variation of memory performance and saccade metrics across the visual field. First, we employed a topographic covariation approach in which we assessed whether asymmetries in the spatial maps underlying visual memory and saccade metrics are associated. Both the initial processing of visual information and the programming of saccadic eye movements occurs in retinotopic coordinates. This facilitates the information flow and allows for the possibility that one map imposes its constraints onto the other system. The answer to this question is unambiguous: visual memory and saccade metrics showed pronounced but independent variations across the visual field. Thus, individual asymmetries seem to be the result of specific constraints within the oculomotor system and within visual working memory, respectively, and not of common constraints shared between the systems.

Saccadic selection and saccade metrics covary on a single-trial level

We assessed the existence of a link between visual working memory and eye movements employing a single-trial covariation approach. To this end, we standardized saccade metrics within each observer and location to remove biases across the visual field. Saccade metrics are typically related to each other (e.g., the main sequence describing the relationship amplitude and peak velocity, Bahill et al., 1975). In our analysis, we included all four assessed saccade metrics (i.e., latency, amplitude, peak velocity, and landing error) as linear predictors of memory performance after factoring out biases between experiments, observers, and locations. This approach successfully uncovered the association between saccade metrics and memory performance. Our analyses suggest that visual working memory and the oculomotor system are linked by communicating within a common functional network: the way we execute an eye movement is associated with how well we remember a stimulus. In line with previous research, we observed that shorter saccade latencies and more accurate saccades were associated with higher memory performance (Hanning et al., 2016; Ohl & Rolfs, 2018). This finding is reminiscent of pre-saccadic selection of external visual signals for which faster saccades also result in better visual performance (Jonikaitis & Deubel, 2011; Jonikaitis & Theeuwes, 2013), linking visual memory and saccades at the level of a saccade's intrinsic consequence (e.g., more efficient allocation of pre-saccadic attention to the target location). Notably, memory performance and saccade latency were associated on a single-trial level but not when relating visual field asymmetries in memory and saccade latency. In fact, the location with the shortest saccade latency was the location with the worst memory performance (i.e., the upper vertical meridian). The apparent discrepancy between these two analyses results from factoring out variations in saccade latencies across the visual field for the single-trial analysis. The standardization of saccade latency therefore allowed us to reveal that shorter saccade latencies are associated with better memory performance at each individual location irrespective of the mean saccade latency at a given location. This result can be accounted for if we assume that two relevant sources contribute to the overall saccade latency. First, the target location is selected as the movement goal. Memory performance for the saccade target benefits more the faster this selection progresses. Second, after the saccade target is selected, a motor command would propagate to the oculomotor system and initialize the movement. The systematic asymmetries of saccade metrics across the visual field may arise during the oculomotor phase of processing, which however, does not relate to visual memory performance.

Interestingly, more accurate saccades in our investigation were associated with better memory performance. Less accurate saccades constitute a deviation from the saccade's intended consequence of targeting the cued location. The present analyses, however, do not allow us to distinguish between different causal mechanisms underlying the observed findings. First, it is possible that more accurate saccades were more closely targeting the underlying cortical space that maintained the memory representation. This view is in line with the idea of sensory recruitment (Harrison & Tong, 2009; Serences et al., 2009; for reviews see Pasternak & Greenlee, 2005; Serences, 2016), and suggests that early visual cortex could constitute an interface between visual working memory and the oculomotor system that accounts for the reported trial-by-trial variations. In consequence, it could explain the marked difference between our results and the findings of Greenwood et al. (2017): while we demonstrate that saccadic selection in memory and saccade metrics covary on an a single-trial level, saccade parameters and crowding remained uncorrelated even after standardization in their study. Arguably, a saccadic landing error is dependent on saccade execution (i.e., there is no saccadic error for saccades that were planned but never executed). Based on this reasoning, this mechanism would suggest that the execution of the saccade affects visual memory performance in addition to the established influences of saccade preparation on visual memory performance (Hanning et al., 2016). Second, it is possible that stronger memory representations lead to more accurate saccades. Note, however, that placeholders were visible throughout the trial and saccades could be performed accurately to these placeholders even without maintaining a memory representation of the oriented stimuli.

Saccade latency and landing error were associated with memory performance exclusively in congruent trials. This selective association suggests that saccade metrics and memory performance are linked beyond the influence of a global performance moderator arising from an observer’s attentive state (e.g., different levels of fatigue). For instance, a heightened attentive state may both decrease saccade latencies and increase overall memory performance. Such a general influence would affect congruent and incongruent trials alike. An association that exclusively manifests on congruent trials provides additional evidence for a tight functional coupling between visual memory and saccades.

We did not observe an association between saccadic peak velocity and memory performance. Thus, we did not observe changes in memory for high-vigor saccades beyond the impact of saccade latency. The lack of an association between peak velocity and memory performance, however, is not surprising given the relatively small variations in peak velocity for the same saccade amplitude in our experiments. Moreover, peak velocity and saccade duration may have larger influences on visual memory through the intra-saccadic stimulation. For these influences to show up one would need to ensure a larger range of saccade amplitudes and more natural backgrounds (Schweitzer, Doering, Seel, Raisch, & Rolfs, 2023).

Future experiments that aim to turn these observed associations between saccade metrics and performance in visual (memory) tasks into causal relationships promise to provide important insights into the large-scale architecture of information processing in active observers. For instance, combining the present experimental protocol with a manipulation that effectively alters saccade latencies (e.g., saccadic gap/overlap paradigm; Saslow, 1967; or rewarding short latency saccades in a subset of trials; Kawagoe et al., 1998) would allow us to test whether faster saccades are causing a superior selection of memory representations. Another limitation of our study is that we cannot further decompose contributions of the different memory load and movement cue delay conditions. We collapsed data across nine different experiments to establish a solid basis for analyzing the variations of memory performance and saccade metrics across the visual field. Consequently, our analyses likely underestimate the memory advantage at locations congruent with the saccade target as we included conditions that act against saccadic selection in visual working memory (e.g., very long movement cue delays and probabilistic manipulations that rendered the saccade target less likely to be probed).

