Dynamic saccade context triggers more stable spatiotopic object-location binding

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Abstract

Despite receiving visual inputs in eye-centered (retinotopic) coordinates, we perceive the world-centered (spatiotopic) locations of objects. There is long-standing debate about how object representations attain visual stability across eye movements, with many studies reporting persistent retinotopic effects even for higher-level object-location binding. But these studies are generally conducted in fairly static experimental contexts. Might spatiotopic object-location binding only emerge in more dynamic saccade contexts? In the present study, we investigated this using the Spatial Congruency Bias paradigm. In a more static (single saccade) context, we found purely retinotopic binding, as before. However, robust spatiotopic binding emerged in the more dynamic (multiple frequent saccades) context. We further isolated specific factors that modulate retinotopic and spatiotopic binding. Our results provide strong evidence that dynamic saccade context can trigger more stable object-location binding in ecologically-relevant spatiotopic coordinates, perhaps via a more flexible brain state which accommodates improved visual stability in the dynamic world.

Key words: spatiotopic, retinotopic, object-location binding, visual stability

Introduction

One of the most fundamental challenges for human behavior is how we integrate and stabilize perceptual information in our ever-changing sensory environments. In particular, we make multiple eye movements every second, constantly displacing and distorting our visual input. Understanding how the human brain attains stable visual perception requires understanding both how spatial information is stabilized across eye movements and how this spatial information is integrated with visual feature and object representations.

As a real-world example, when we are searching for a red pen on a desk, we are able to not only recognize the shape and color of the pen but also the location of the pen. A great deal of research has gone into understanding how information about object identity and location are combined, often called object-location binding (Treisman, 1996). Traditionally, information regarding the 'where' and 'what' of an object has been considered to be processed through separate cognitive and neural processes (Goodale & Milner, 1992; Mishkin & Ungerleider, 1982). However, increasing studies have found interactions between object identity and spatial location during behavioral and neuroimaging studies (Carlson et al., 2011; Cichy et al., 2011; Gardner et al., 2008; Golomb & Kanwisher, 2012b; Gronau et al., 2008; Harris et al., 2020; Kovacs & Harris, 2019; Schneegans & Bays, 2017; Schwarzlose et al., 2008; Treisman & Gelade, 1980; Treisman & Zhang, 2006). Moreover, even when location is irrelevant or disadvantageous to the task, various behavioral paradigms have found that location can still be bound to object representations (Chen, 2009; Golomb et al., 2014; Tsal & Lavie, 1988). Thus, spatial location can be automatically encoded and bound to an object's representation during object recognition.

However, as we view the world and move our eyes, the input location of objects onto our eyes is constantly changing. This prompts the question, what is the spatial reference frame for object-location binding? When searching for the pen on the desk, we perceive the pen as having a static position in the world (spatiotopic, world-centered coordinates), even when eye movements change the pen's location on the retina (retinotopic, eye-centered coordinates). Thus, our brains should have the ability to link together an object's identity and its spatiotopic location when we are viewing something in the real world. However, evidence for spatiotopic object-location binding has proved elusive.

Even outside the context of object-location binding, it is controversial whether and how the brain represents spatial information in spatiotopic coordinates. While there is some evidence of neurons with spatiotopic selectivity in the parietal cortex (Duhamel et al., 1997; Snyder et al., 1998), most neurons involved in visual processing have retinotopic receptive fields that must remap, sometimes predictively (Duhamel et al., 1992), with each eye movement. It is still unresolved how object features and identity are processed across eye movements: is object-location binding instantiated in spatiotopic and/or retinotopic coordinates? If the latter, is binding automatically and predictively remapped, or is binding re-instantiated with each fixation? This puzzle has been referred to as the 'hard binding problem' (Cavanagh et al., 2010; Golomb & Mazer, 2021).

One recent approach to measure the spatial reference frame of object-location binding (Shafer-Skelton et al., 2017) used the Spatial Congruency Bias paradigm (Golomb et al., 2014), a behavioral paradigm that provides a robust measure of object-location binding. In the standard Spatial Congruency Bias task, participants are asked to judge whether two objects presented sequentially were of the same identity or not. Although object location is irrelevant to the task, if

the two sequential objects appeared in the same location, participants are more likely to judge them as the same identity, in contrast to if they appeared in different locations, showing that object location is automatically bound to and fundamentally influences perception of object identity. The Spatial Congruency Bias influences visual judgments ranging from orientation, color, shape, letters, facial identity, and expressions (Cave & Chen, 2017; Golomb et al., 2014; Shafer-Skelton et al., 2017; Starks et al., 2020), and it has been used to probe various aspects of object-location binding (Babu et al., in press; Bapat et al., 2017; Finlayson & Golomb, 2016; Gao et al., under review).

To investigate object-location binding across eye movements, Shafer-Skelton et al (2017) added a saccade during the delay between objects to distinguish retinotopic and spatiotopic bindings (Shafer-Skelton et al., 2017). Strikingly, they found that the Spatial Congruency Bias was preserved across the saccade, but entirely based in retinotopic coordinates, with no evidence for spatiotopic object-location binding even at longer post-saccade delays or for complex objects requiring higher-level processing (Shafer-Skelton et al., 2017).

Why don't we find spatiotopic object-location binding across saccades, when that is clearly the more ecologically relevant coordinate system for behavior? One option is that despite ecological relevance, visual information is simply always coded in native retinotopic coordinates. But an alternative option is that spatiotopic object-location binding might emerge only under certain contexts, and the prior studies were not designed in a way to tap into this. For example, the Shafer-Skelton et al (2017) study and other studies referenced above tend to rely on fairly static contexts to explore reference frames, where participants are asked to fixate on one location for an extended period of time, and perhaps execute a single saccade on each trial. In

contrast, in real life we are constantly executing multiple eye movements in rapid succession. Might these dynamic contexts play a role in visual stability?