While the mandatory shift of attention prior to saccade onset likely plays an important role in accounting for the observed influence on memory performance, there are differences between saccadic selection in memory and pre-saccadic attention shifts in vision. First, we observed a performance benefit across the entire visual field while pre-saccadic attention benefits in vision can be absent at the upper vertical meridian (Hanning et al., 2022). Second, pre-saccadic attention shifts, however, enhance visual performance at the intended target location independent of saccade accuracy on a given trial (Deubel & Schneider, 1996). Similarly, the prediction of the target stimulus in the fovea is unrelated to the specific saccade metrics (Kroell & Rolfs, 2022). In contrast to these findings, we here revealed an association of saccadic error and memory performance. Notably, linking saccade metrics, and hence the specific way in which an action is performed, to visual memory performance allows us to distinguish saccadic selection from covertly attending maintained representations in visual working memory in response to informative retro-cues (Griffin & Nobre, 2003; Landman et al., 2003; for a review see Souza & Oberauer, 2016). The link between saccade metrics and visual working memory performance is specific to an overt selection mechanism and therefore adds to the multiple differences between saccadic selection and covertly selecting representations in memory (for a detailed discussion see Heuer et al., 2020 and Ohl & Rolfs, 2017). One major difference is that benefits arising from informative retro-cues are strategic while memory advantages through saccadic selection are automatic and occur even if it is disadvantageous to prioritize information at the saccade target location (Ohl & Rolfs, 2017, 2020). Moreover, saccadic selection in memory is strongest right after disappearance of the memory array and decreases over the course of one second after memory array offset (Ohl & Rolfs, 2017). This contrasts with the time course observed for retro-cueing which is effective even several seconds after the stimulus has disappeared from view (Astle et al., 2012). Another difference is the role of memory load for the two selection mechanisms. While the costs and benefits for covertly attending to memory representations vary strategically as a function of memory load (Souza & Oberauer, 2016), the memory advantage following saccadic selection was independent of memory load (Ohl & Rolfs, 2020). In summary, these differences point to distinct mechanisms that underly saccadic selection in visual memory and covertly attending to memory representations.

Recent developments in our understanding of visual working memory stressed its functional role in linking visual signals to future actions (Heuer et al., 2020; Myers et al., 2017; Olivers & Roelfsema, 2020; van Ede, 2020; van Ede & Nobre, 2023), for instance by showing how action plans prioritize visual working memory representations (Trentin et al., 2023). This change in perspective suggests that the need to understand the control of memory contents through actions is as important as understanding the capacity limits of visual working memory (van Ede & Nobre, 2023). The mechanisms that select internal representations play a crucial role here, as does the level at which selection occurs (e.g., features vs. objects) and the way selection serves future actions (e.g., making them faster and more accurate). Selection can be top-down using informative cues (Griffin & Nobre, 2003; Landman et al., 2003) or as demonstrated here using actions such as saccadic eye movements or hand movements

(Hanning & Deubel, 2018; Heuer et al., 2017; Heuer & Schubö, 2017; see Heuer et al., 2020 for review), even in the absence of informative cues. Actions impact the selection of external visual information by enhancing visual performance at the saccade target location (Deubel & Schneider, 1996; Kowler et al., 1995; Rolfs & Carrasco, 2012; see Li et al., 2021 for review), for instance, by sharpening orientation tuning (Li et al., 2016; Ohl et al., 2017) and reshaping the peripheral sensitivity profile at the saccade target (Kroell & Rolfs, 2021). It is promising to assess in future studies how both selection mechanisms interact in a natural situation. An orchestrated and flexible selection between visual and remembered, task-relevant information would further lay out how finely vision, memory, and actions are attuned to each other to prepare effective actions in a complex visual environment.

Constraints on generality

Our study shows that saccadic selection in visual working memory is a robust behavior that is present in a large portion of the recruited healthy adults and across all directions in the visual field. Since the age range of our sample was limited, it is unknown what role this selection mechanism plays in elderly people or how it developed during childhood and adolescence. Similarly, it is unknown how saccadic selection in visual memory behaves in various patient groups. However, future studies of selective disorders—either in visual memory or in the oculomotor system—can improve our understanding of how saccade metrics and visual memory at the single-trial level are causally linked. Moreover, while we tested participants' memory for an isolated visual feature (i.e., oriented Gabors), future studies should compare whether saccades are equally effective in selecting entire objects of increasing complexity. Importantly, action-based selection in visual working memory has been observed for hand movements, suggesting that the findings reported here may well generalize across different actions (see Heuer et al., 2020 for a review).

References

Aagten-Murphy, D., & Bays, P. M. (2018). Functions of memory across saccadic eye movements. In T. Hodgson (Hrsg.), *Processes of visuospatial attention and working memory* (Bd. 41, S. 155–183). Springer International Publishing. https://doi.org/10.1007/7854_2018_66

Abrams, J., Nizam, A., & Carrasco, M. (2012). Isoeccentric locations are not equivalent: The extent of the vertical meridian asymmetry. *Vision Research*, *52*(1), 70–78. https://doi.org/10.1016/j.visres.2011.10.016

Anderson, J. E., Leslie Cameron, E., & Levine, M. W. (2014). A method for quantifying visual field inhomogeneities. *Vision Research*, *105*, 112–120. https://doi.org/10.1016/j.visres.2014.09.010

Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2012). Orienting attention to locations in mental representations. *Attention, Perception, & Psychophysics*, *74*, 146–162.

Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye movements. *Mathematical Biosciences*, *24*(3–4), 191–204. https://doi.org/10.1016/0025-5564(75)90075-9

Bahle, B., Matsukura, M., & Hollingworth, A. (2018). Contrasting gist-based and template-based guidance during real-world visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(3), 367–386. https://doi.org/10.1037/xhp0000468

Baldwin, A. S., Meese, T. S., & Baker, D. H. (2012). The attenuation surface for contrast sensitivity has the form of a witch's hat within the central visual field. *Journal of Vision*, *12*(11), 23. https://doi.org/10.1167/12.11.23

Barbot, A., Xue, S., & Carrasco, M. (2021). Asymmetries in visual acuity around the visual field. *Journal of Vision*, *21*(1), 2. https://doi.org/10.1167/jov.21.1.2

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, *321*(5890), 851–854. https://doi.org/10.1126/science.1158023

Beck, V. M., Hollingworth, A., & Luck, S. J. (2012). Simultaneous control of attention by multiple working memory representations. *Psychological Science*, *23*(8), 887–898. https://doi.org/10.1177/0956797612439068

Benson, N. C., Kupers, E. R., Barbot, A., Carrasco, M., & Winawer, J. (2021). Cortical magnification in human visual cortex parallels task performance around the visual field. *eLife*, *10*, e67685. https://doi.org/10.7554/eLife.67685

Bhidayasiri, R., Riley, D. E., Somers, J. T., Lerner, A. J., Buttner-Ennever, J. A., & Leigh, R. J. (2001). Pathophysiology of slow vertical saccades in progressive supranuclear palsy. *Neurology*, *57*(11), 2070–2077. https://doi.org/10.1212/WNL.57.11.2070

Brainard, D. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/doi:10.18637/jss.v080.i01

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research*, *42*(8), 949–967. https://doi.org/10.1016/S0042-6989(02)00039-1

Carrasco, M., Roberts, M., Myers, C., & Shukla, L. (2022). Visual field asymmetries vary between children and adults. *Current Biology*, *32*(11), R509–R510. https://doi.org/10.1016/j.cub.2022.04.052

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial vision*, *15*(1), 61–75.

Carrasco, M., Williams, P. E., & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: Support for signal enhancement. *Journal of Vision*, *2*(6), 467–479. https://doi.org/10.1167/2.6.4

Corbett, J. E., & Carrasco, M. (2011). Visual Performance Fields: Frames of Reference.

PLOS ONE, *6*(9), e24470. https://doi.org/10.1371/journal.pone.0024470

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617. https://doi.org/10.3758/BF03195489

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*(1), 87–114. https://doi.org/10.1017/S0140525X01003922

Curcio, C. A., & Allen, K. A. (1990). Topography of ganglion cells in human retina. *Journal of Comparative Neurology*, *300*(1), 5–25. https://doi.org/10.1002/cne.903000103

Curcio, C. A., Sloan, K. R., Kalina, R. E., & Hendrickson, A. E. (1990). Human photoreceptor topography. *Journal of Comparative Neurology*, *292*(4), 497–523. https://doi.org/10.1002/cne.902920402

Danckert, J., & Goodale, M. A. (2001). Superior performance for visually guided pointing in the lower visual field. *Experimental Brain Research*, *137*(3), 303–308. https://doi.org/10.1007/s002210000653

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837. https://doi.org/10.1016/0042-6989(95)00294-4

Draschkow, D., Nobre, A. C., & van Ede, F. (2022). Multiple spatial frames for immersive working memory. *Nature Human Behaviour*, *6*(4), 536–544. https://doi.org/10.1038/s41562-021-01245-y

Edgar, G. K., & Smith, A. T. (1990). Hemifield Differences in Perceived Spatial Frequency. *Perception*, *19*(6), 759–766. https://doi.org/10.1068/p190759

Efron, B., & Morris, C. (1977). Stein's Paradox in Statistics. *SCIENTIFIC AMERICAN*, 10.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences*, *103*(18), 7192–7197.

Foerster, R. M., & Schneider, W. X. (2020). Oculomotor capture by search-irrelevant features in visual working memory: On the crucial role of target–distractor similarity. *Attention, Perception, & Psychophysics*, *82*(5), 2379–2392. https://doi.org/10.3758/s13414-020-02007-0

Fracasso, A., Buonocore, A., & Hafed, Z.M. (2022). Peri-saccadic visual sensitivity is higher in the upper visual field. *bioRxiv*, 2022.07.05.498850. https://doi.org/10.1101/2022.07.05.498850

Fuller, S., & Carrasco, M. (2009). Perceptual consequences of visual performance fields: The case of the line motion illusion. *Journal of Vision*, *9*(4), 13. https://doi.org/10.1167/9.4.13

Fuller, S., Rodriguez, R. Z., & Carrasco, M. (2008). Apparent contrast differs across the vertical meridian: Visual and attentional factors. *Journal of Vision*, *8*(1), 16. https://doi.org/10.1167/8.1.16

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–472.