Some recent findings hint that this may be the case, including an intriguing observation from an fMRI study that decoding of stimulus location in early visual cortex appeared to be eye-position dependent during stable fixation blocks, but became more tolerant during blocks where participants made multiple repeated saccades (Zhang et al., 2020). Some computational models have proposed that visual stability relies on both active and passive feedback mechanisms (Bergelt & Hamker, 2019; Sun & Goldberg, 2016), consistent with findings that active eye movements may provide important cues for integration of visual information (Golomb et al., 2011; Ross & Ma-Wyatt, 2003; Wexler & Van Boxtel, 2005). To our knowledge, it has never been investigated whether more dynamic contexts with multiple active eye movements may provide additional stability to form a more stable state, which could be particularly valuable during object recognition. This raises our crucial question: can a dynamic context with frequent eye movements help to trigger spatiotopic object-location binding? We hypothesize that our visual system has the ability to bind object information to spatiotopic coordinates under more dynamic saccade contexts, which are more ecological. Perhaps previous studies only found retinotopic effects because they did not fully induce the spatiotopic binding mechanism.

In the present study, our goal is to revisit the behavioral object-location binding question and ask whether dynamic saccade context, in contrast to more static contexts, can trigger spatiotopic object-location binding. In Experiment 1, we tested a dynamic saccade context where participants performed continual eye movements during the task and were asked to judge if two objects presented sequentially were the same identity or not at the end of each trial. In comparison, Experiment 2 was a control version of the task testing a static condition where

participant were asked to conduct only a single saccade during the delay between the two stimuli. We hypothesized that if the dynamic saccade context could trigger spatiotopic object-location binding, we might see a spatiotopic bias in Experiment 1; otherwise, we would expect similar retinotopic-only results in Experiment 1 and Experiment 2. To preview our results, we did in fact find a spatiotopic bias in Experiment 1, while replicating the previous retinotopic-only bias in Experiment 2. We then conducted two additional experiments (Experiment 3 and Experiment 4) to further isolate specific factors that might contribute to the influence of dynamic saccade context on spatiotopic object-location binding.

Results

Experiments 1 and 2: Dynamic saccade vs static fixation contexts.

Experiments 1 and 2 aimed to test whether dynamic saccade context can trigger spatiotopic object-location binding. In Experiment 1 (dynamic saccade context), participants were asked to perform a sequence of 8 eye movements on each trial (Figure 1A). At two points in the sequence, object stimuli appeared on the screen. Participants had to judge whether the two objects were the same or different identity. In Experiment 2 (static context), rather than the sequence of 8 saccades, participants were asked to conduct only one saccade in the middle of the trial, and the two object stimuli were presented during static fixation periods (Figure 1B). Experiment 2 is the same single-saccade Spatial Congruency Bias task that was used in Shafer-Skelton et al., 2017, but here we designed the timing, stimuli, and experimental design of the trials to perfectly match those in Experiment 1. In other words, Experiment 2 was identical to Experiment 1, save for the dynamic saccade context manipulation.