Goldring, J., & Fischer, B. (1997). Reaction times of vertical prosaccades and antisaccades in gap and overlap tasks. *Experimental brain research*, *113*(1), 88–103. https://doi.org/10.1007/BF02454145

Greene, H. H., Brown, J. M., & Dauphin, B. (2014). When do you look where you look? A visual field asymmetry. *Vision Research*, *102*, 33–40. https://doi.org/10.1016/j.visres.2014.07.012

Greenwood, J. A., Szinte, M., Sayim, B., & Cavanagh, P. (2017). Variations in crowding, saccadic precision, and spatial localization reveal the shared topology of spatial vision. *Proceedings of the National Academy of Sciences*, *114*(17), E3573–E3582. https://doi.org/10.1073/pnas.1615504114

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194. https://doi.org/10.1162/089892903322598139

Hanning, N. M., & Deubel, H. (2018). Independent effects of eye and hand movements on visual working memory. *Frontiers in Systems Neuroscience*, *12*, 37. https://doi.org/10.3389/fnsys.2018.00037

Hanning, N. M., Himmelberg, M. M., & Carrasco, M. (2022). Presaccadic attention enhances contrast sensitivity, but not at the upper vertical meridian. *IScience*, *25*(2), 103851. https://doi.org/10.1016/j.isci.2022.103851

Hanning, N. M., Jonikaitis, D., Deubel, H., & Szinte, M. (2016). Oculomotor selection underlies feature retention in visual working memory. *Journal of Neurophysiology*, *115*(2), 1071–1076. https://doi.org/10.1152/jn.00927.2015

Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632–635. https://doi.org/10.1038/nature07832

Hafed, Z. M., Chen, C. Y. (2016). Sharper, stronger, faster upper visual field representation in primate superior colliculus. *Current Biology, 26*(13), 1647–1658. https://doi.org/10.1016/j.cub.2016.04.059.

Henderson, J. M., & Hollingworth, A. (2003). Eye movements and visual memory: Detecting changes to saccade targets in scenes. *Perception & Psychophysics*, *65*(1), 58–71.

Henderson, M., & Serences, J. T. (2021). Biased orientation representations can be explained by experience with nonuniform training set statistics. *Journal of Vision*, *21*(8), 1–22. https://doi.org/10.1167/jov.21.8.10

Heuer, A., Crawford, J. D., & Schubö, A. (2017). Action relevance induces an attentional weighting of representations in visual working memory. *Memory & Cognition*, *45*(3), 413–427. https://doi.org/10.3758/s13421-016-0670-3

Heuer, A., Ohl, S., & Rolfs, M. (2020). Memory for action: A functional view of selection in visual working memory. *Visual Cognition*, *28*(5–8), 388–400. https://doi.org/10.1080/13506285.2020.1764156

Heuer, A., & Schubö, A. (2017). Selective weighting of action-related feature dimensions in visual working memory. *Psychonomic Bulletin & Review*, *24*(4), 1129–1134. https://doi.org/10.3758/s13423-016-1209-0

Himmelberg, M. M., Winawer, J., & Carrasco, M. (2020). Stimulus-dependent contrast sensitivity asymmetries around the visual field. *Journal of Vision*, *20*(9), 18. https://doi.org/10.1167/jov.20.9.18

Himmelberg, M. M., Winawer, J., & Carrasco, M. (2023). Polar angle asymmetries in visual perception and neural architecture. *Trends in Neurosciences, 46*(64), 445–458.

Hollingworth, A., & Luck, S. J. (2009). The role of visual working memory (VWM) in the control of gaze during visual search. *Attention, Perception, & Psychophysics*, *71*(4), 936–949. https://doi.org/10.3758/APP.71.4.936

Hollingworth, A., Richard, A. M., & Luck, S. J. (2008). Understanding the function of visual short-term memory: Transsaccadic memory, object correspondence, and gaze correction. *Journal of Experimental Psychology: General*, *137*(1), 163–181. https://doi.org/10.1037/0096-3445.137.1.163

Honda, H., & Findlay, J. M. (1992). Saccades to targets in three-dimensional space: Dependence of saccadic latency on target location. *Perception & Psychophysics, 52*(2), 167–174. https://doi.org/10.3758/BF03206770

Ince, R. A., Paton, A. T., Kay, J. W., & Schyns, P. G. (2021). Bayesian inference of population prevalence. *ELife*, *10*, 1–22. https://doi.org/10.7554/eLife.62461

Irving, E. L., & Lillakas, L. (2019). Difference between vertical and horizontal saccades across the human lifespan. *Experimental Eye Research*, *183*, 38–45. https://doi.org/10.1016/j.exer.2018.08.020

Irwin, D. E. (1991). Information integration across saccadic eye movements. *Cognitive Psychology*, *23*(3), 420–456. https://doi.org/10.1016/0010-0285(91)90015-G

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, *22*(3), 339–347. https://doi.org/10.1177/0956797610397666

Jonikaitis, D., Klapetek, A., & Deubel, H. (2017). Spatial attention during saccade decisions. *Journal of Neurophysiology*, *118*(1), 149–160.

Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology*, *110*(7), 1525–1534. https://doi.org/10.1152/jn.00275.2013

Kawagoe, R., Takikawa, Y., & Hikosaka, O. (1998). Expectation of reward modulates cognitive signals in the basal ganglia. *Nature Neuroscience*, *1*(5), 411-416.

Kleiner, M., Brainard, D. H., Pelli, D. G., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, *36*(14), 1–16.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916. https://doi.org/10.1016/0042-6989(94)00279-U

Kroell, L. M., & Rolfs, M. (2021). The peripheral sensitivity profile at the saccade target reshapes during saccade preparation. *Cortex*, *139*, 12–26.