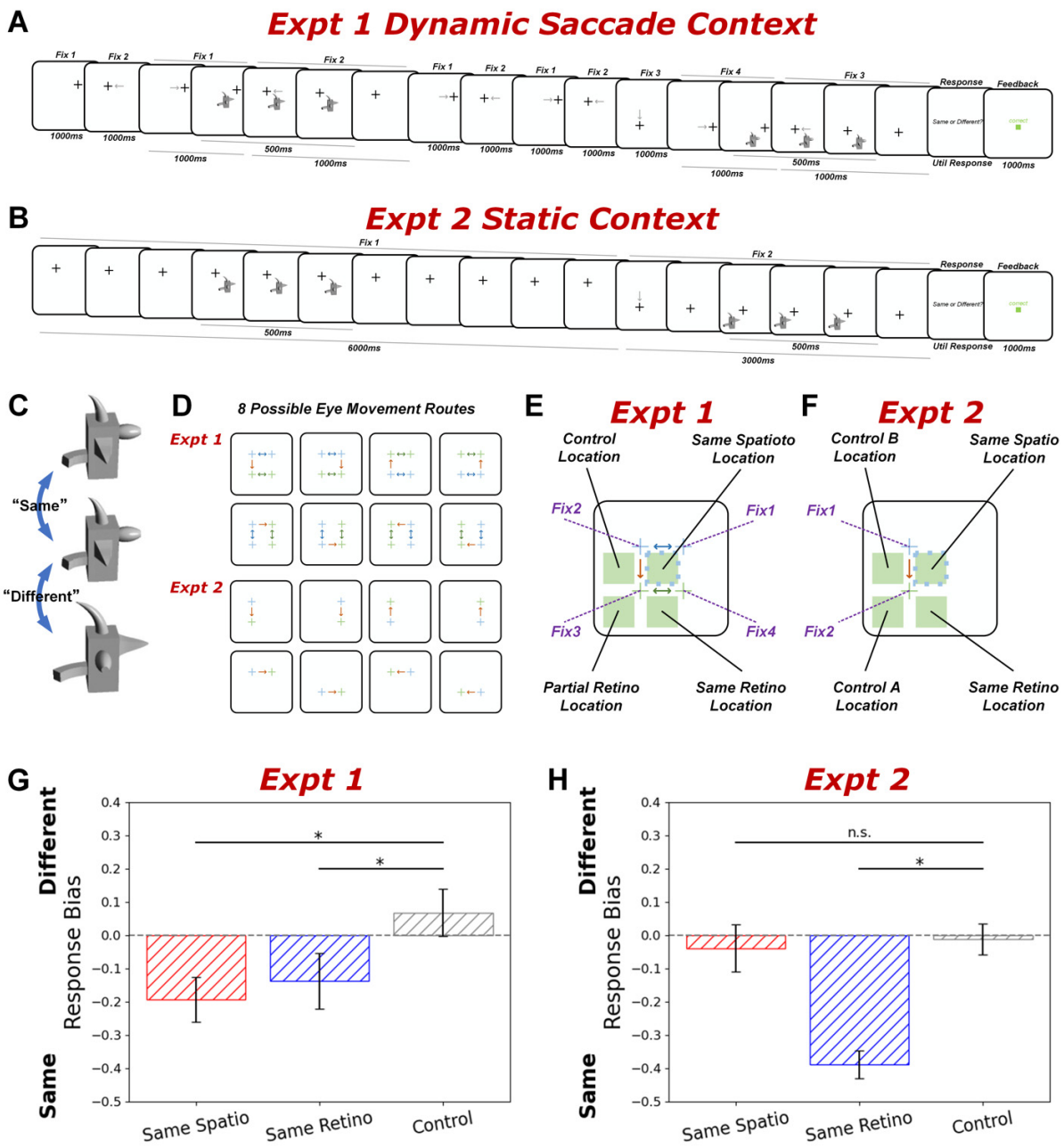

Figure 1. Methods and results of Experiment 1 and 2. (A) Trial timing for Experiment 1. While doing dynamic saccades, subjects saw two sequential object presentations. Subjects completed 8 saccades on each trial, two of which happened during the time the two stimuli appeared. The task was to judge whether two stimuli were the same or different identity. (B) Trial timing for Experiment 2. Subjects saw two sequential object presentations on each trial. Subjects completed only 1 saccade during the delay between two stimuli on each trial. The task was to judge whether two stimuli were the same or different identity. (C) Sample identity stimuli from a certain shape morph family. Left two stimuli are different, and right two stimuli are same. (D) 8 possible eye movement routes in two experiments. The brown arrow in Expt 1 was a critical saccade in an orthogonal direction to Fixation 3, which was consistent with the only arrow in Expt 2. (E) An illustration of 4 possible location conditions for Experiment 1. For a given Stimulus

1 location (blue dotted square), there were four possible locations for Stimulus 2 (indicated by four squares): Same Spatiotopic Location (same screen position as Stimulus 1), Same Retinotopic Location (same location as Stimulus 1 relative to 2 fixations during stimulus), Partial Retinotopic Location, and Control Location (different spatiotopic and retinotopic location). (F) An illustration of 4 possible location conditions for Experiment 2. For a given Stimulus 1 location (yellow dotted square), there were four possible locations for Stimulus 2 (indicated by four squares): Same Spatiotopic Location (same screen position as Stimulus 1), Same Retinotopic Location (same location as Stimulus 1 relative to the fixation), Control A Location (different spatiotopic and retinotopic location), and Control B Location (different spatiotopic and retinotopic location). (G) Response bias (criterion) on the identity task plotted for Same Spatiotopic, Same Retinotopic, and Control location conditions, for Experiment 1. A more negative response bias indicates a greater tendency to respond 'Same Identity'. (H) Response bias (criterion) on the identity task plotted Same Spatiotopic, Same Retinotopic, and Control (the average of Control A and Control B) location conditions, for Experiment 2. Error bars are standard error of the mean. Asterisk indicates p<.05 (paired t-tests between different conditions). Spatio = Spatiotopic; Retino = Retinotopic. See Supplemental Materials for tables *with full results for all behavioral measures and conditions.*

The task in the two experiments was to judge whether the identities of the two objects were the same or different; the objects could appear in different locations, but location was irrelevant to the task. In both experiments, the critical location conditions were Same Spatiotopic location (objects 1 and 2 appeared in the same absolute screen location) and Same Retinotopic location (objects 1 and 2 appeared in the same eye-centered location), which were compared to Control locations (object 2 appeared in a location that was different from object 1 in both retinotopic and spatiotopic coordinates; Figures 1A-B). To assess object-location binding, we calculated the Spatial Congruency Bias (SCB: Golomb et al., 2014).

The results in Experiment 1 revealed that participants were more likely to report the objects as the same identity when they appeared in the same spatiotopic or same retinotopic locations, compared to the control location (Figure 1G). Paired t-tests revealed a significant spatiotopic SCB (difference in response bias for Control vs. Same Spatiotopic, $t(15) = 3.6060$, $p = 0.0026$, $d = 0.9366$, $BF_{10} = 16.937$), and a significant retinotopic SCB (Control vs. Same Retinotopic, $t(15) = 2.6115$, $p = 0.0196$, $d = 0.6571$, $BF_{10} = 3.152$), with no significant difference between spatiotopic and retinotopic biases: $t(15) = -0.6686$, $p = 0.5139$, $d = 0.1822$, $BF_{10} =$

0.311). This contrasts with the results from Shafer-Skelton et al. (2017), which only found a significant retinotopic SCB in the more static single-saccade context.

To test whether it was in fact the dynamic saccade context that triggered spatiotopic object-location binding, we conducted Experiment 2 with an otherwise identical design but without the dynamic saccade context. In Experiment 2 (static context), we only found a significant retinotopic SCB (Control vs. Same Retinotopic: $t(15) = 8.8710$, $p < 0.001$, $d = 2.1290$, $BF_{10} = 65580$), similar to Shafer-Skelton et al, with no significant spatiotopic SCB (Control vs. Same Spatiotopic: $t(15) = 0.4661$, $p = 0.6478$, $d = 0.1113$, $BF_{10} = 0.281$) (Figure 1D), and a significantly greater retinotopic than spatiotopic bias ($t(15) = -5.5787$, $p < 0.001$, $d = 1.5088$, $BF_{10} = 503$).