Kupers, E. R., Benson, N. C., Carrasco, M., & Winawer, J. (2022). Asymmetries around the visual field: From retina to cortex to behavior. *PLOS Computational Biology*, *18*(1), e1009771. https://doi.org/10.1371/journal.pcbi.1009771

Kupers, E. R., Carrasco, M., & Winawer, J. (2019). Modeling visual performance differences 'around' the visual field: A computational observer approach. *PLOS Computational Biology*, *15*(5), e1007063. https://doi.org/10.1371/journal.pcbi.1007063

Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research*, *43*(2), 149–164. https://doi.org/10.1016/S0042-6989(02)00402-9

Lestrange-Anginieur, E. D., & Kee, C. (2020). Investigation of the impact of blur under mobile attentional orientation using a vision simulator. *PLOS ONE*, *15*(6), e0234380. https://doi.org/10.1371/journal.pone.0234380

Levine, M. W., & McAnany, J. J. (2005). The relative capabilities of the upper and lower visual hemifields. *Vision Research*, *45*(21), 2820–2830. https://doi.org/10.1016/j.visres.2005.04.001

Li, H.-H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology*, *26*(12), 1564–1570. https://doi.org/10.1016/j.cub.2016.04.028

Li, H.-H., Hanning, N. M., & Carrasco, M. (2021). To look or not to look: Dissociating presaccadic and covert spatial attention. *Trends in Neurosciences*, *44*(8), 669–686. https://doi.org/10.1016/j.tins.2021.05.002

Liu, T., Heeger, D. J., & Carrasco, M. (2006). Neural correlates of the visual vertical meridian asymmetry. *Journal of Vision*, *6*(11), 12. https://doi.org/10.1167/6.11.12

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–281. https://doi.org/10.1038/36846

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences*, *17*(8), 391–400. https://doi.org/10.1016/j.tics.2013.06.006

Marois, R., & Ivanoff, J. (2005). Capacity limits of information processing in the brain. *Trends in Cognitive Sciences*, *9*(6), 296–305. https://doi.org/10.1016/j.tics.2005.04.010

McAnany, J. J., & Levine, M. W. (2007). Magnocellular and parvocellular visual pathway contributions to visual field anisotropies. *Vision Research*, *47*(17), 2327–2336. https://doi.org/10.1016/j.visres.2007.05.013

Montaser-Kouhsari, L., & Carrasco, M. (2009). Perceptual asymmetries are preserved in short-term memory tasks. *Attention, Perception & Psychophysics*, *71*(8), 1782–1792. https://doi.org/10.3758/APP.71.8.1782

Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. *Trends in Cognitive Sciences*, *21*(6), 449–461. https://doi.org/10.1016/j.tics.2017.03.010

Nazir, T. A. (1992). Effects of lateral masking and spatial precueing on gap-resolution in central and peripheral vision. *Vision Research*, *32*(4), 771–777. https://doi.org/10.1016/0042-6989(92)90192-L

Ohl, S., Brandt, S. A., & Kliegl, R. (2013). The generation of secondary saccades without postsaccadic visual feedback. *Journal of Vision*, *13*(5), 1–13. https://doi.org/10.1167/13.5.11

Ohl, S., Kuper, C., & Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. *Journal of Vision*, *17*(13), 1–11. https://doi.org/10.1167/17.13.2

Ohl, S., & Rolfs, M. (2017). Saccadic eye movements impose a natural bottleneck on visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*(5), 736–748.

Ohl, S., & Rolfs, M. (2018). Saccadic selection of stabilized items in visuospatial working memory. *Consciousness and Cognition*, *64*, 32–44.

Ohl, S., & Rolfs, M. (2020). Bold moves: Inevitable saccadic selection in visual short-term memory. *Journal of Vision*, *20*(2), 1–14. https://doi.org/10.1167/jov.20.2.11

Olivers, C. N. L., Meijer, F., & Theeuwes, J. (2006). Feature-based memory-driven attentional capture: Visual working memory content affects visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(5), 1243–1265. https://doi.org/10.1037/0096-1523.32.5.1243

Olivers, C. N. L., & Roelfsema, P. R. (2020). Attention for action in visual working memory. *Cortex*, *131*, 179–194. https://doi.org/10.1016/j.cortex.2020.07.011

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*(4), 369–378. https://doi.org/10.3758/BF03210419

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, *6*(2), 97–107. https://doi.org/10.1038/nrn1603

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.

Pointer, J. S., & Hess, R. F. (1989). The contrast sensitivity gradient across the human visual field: With emphasis on the low spatial frequency range. *Vision Research*, *29*(9), 1133–1151. https://doi.org/10.1016/0042-6989(89)90061-8

Purokayastha, S., Roberts, M., & Carrasco-Queijeiro, M. (2020). *Voluntary attention improves performance similarly around the visual field*. PsyArXiv. https://doi.org/10.31234/osf.io/6fkys

R Core Team. (2022). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. URL https://www.R-project.org/.

Roberts, M., Ashinoff, B. K., Castellanos, F. X., & Carrasco, M. (2018). When attention is intact in adults with ADHD. *Psychonomic Bulletin & Review*, *25*(4), 1423–1434. https://doi.org/10.3758/s13423-017-1407-4

Roberts, M., Cymerman, R., Smith, R. T., Kiorpes, L., & Carrasco, M. (2016). Covert spatial attention is functionally intact in amblyopic human adults. *Journal of Vision*, *16*(15), 30. https://doi.org/10.1167/16.15.30

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *32*(40), 13744–13752. https://doi.org/10.1523/JNEUROSCI.2676-12.2012

Rolfs, M., & Ohl, S. (2021). Moving fast and seeing slow? The visual consequences of vigorous movement. *Behavioral & Brain Sciences*, *44*.