A 2 × 2 ANOVA on the SCB measures with a within-subjects factor of Reference frame (Spatiotopic or Retinotopic) and an across-subjects factor of Experiment Context (dynamic saccade or static fixation) confirmed a significant interaction between reference frame and experimental context ($F(1, 30) = 15.213$, $p < 0.001$, $\eta^2 = 0.337$). The main effect for reference frame was also significant ($F(1, 30) = 8.032$, $p = 0.008$, $\eta^2 = 0.211$), while the main effect of experiment context was not ($F(1, 30) = 0.170$, $p = 0.683$, $\eta^2 = 0.006$).

Thus, these results suggest that dynamic saccade context can indeed play a critical role in creating spatiotopic object-location binding. Comparatively, static context only triggered retinotopic object-location binding.

Experiment 3 and 4: Which factors contribute to dynamic saccade context?

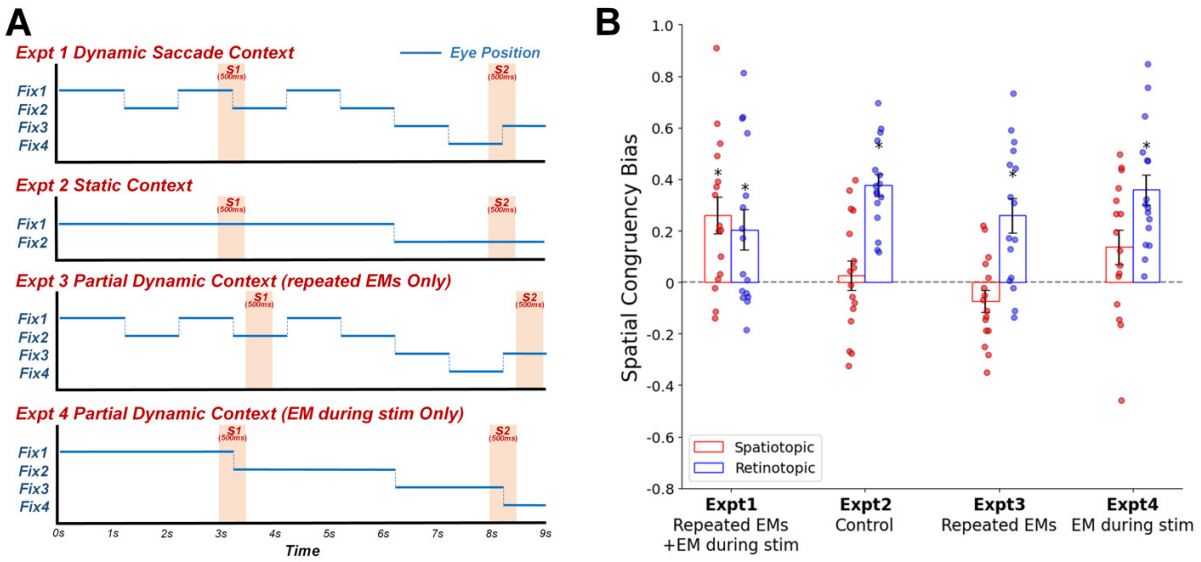

Figure 2. (A) Trial timing for all four experiments. The X-axis represents the time for each trial. The Y-axis represents the four possible fixation locations. The blue lines indicate eye positions during the task. The orange blocks indicate two stimuli on each trial. (B) Spatial congruency bias on the identity task plotted for spatiotopic and retinotopic conditions (spatiotopic congruency bias: Control bias minus Same Spatiotopic bias; retinotopic congruency bias: Control bias minus Same Retinotopic bias). Error bars are standard error of the mean. Asterisk indicates p<.05 (one-sample t-test for each condition). Spatio = Spatiotopic; Retino = Retinotopic; EM = eye movement, stim = stimulus. See Supplemental Materials for tables with full results for all behavioral measures and conditions.

Based on Experiments 1 and 2, we found that static context could only trigger retinotopic object-location binding, but dynamic saccade context could trigger both spatiotopic and retinotopic object-location binding. Design-wise, there were two factors that comprised the dynamic saccade context in Experiment 1: the presence of multiple repeated eye movements, and the fact that stimuli were presented peri-saccadically, with stimulus appearance timed to straddle an eye movement (Figure 2A). To test whether one or both of these factors was critical for triggering spatiotopic object-location binding, we separately manipulated these two factors in Experiments 3 and 4. In Experiment 3 (repeated eye movements only), subjects did 8 sequential saccades on each trial, as in Experiment 1. But here, the stimuli were timed to appear while subjects were stably fixating on one location, as in Experiment 2. In other words, the eye movements occurred

before and after, but not during, stimulus presentation in Experiment 3. Contrastingly, in Experiment 4, an eye movement occurred during the stimulus presentation, as in Experiment 1, but here subjects only did 3 saccades on each trial (the minimum necessary for the manipulation; Figure 2A). If being in a dynamic context with multiple repeated eye movements enhances or induces spatiotopic object-location binding, we would expect that Experiment 3 should show a significant spatiotopic SCB, similar to Experiment 1. On the other hand, if the critical aspect of the dynamic context is having eye movements during the stimulus presentation, then we would expect that Experiment 4 should resemble Experiment 1 with a spatiotopic SCB. Finally, if both factors are necessary for spatiotopic object-location binding, we would expect both Experiments 3 and 4 to more closely resemble Experiment 2, with only a retinotopic SCB.

To facilitate comparison across experiments, Figure 2B plots the spatiotopic and retinotopic SCBs for each experiment. Experiment 3 revealed a significant retinotopic SCB ($t(15) = 3.8460$, $p = 0.0016$, $d = 0.9615$, $BF_{10} = 25.739$), but no significant spatiotopic SCB ($t(15) = -1.7728$, $p = 0.0966$, $d = -0.4432$, $BF_{10} = 0.913$), and the retinotopic SCB was significantly stronger than the spatiotopic SCB ($t(15) = 5.7404$, $p < 0.0001$, $d = 1.3849$, $BF_{10} = 655.613$). Experiment 4 also revealed a significant retinotopic SCB ($t(15) = 6.0155$, $p < 0.001$, $d = 1.5039$, $BF_{10} = 1024.426$). The spatiotopic SCB was not significant ($t(15) = 2.0673$, $p = 0.0564$, $d = 0.5168$, $BF_{10} = 1.370$), but the Bayes factors suggested inconclusive evidence, with neither strong evidence for the presence or absence of a spatiotopic congruency bias. The retinotopic SCB was significantly greater than the spatiotopic SCB ($t(15) = -2.7880$, $p = 0.0138$, $d = -0.8844$, $BF_{10} = 4.201$).

The results of Experiments 3 and 4 suggest that both factors – multiple repeated eye movements and eye movements during the stimulus – are important for triggering spatiotopic

object-location binding, such that the two dynamic saccade factors may each be necessary, but not individually sufficient, to induce reliable spatiotopic binding. In constrast, retinotopic object-location binding was present in all contexts.

Across experiments analysis. In order to further compare object-location binding under these different conditions, we conducted an analysis across all four experiments to quantify how the two different factors (repeated eye movements and eye movement during stimulus) influence object-location binding. We first performed a 2 × 2 × 2 ANOVA with a within-subjects factor of Reference frame (Spatiotopic or Retinotopic) and across-subjects factors of Repeated eye movements factor (present or not) and Eye movement during stimulus factor (present or not). A significant main effect was found for reference frame ($F(1, 60) = 35.172$, $p < 0.001$, $\eta^2 = 0.370$). The main effects of repeated eye movements factor and eye movement during stimulus factor were not significant (repeated eye movements factor: $F(1, 60) = 1.527$, $p = 0.221$, $\eta^2 = 0.025$; eye movement during stimulus factor: $F(1, 60) = 3.390$, $p = 0.0710$, $\eta^2 = 0.053$), but there were significant interactions between reference frame and repeated eye movements factor ($F(1, 60) = 4.244$, $p = 0.044$, $\eta^2 = 0.066$), and reference frame and eye movement during stimulus factor ($F(1, 60) = 12.953$, $p < 0.001$, $\eta^2 = 0.178$). However, the interaction between the two across-subjects factors was not significant ($F(1, 60) = 0.859$, $p = 0.358$, $\eta^2 = 0.014$), nor was the 3-way interaction ($F(1, 60) = 3.307$, $p = 0.074$, $\eta^2 = 0.052$).

We followed with two separate 2 (Repeated eye movements factor) × 2 (Eye movement during stimulus factor) ANOVAs to assess how these two factors influence spatiotopic and retinotopic object-location binding respectively. For spatiotopic, a significant main effect was found for the eye movement during stimulus factor ($F(1, 60) = 13.538$, $p < 0.001$, $\eta^2 = 0.184$),

but not for the repeated eye movements factor ($F(1, 60) = 0.037$, $p = 0.848$, $\eta^2 = 0.001$). For retinotopic, a significant main effect was found for the repeated eye movements factor ($F(1, 60) = 4.616$, $p = 0.036$, $\eta^2 = 0.071$) but not for the eye movement during stimulus factor ($F(1, 60) = 0.328$, $p = 0.569$, $\eta^2 = 0.005$). There was no significant interaction between the two factors for either case (spatiotopic: $F(1, 60) = 3.445$, $p = 0.068$, $\eta^2 = 0.054$, retinotopic: $F(1, 60) = 0.086$, $p = 0.771$, $\eta^2 = 0.001$).

These across-experiments results suggest that both factors influence object-location binding. Having an eye movement during stimulus presentation seems to have a stronger effect on forming more stable spatiotopic object-location binding than the repeated eye movements factor. But as noted earlier, only in the experiment where both factors were present (Experiment 1) was spatiotopic object-location binding reliably triggered. Retinotopic object-location binding, on the other hand, was consistently significant in all four experiments, though the repeated eye movements factor might weaken the magnitude of the effect.

Sensitivity effects. The primary focus of this study was to examine the spatial congruency bias measure, which reflects a fundamental influence of object location on object identity judgement, to explore how dynamic saccade context influences object-location binding. However, the design also allows us to examine facilitation effects using the sensitivity measure d-prime. Some previous SCB studies have found a same-location sensitivity effect that co-existed with the spatial congruency bias, while others found only a spatial congruency bias but no sensitivity effect. Table S1 lists the sensitivity effects for the spatiotopic and retinotopic conditions, defined as the difference in sensitivity compared to the control location. The only significant sensitivity effect was retinotopic in Experiment 3. Consistent with the prior studies using the SCB

paradigm, the sensitivity measure thus appears to be a less consistent measure, especially compared to the SCB measure, which has proven to be a reliable and theoretically meaningful measure of object-location binding specifically (Cave & Chen, 2017; Golomb et al., 2014; Shafer-Skelton et al., 2017; Starks et al., 2020) .

Discussion

The current study revealed a striking effect with potentially broad theoretical implications: that dynamic saccade context can trigger spatiotopic object-location binding, whereas more static contexts produce retinotopic-only binding. We used the Spatial Conguency Bias behavioral paradigm (Golomb et al., 2014) to test the reference frame of object-location binding. For real-world visual stability, it would seem more important to encode an object's identity with the stable spatiotopic location, instead of the constantly-changing retinotopic location. Yet a previous series of studies using this paradigm to test whether object-location binding was tied to retinotopic and/or spatiotopic coordinates revealed purely retinotopic object-location binding, for stimuli ranging from gabors to novel objects to faces (Shafer-Skelton et al., 2017). However, these previous studies used a standard saccade manipulation where a single saccade occurred in the middle of each trial, during the delay when the stimulus disappeared. We speculated that a more dynamic saccade context might be more ecologically relevant and similar to our real lives. Thus, our current study used a novel experimental design to manipulate the number and timing of eye movements while subjects performed an object identity task.