Rolfs, M., & Schweitzer, R. (2022). Coupling perception to action through incidental sensory consequences of motor behaviour. *Nature Reviews Psychology*, *1*(2), 112–123. https://doi.org/10.1038/s44159-021-00015-x

Rosén, R., Lundström, L., Venkataraman, A. P., Winter, S., & Unsbo, P. (2014). Quick contrast sensitivity measurements in the periphery. *Journal of Vision*, *14*(8), 3. https://doi.org/10.1167/14.8.3

Rouder, J. N., & Lu, J. (2005). An introduction to Bayesian hierarchical models with an application in the theory of signal detection. *Psychonomic Bulletin & Review*, *12*(4), 573–604. https://doi.org/10.3758/BF03196750

Rubin, N., Nakayama, K., & Shapley, R. (1996). Enhanced Perception of Illusory Contours in the Lower Versus Upper Visual Hemifields. *Science*, *271*(5249), 651–653.

https://doi.org/10.1126/science.271.5249.651

Saslow, M. G. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *Journal of the Optical Society of America*, *57*(8), 1024-1029.

Schmidtmann, G., Logan, A. J., Kennedy, G. J., Gordon, G. E., & Loffler, G. (2015). Distinct lower visual field preference for object shape. *Journal of Vision*, *15*(5), 18. https://doi.org/10.1167/15.5.18

Schut, M. J., Van der Stoep, N., Postma, A., & Van der Stigchel, S. (2017). The cost of making an eye movement: A direct link between visual working memory and saccade execution. *Journal of Vision*, *17*(6), 15. https://doi.org/10.1167/17.6.15

Schweitzer, R., Doering, M., Seel, T., Raisch, J., & Rolfs, M. (2023). Saccadic omission revisited: What saccade-induced smear looks like. *bioRxiv*, 2023-03.

Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*, *128*, 53–67. https://doi.org/10.1016/j.visres.2016.09.010

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science*, *20*(2), 207–214. https://doi.org/10.1111/j.1467-9280.2009.02276.x

Shadmehr, R., & Ahmed, A. A. (2020). *Vigor: Neuroeconomics of movement control*. MIT Press.

Shao, N., Li, J., Shui, R., Zheng, X., Lu, J., & Shen, M. (2010). Saccades elicit obligatory allocation of visual working memory. *Memory & Cognition*, *38*(5), 629–640. https://doi.org/10.3758/MC.38.5.629

Silva, M. F., Brascamp, J. W., Ferreira, S., Castelo-Branco, M., Dumoulin, S. O., & Harvey, B. M. (2018). Radial asymmetries in population receptive field size and cortical magnification factor in early visual cortex. *NeuroImage*, *167*, 41–52. https://doi.org/10.1016/j.neuroimage.2017.11.021

Smith, D. T. (2022). A horizontal–vertical anisotropy in spatial short-term memory. *Visual Cognition*, *30*(4), 245–253. https://doi.org/10.1080/13506285.2022.2042446

Song, H., Chui, T. Y. P., Zhong, Z., Elsner, A. E., & Burns, S. A. (2011). Variation of Cone Photoreceptor Packing Density with Retinal Eccentricity and Age. *Investigative Ophthalmology & Visual Science*, *52*(10), 7376–7384. https://doi.org/10.1167/iovs.11-7199

Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics*, *78*(7), 1839–1860. https://doi.org/10.3758/s13414-016-1108-5

Stan Development Team. (2021). *RStan: The R interface to Stan. R package version 2.21.3.*

Stanford, T. R., Shankar, S., Massoglia, D. P., Costello, M. G., & Salinas, E. (2010). Perceptual decision making in less than 30 milliseconds. *Nature Neuroscience*, *13*(3), 379–385.

Talgar, C. P., & Carrasco, M. (2002). *Vertical meridian asymmetry in spatial resolution: Visual and attentional factors*. *9*(4), 714–722.

Tas, A. C., Luck, S. J., & Hollingworth, A. (2016). The relationship between visual attention and visual working memory encoding: A dissociation between covert and overt orienting. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(8), 1121–1138. https://doi.org/10.1037/xhp0000212

Thomas, N. A., & Elias, L. J. (2011). Upper and lower visual field differences in perceptual asymmetries. *Brain Research*, *1387*, 108–115. https://doi.org/10.1016/j.brainres.2011.02.063

Tiadi, A., Seassau, M., Bui-Quoc, E., Gerard, C. L., & Bucci, M. P. (2014). Vertical saccades in dyslexic children. *Research in developmental disabilities*, *35*(11), 3175–3181. https://doi.org/10.1016/j.ridd.2014.07.057

Tootell, R. B., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. *Journal of Neuroscience*, *8*(5), 1531–1568. https://doi.org/10.1523/JNEUROSCI.08-05-01531.1988

Trentin, C., Slagter, H. A., & Olivers, C. N. (2023). Visual working memory representations bias attention more when they are the target of an action plan. *Cognition*, *230*, 105274.

Tzelepi, A., Laskaris, N., Amditis, A., & Kapoula, Z. (2010). Cortical activity preceding vertical saccades: a MEG study. *Brain research*, *1321*, 105–116. https://doi.org/10.1016/j.brainres.2010.01.002

Udale, R., Tran, M. T., Manohar, S., & Husain, M. (2022). Dynamic In-Flight Shifts of Working Memory Resources Across Saccades. *Journal of Experimental Psychology: Human Perception and Performance*, *48*(1), 21–36.