Indeed, here when we employed a dynamic saccade context with multiple eye movements during the task, we found both strong spatiotopic and retinotopic spatial congruency biases. In contrast, in Experiment 2 we conducted a static context experiment similar to the Shafer-Skelton et al (2017) study, we replicated the finding of only retinotopic object-location binding. Thus, the presence of a more dynamic saccade context can starkly influence the reference frame of object-location binding, allowing spatiotopic effects to robustly emerge.

Our full set of results suggests that only the most dynamic and ecological experimental condition (Experiment 1), triggered reliable spatiotopic object representations (i.e., a spatiotopic

Spatial Congruency Bias). If there was only one saccade in the middle of the trial (static condition, Experiment 2), or only partially-dynamic conditions (repeated eye movements factor only, Experiment 3, or eye movement during stimulus factor only, Experiment 4), there was only retinotopic object-location binding.

Previous studies testing other aspects of visual perception have found mixed evidence for spatiotopic effects. Although some studies have found evidence of spatiotopic effects in visual memory, adaptation, and feature integration (Demeyer et al., 2009, 2010, 2011; Ezzati et al., 2008; Fairhall et al., 2017; Fischer & Whitney, 2014; Harrison & Bex, 2014; Hayhoe et al., 1991; Melcher & Morrone, 2003; Mikellidou et al., 2021; Prime et al., 2006; Steinberg et al., 2022; Turi & Burr, 2012; Van Eccelpoel et al., 2008; Wijdenes et al., 2015; Wittenberg et al., 2008; Wolfe & Whitney, 2015; Zimmermann et al., 2013), other studies only observed retinotopic evidence (Afraz & Cavanagh, 2009; Collins, 2019; Golomb et al., 2008; Golomb & Kanwisher, 2012a; Hui et al., 2020; McKyton et al., 2009; Shafer-Skelton et al., 2017; Shafer-Skelton & Golomb, 2018; Sheremata et al., 2023). As such, there has been a lot of debate over the years regarding reference frames for visual cognition across saccades (Cavanagh et al., 2010; Golomb & Mazer, 2021; Lappi, 2016; Marino & Mazer, 2016). Largely missing is an understanding of what factors are contributing to these different findings, and whether they can be effectively manipulated.

Here we took the novel approach of testing the role of dynamic saccade context, and isolating this factor across experiments using an otherwise identical design. Not only did we find both retinotopic and spatiotopic biases in dynamic saccade context, but also we replicated the prior finding of only retinotopic bias in static context (Shafer-Skelton et al., 2017). These results

suggest that there can be different reference frameworks of object-location binding under different conditions.

We find these clear conclusions for object-location binding, but our findings could also have implications for spatiotopic processing and remapping more broadly. An intriguing possibility is that the static vs dynamic saccade context may also explain why primarily retinotopic object representations have been found in some neuroimaging studies (Gardner et al., 2008; Golomb & Kanwisher, 2012b; Lu et al., 2022). Accordingly, it is possible that more spatiotopic neural representations might also emerge in more dynamic brain states.

The behavioral findings we report here may also provide some insight into and future directions for exploring the neural mechanisms of object-location binding across saccades. Various neural mechanisms underlying object-location binding have been proposed, including joint representations of object location and identity in feature-selective ventral areas (Gardner et al., 2008; Golomb & Kanwisher, 2012b; Majima et al., 2017; Reynolds & Desimone, 1999; Riesenhuber & Poggio, 1999; Vaziri-Pashkam & Xu, 2019), latent representations of task-irrelevant location decodable from different neural signals (Bae & Luck, 2018; Foster et al., 2017), synchronization of brain activity (Raffone & Wolters, 2001; Von Der Malsburg, 1999), and conjunctive coding (Op & Vogels, 2000; S. C. Rao et al., 1997). Most of this work has avoided the complication of eye movements and how our visual system establishes and maintains links between object identity and location across saccades.

In terms of this “hard binding problem” (Cavanagh et al., 2010), a few solutions have been speculated. One way spatiotopic object-location binding could be achieved is through a ‘remapping’ mechanism that updates both spatial location and feature/identity information with each saccade. Spatial remapping is well established (Duhamel et al., 1992; Hartmann et al.,

2017; Nakamura & Colby, 2002; Neupane et al., 2016; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997, 2001), but feature remapping is still unresolved (Cavanagh et al., 2010; Golomb, 2019; Golomb & Mazer, 2021; Lescroart et al., 2016; Melcher, 2007; O'Herron & von der Heydt, 2013; Subramanian & Colby, 2014). An alternative way to achieve spatiotopic binding is that the binding could be converted to a more stable spatiotopic state, and then would not need to be remapped or rebound with each saccade. We refer to this possibility as 'spatiotopic state conversion'. While it is possible in principle that this spatiotopic state could overwrite or remove retinotopic location binding altogether, our results suggest that it is more likely this spatiotopic binding would occur in addition to retinotopic representations. However, as noted above, neural evidence for large-scale spatiotopic organization has also proved controversial (Crespi et al., 2011; D'Avossa et al., 2007; Gardner et al., 2008; Golomb & Kanwisher, 2012b; McKyton & Zohary, 2007). Thus, it is difficult to differentiate the specific mechanism of spatiotopic object-location binding through our current study, but our study does suggest that the incorporation of more dynamic saccade context might prove insightful for neural studies of visual stability as well.

Finally, our current study isolated two ecologically key factors -- repeated eye movements and eye movement during stimulus – that can contribute to dynamic saccade context at the behavioral level. To our knowledge, this is the first time these factors have been isolated in this way. For example, a previous study on 3D spatial representations found that experimental blocks in which participants made repeated eye movements while viewing the stimulus induced more tolerant spatial position representations in human visual cortex, compared to experimental blocks containing no eye movements (Zhang et al., 2020). However, multiple factors simultaneously varied between these conditions. Moreover, the eye movements in that study

were guided in such a way that overlapping retinotopic visual stimulation could have partially accounted for the results; in contrast, in the current study, the critical eye movement separating the retinotopic and spatiotopic locations was in an orthogonal direction to the repeated saccades and saccade during the stimulus. For example, for the trial shown in Figure 1, Stimulus 1 appeared in the lower visual field; saccades made during the first half of the trial could have resulted in an expanded retinotopic area of stimulation spread across the lower visual field (hence the Partial Retinotopic condition), but after the critical saccade in the middle of the trials, the Same Spatiotopic location is now located in the upper visual field, a previously unstimulated retinotopic location. Another prior behavioral study explored spatial memory across eye movements and found that having a 2-second period of free viewing a background scene before the spatial memory stimulus could help facilitate spatiotopic memory (Steinberg et al., 2022), which the authors attributed to the availability of semantic content. Our current findings suggest the possibility that the eye movements themselves could have boosted spatiotopic processing; indeed, at least numerically it appeared that free viewing a blank screen for the same 2-second period also produced slightly improved spatiotopic memory, though a more conclusive test of this possibility would require comparing a preview with free viewing compared to an equivalent duration preview with static fixation.

According to our behavioral findings from four experiments, there might be a dynamic system of object-location binding. Object features seem to be bound to an object's native retinotopic location by default, and remain tied to retinotopic coordinates in more static contexts. But in more dynamic saccade contexts, spatiotopic object-location binding can also develop, suggesting that object representations can be automatically remapped or converted to reflect spatiotopic coordinates. Although the exact mechanism(s) supporting this spatiotopic binding

remains to be investigated, we speculate there might be a mechanism whereby an eye movement during the stimulus could be thought of as a gating factor; when present, that triggers the opening of the formation of the spatiotopic representation (but doesn't influence the existing retinotopic representation). However, opening the gate alone is not enough to reliably trigger spatiotopic binding, and repeated eye movements can thus induce a stronger dynamic brain state that encourages the brain to process the dynamic inputs to maintain visual stability, reinforcing more stable spatiotopic representations, while weakening the retinotopic representations (since repeated eye movements may result in a blurring of retinotopic input if not perfectly aligned).

As discussed above, the current study provides novel behavioral evidence for a critical role of dynamic saccade context, but future neural and computational work will be needed to build off these findings and probe which mechanism(s) elicit spatiotopic object-location binding in dynamic saccade context. An intriguing question is how this finding of dynamic saccade context triggering more stable object-location binding relates to different sources of remapping-related feedback, including the interplay between rapid, active corollary discharge signals and slower, more passive proprioceptive feedback signals (Bergelt & Hamker, 2019; H. M. Rao et al., 2016; Sun & Goldberg, 2016; Wurtz, 2008); information transfer across neural populations (So & Shadlen, 2022); and/or attentional pointers (Cavanagh et al., 2010).

In addition, the finding of dynamic saccade context triggering more stable spatiotopic effects may not be specific to object location binding. It is worth exploring whether this principle extends to perception of other visual features (low-level features: shape, orientation, color, etc.; high-level features: facial identity and expression, etc.), other forms of binding (property binding, part binding, range binding, hierarchical binding, conditional binding, and temporal binding) (Treisman, 1996), and other types of visual stability (generally spatial representations

across saccadic eye movements, during self-motion, and during the continuous tracking of moving objects) (Bridgeman, 2011), as well as how dynamic saccade context might interact with other cues for visual stability, such as visual landmarks (Deubel, 2004; McConkie & Currie, 1996; Verfaillie, 1997), and working memory.

In sum, our study offers a novel step forward in understanding the complex challenges of visual stability across eye movements and object-location binding. We provide strong evidence for dynamic saccade contexts, including both repeated eye movements and eye movement during stimulus, triggering an integrative brain state that creates a more stable object-location binding. In the real world, we indeed make eye movements during stimulus and repeated eye movements while observing the world. To some extent, our behavioral results confirm that these two factors are essential components of the dynamic saccade context triggering spatiotopic binding. These findings provide strong evidence that dynamic saccade context can trigger an integrative and dynamic brain state to form more stable object-location binding, which is crucial to improved understanding of how the brain achieves visual stability and how we form a stable perception of the dynamic world.

Method

Subjects. The research was approved by the Ohio State University Behavioral and Social Sciences Institutional Review Board. Each of the four experiments included 16 subjects (with a different set of subjects in each experiment). All subjects reported normal or corrected-to-normal vision and gave informed consent. Subjects were compensated with course credit or payment. Sample size was chosen in advance based on power analyses of previous spatial congruency bias studies. A power analysis of the original spatial congruency bias effect (Experiment 1 of Golomb

et al., 2014), which had an effect size of dz = 1.01 for the comparison of SameLocation versus DifferentLocation bias, estimated *N*=13 would be needed to achieve .9 power. Also, a power analysis of previous spatial congruency bias effect with one saccade (Experiment 4 of Shafer-Skelton et al., 2017), which had an effect size of dz = 0.92 for the comparision of RetinotopicLocation and ControlLocation, estimated *N* = 15 would be needed to achieve .9 power. We set sample size at N = 16 (matching prior studies), which should have sufficient power. Additional subjects completed the experiment but were excluded due to poor task performance (overall accuracy < 55% or hit rate < 50% or false alarm rate > 50 %; predetermined threshold).

Experimental setup. Stimuli were presented using Psychtoolbox extension (Brainard, 1997) for MATLAB (Math Works), on a 21-in (53.34-cm) flat screen CRT monitor. Subjects were seated at a chinrest 60 cm from the monitor.

Eye tracking. Eye position was monitored with an EyeLink 1000 eye-tracking system recording pupil and corneal reflection position. Fixation was monitored for all experiments.