Van der Stigchel, S., & Hollingworth, A. (2018). Visuospatial Working Memory as a Fundamental Component of the Eye Movement System. *Current Directions in Psychological Science*, *27*(2), 136–143. https://doi.org/10.1177/0963721417741710

van Ede, F. (2020). Visual working memory and action: Functional links and bi-directional influences. *Visual Cognition*, *28*(5–8), 401–413. https://doi.org/10.1080/13506285.2020.1759744

van Ede, F., Board, A. G., & Nobre, A. C. (2020). Goal-directed and stimulus-driven selection of internal representations. *Proceedings of the National Academy of Sciences*, *117*(39), 24590–24598. https://doi.org/10.1073/pnas.2013432117

van Ede, F., Chekroud, S. R., & Nobre, A. C. (2019). Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour*, *3*(5), 462–470. https://doi.org/10.1038/s41562-019-0549-y

van Ede, F., & Nobre, A. C. (2023). Turning attention inside out: How working memory serves behavior. *Annual Review of Psychology, 74,* 137–165.

Van Essen, D. C., Newsome, W. T., & Maunsell, J. H. R. (1984). The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability. *Vision Research*, *24*(5), 429–448. https://doi.org/10.1016/0042-6989(84)90041-5

van Loon, A. M., Olmos-Solis, K., & Olivers, C. N. L. (2017). Subtle eye movement metrics reveal task-relevant representations prior to visual search. *Journal of Vision*, *17*(6), 1–15. https://doi.org/10.1167/17.6.13

Von Grünau, M., & Dubé, S. (1994). Visual search asymmetry for viewing direction. *Perception & Psychophysics*, *56*(2), 211–220. https://doi.org/10.3758/BF03213899

Watson, A. B. (2014). A formula for human retinal ganglion cell receptive field density as a function of visual field location. *Journal of Vision*, *14*(7), 15. https://doi.org/10.1167/14.7.15

Yan, Y., Zhaoping, L., & Li, W. (2018). Bottom-up saliency and top-down learning in the primary visual cortex of monkeys. *Proceedings of the National Academy of Sciences*, *115*(41), 10499–10504.

Zhou, W., & King, W. M. (2002). Attentional sensitivity and asymmetries of vertical saccade generation in monkey. *Vision Research, 42*(6), 771–779. https://doi.org/10.1016/S0042-6989(01)00319-4

Table 1. Estimates (in logits) of the Bayesian hierarchical model *bhm1* for predicting memory performance as a function on congruency.

Group-level effects for observers:	Estimate	Lower CI$_{95\%}$	Upper CI$_{95\%}$
Sd(Intercept)	0.48	0.40	0.57
Sd(Congruency)	0.26	0.20	0.33
Cor(Intercept, Congruency)	0.50	0.24	0.71
Group-level effects for experiments:	Estimate	Lower CI$_{95\%}$	Upper CI$_{95\%}$
Sd(Intercept)	0.21	0.02	0.49
Sd(Congruency)	0.12	0.01	0.29
Cor(Intercept, Congruency)	-0.21	-0.96	0.77
Population-level effects:	Estimate	Lower CI$_{95\%}$	Upper CI$_{95\%}$
Intercept	**0.72**	**0.53**	**0.92**
Congruency (dummy coded)	**0.41**	**0.29**	**0.53**

Table 2. Bayesian hierarchical model *bhm2* for comparing memory performance at the horizontal vs. vertical meridian (dummy coded with vertical meridian as 0 and horizontal meridian as 1) as a function of congruency (dummy coded with incongruent trials as 0 and congruent trials as 1) between saccade target and memory test location. For estimates of the group-level effects (observers and experiments) see OSF link.

Population-level effects:	Estimate	Lower $CI_{95\%}$	Upper $CI_{95\%}$
Intercept_vertical	**0.60**	**0.44**	**0.77**
Meridian_horizontal (dummy coded)	**0.30**	**0.12**	**0.48**
Congruency (dummy coded)	**0.50**	**0.37**	**0.64**
Meridian x Congruency	0.10	-0.08	0.29

Table 3. Estimates (in logits) of the Bayesian hierarchical model *bhm3* for comparing memory performance at the upper and lower visual field (dummy coded with upper field as 0 and lower field as 1) as a function of congruency (dummy coded with incongruent trials as 0 and congruent trials as 1) between saccade target and memory test location. For estimates of the group-level effects (observers and experiments) see OSF link.

Population-level effects:	Estimate	Lower $CI_{95\%}$	Upper $CI_{95\%}$
Intercept (upper field)	**0.65**	**0.46**	**0.84**
Visual field_lower (dummy coded)	0.06	-0.05	0.16
Congruency (dummy coded)	**0.31**	**0.19**	**0.44**
Visual field x Congruency	**0.15**	**0.04**	**0.26**

Table 4. Estimates (in logits) of the Bayesian hierarchical model *bhm4* for predicting memory performance as a function of memory test location and congruency between locations of the movement cue and memory test. For estimates of the group-level effects (observers and experiments) see OSF link.

Population-level effects:	Estimate	Lower $CI_{95\%}$	Upper $CI_{95\%}$
Intercept_North	0.59	0.41	0.78
Location_E	**0.20**	**0.03**	**0.37**
Location_SE	0.10	-0.04	0.25
Location_S	0.03	-0.08	0.14
Location_SW	**0.27**	**0.13**	**0.40**
Location_W	**0.49**	**0.31**	**0.67**
Location_NW	**0.19**	**0.07**	**0.32**
Location_NE	0.03	-0.07	0.14
Congruency_N (dummy coded)	**0.40**	**0.25**	**0.56**
Congruency x Location_E	0.22	-0.03	0.48
Congruency x Location_SE	-0.03	-0.22	0.17
Congruency x Location_S	**0.24**	**0.07**	**0.42**
Congruency x Location_SW	0.03	-0.16	0.24
Congruency x Location_W	0.11	-0.10	0.33
Congruency x Location_NW	-0.11	-0.28	0.06
Congruency x Location_NE	-0.15	-0.32	0.02

Table 5. Estimates Bayesian hierarchical model *bhm5* – *bhm8* for predicting memory performance as a function of standardized (within-location) saccade latency, saccade amplitude, saccade peak velocity, and saccadic landing error. For estimates of the group-level effects (observers and experiments) and family specific parameters see OSF link.

Population-level:				
	Latency	*Amplitude*	*Peak Velocity*	*Landing error*
	Estim. [95% CI]	Estim. [95% CI]	Estim. [95% CI]	Estim. [95% CI]
Intercept_North	**209 [196, 220]**	**5.27 [5.12, 5.42]**	**324 [305, 341]**	**1.34 [1.26, 1.41]**
Location_E	-1.7 [-4.5, 1.1]	**0.42 [.27, .57]**	**21.4 [9.9, 33.1]**	-0.01 [-.14, .12]
Location_SE	**3.7 [0.6, 6.8]**	**0.68 [.53, .83]**	**39.2 [22.1, 56.5]**	**0.25 [.07, .42]**
Location_S	**11.1 [7.9, 14.3]**	**0.55 [.36, .74]**	-1.6 [-16.6, 14.0]	0.21 [-.03, .44]
Location_SW	**5.3 [2.3, 8.3]**	**0.51 [.37, .65]**	**19.1 [6.3, 31.9]**	**0.25 [.13, .38]**
Location_W	0.3 [-2.9, 3.6]	**0.31 [.18, .45]**	**13.5 [2.0 25.1]**	-0.05 [-.17, .06]
Location_NW	-0.3 [-2.6, 2.1]	0.06 [-.03, .14]	3.8 [-5.1, 12.2]	0.06 [-.00, .12]
Location_NE	-1.5 [-3.7, 0.7]	**0.16 [.05, .28]**	**11.6 [1.4, 21.6]**	**0.09 [.02, .17]**
Congruency_N	-1.2 [-3.0, 0.6]	0.06 [-.03, .15]	3.2 [-7.8, 14.1]	-0.03 [-.10, .03]
Cong. x Loc_E	1.0 [-1.0, 3.1]	-0.06 [-.15, .02]	-6.3 [-21.6, 8.8]	-0.01 [-.07, .06]
Cong. x Loc_SE	-0.1 [-2.0, 1.8]	-0.03 [-.12, .07]	0.8 [-16.7, 19.1]	-0.01 [-.06, .04]
Cong. x Loc_S	0.6 [-2.6, 3.8]	-0.03 [-.14, .07]	-7.4 [-23.0, 8.6]	0.02 [-.04, .08]
Cong. x Loc_SW	-0.2 [-2.4, 2.0]	0.06 [-.07, .18]	10.4 [-14.9, 35.5]	-0.01 [-.06, .05]
Cong. x Loc_W	0.8 [-1.3, 2.8]	-0.05 [-.14, .05]	-2.9 [-18.7, 13.1]	0.02 [-.03, .08]
Cong. x Loc_NW	0.1 [-2.0, 2.3]	-0.04 [-.13, .05]	-10.9 [-26.4, 5.0]	0.00 [-.07, .05]
Cong. x Loc_NE	-0.03 [-2.0, 1.9]	-0.03 [-.11, .06]	-0.5 [-17.2, 16.3]	0.01 [-.06, .06]

Table 6. Estimates of Bayesian hierarchical model *bhm9 – bhm12* for associating location specific median posterior probabilities for memory performance and centered saccade metrics as a function of congruency (dummy coded with incongruent trials as 0 and congruent trials as 1) between saccade target and memory test location. Note, that these models did not include group-level effects. For estimates of the family specific parameters see OSF link.

Population-level:				
	Latency	*Amplitude*	*Landing error*	*Peak Velocity*
	Estim. [95% CI]	Estim. [95% CI]	Estim. [95% CI]	Estim. [95% CI]
Intercept (incong)	**0.68 [.65, .71]**	**0.68 [.65, .71]**	**0.68 [.65, .71]**	**0.68 [.64, .71]**
Metric (incong)	-0.00 [-.01 .01]	0.01 [-.13 .15]	-0.09 [-.38 .20]	-0.00 [-.00 .00]
Congruency	**0.09 [.04, .13]**	**0.09 [.04, .13]**	**0.08 [.04, .13]**	**0.09 [.04, .14]**
Cong. x Metric	0.00 [-.01, .01]	0.05 [-.14, .25]	0.02 [-.39, .43]	-0.00 [-.00, .00]

Table 7. Estimates of Bayesian hierarchical model *bhm13* for trial-by-trial analysis associating memory performance and standardized (z-transformed) saccade metrics as a function of congruency (dummy coded with incongruent trials as 0 and congruent trials as 1) between saccade target and memory test location. For estimates of the family specific parameters see OSF link.

Population-level effects:	Estimate	Lower $CI_{95\%}$	Upper $CI_{95\%}$
Intercept (incongruent)	**0.72**	**0.50**	**0.93**
Saccade latency (incongruent)	-0.01	-0.04	0.02
Saccade amplitude (incongruent)	0.00	-0.02	0.02
Saccade peak velocity (incongruent)	0.01	-0.02	0.03
Landing error (incongruent)	0.02	-0.02	0.05
Congruency	**0.41**	**0.29**	**0.54**
Congruency x saccade latency	**-0.11**	**-0.17**	**-0.06**
Congruency x saccade amplitude	0.06	-0.01	0.13
Congruency x saccade peak velocity	0.02	-0.04	0.07
Congruency x landing error	**-0.10**	**-0.15**	**-0.04**