Stimuli. Stimuli were the same as those in Golomb et al., 2014, from the Tarr stimulus set (stimulus images courtesy of Michael J. Tarr, Center for the Neural Basis of Cognition and Department of Psychology, Carnegie Mellon University, http://www.tarrlab.org). Stimuli were drawn from ten families of shape morphs; within each family, the "body" of the shape remained constant, while the "appendages" could vary in shape, length, or relative location. The Stimulus 1 shape was randomly chosen for each trial. On Same Shape trials, the Stimulus 2 shape was an identical image. On Different Shape trials, the second shape was chosen as a different shape from the same morph family (Figure 1C). We used the easiest morph level (the two images with the greatest morph distance within a family) for all subjects instead of individually staircasing

task difficulty because in Golomb et al., 2014 and Shafer-Skelton et al., 2017, participants were already within the desired accuracy range at this easiest morph level (maximum staircase value) in both no-saccade and saccade tasks. Stimuli were sized 6.25°×6.25°, and stimulus orientation was never varied.

General procedure. All experiments used the same stimuli, and subjects needed to follow the fixation point throughout the task. There were four possible fixation locations, centered on the screen and forming the corners of an invisible 10°×10° square, and nine possible stimulus locations, forming a 3×3 grid such that each fixation location had four adjacent stimulus locations of equal eccentricity with 7.06° (Figure 1B). Before the main task, subjects were asked to do a saccade pre-task and a practice task. For the saccade task, the location of fixation changed (from 4 possible fixation locations, only vertical or horizontal change) 50 times (once per second), and subject followed the fixation changes to do 50 saccades. We calculated the mean saccade time for each subject as the individual saccade reaction time used in the main task. For the practice task, each subject completed eight trials which were consistent with the trial in the main task.

Experiment 1: Dynamic saccade context. Figure 1A shows a sample trial timeline for Experiment 1. On each trial, the fixation cross first jumped back and forth between two Fixations (Fixation 1 and Fixation 2). During this first part of the trial, Stimulus 1 was presented. Then there was a critical saccade in an orthogonal direction to Fixation 3. Then the fixation cross jumped back and forth between Fixations 3 and 4; during this second part of the trial, Stimulus 2 was presented. The fixation cross stayed at each location for 1000ms. The fixation cross started at Fixation 1, and it changed 5 times between Fixation 1 and Fixation 2. Then the fixation cross

jumped from Fixation 2 to Fixation 3, then changed twice between Fixation 3 and Fixation 4. Subjects were asked to follow the fixation cross throughout the task (monitored via eye-tracking). There were 8 possible eye movement routes (Figure 1D).

Each object stimulus was shown for 500ms, and was designed to straddle an eye movement, such that the eye movement would occur during the stimulus presentation for full dynamic context. Ideally Stimulus 1 would be shown from approximately 250ms before to 250ms after the 3rd saccade, with Stimulus 2 straddling the 8th saccade with similar timing. Because there is variability in saccadic reaction times across individuals and trials, we did the following: First, we estimated each individual's average saccade reaction time (aSRT) from the saccade pre-task. Then, in the main task, we used the individualized aSRT to determine the onset of the stimulus relative to the saccade cue. For example, if saccade 3 was cued at t=3000ms, and that subject's aSRT was 185ms, then Stimulus 1 would be presented at 2935ms (saccade cue onset + aSRT - 250). We used an eye-tracker to monitor eye position to make sure the subjects made the saccade while the stimulus was presented. Moreover, if at any point the subject's fixation deviated greater than 2° from the current fixation, the trial was aborted and repeated later in the block.

After the last fixation, subjects saw the question 'Same or Different' and were instructed to make a two-alternative forced choice same/different judgement comparing the two objects' identities (shapes: Figure 1C); location was irrelevant to the task. Subjects responded by button press ('j' for 'Same' and 'k' for 'Different') and were presented with visual feedback ('correct' or 'incorrect' in green or red on the screen). They were also provided feedback if they broke fixation at any time during the trial ('Please do the saccade faster!' on the screen) or didn't give a response within 3 seconds ('No response' on the screen).

Stimulus 2 could appear in one of four possible location conditions (25% trials for each) (Figure 1E). The two main conditions of interest were Same Spatiotopic Location (the same absolute screen location as Stimulus 1) and Same Retinotopic Location (the same location as Stimulus 1 relative to 2 fixations during stimulus). These were compared to the Control Location condition (different spatiotopic and retinotopic location but at an equal eccentricity from Fixation 2). Finally, because the stimulus straddled the saccade and could have stimulated two different retinotopic positions, we also included a Partial Retinotopic Location condition (the same retinotopic location as Stimulus 1 relative to only one of 2 fixations during stimulus). We did not have clear hypotheses for this condition and do not analyze it further, but it was important to include as a separate condition so as not to contaminate either the Control Location or Same Retinotopic Location conditions.

The location of Stimulus 1 was chosen from one of two possible locations for a given eye movement route (based on the saccade from Fixation 2 to Fixation 3, such that all four Stimulus 2 location conditions were possible). For example, if Fixation 1 and Fixation 2 were the upper-right and upper-left fixation positions and the saccade from Fixation 2 to Fixation 3 was downward, Stimulus 1 could appear in either the middle-left or middle-middle position on the screen, such that the Same Spatiotopic, Same Retinotopic, Partial Retinotopic, and Control locations of Stimulus 2 were located at equal eccentricity from Fixation 3, which was the bottom-left fixation position. The identity of Stimulus 1 was chosen randomly, and Stimulus 2 could have either the same or different identity as Stimulus 1. These sixteen conditions (two Stimulus 1 location conditions × four Stimulus 2 location conditions × two identity conditions), along with eight possible eye movement routes, were counterbalanced and equally likely.

Subjects completed 8 blocks and 32 trials per block (256 trials in total, two trials for each of the 128 Stimulus 1 locations × Stimulus 2 location × identity × eye movement route conditions, in randomized order and randomly divided into 8 blocks), in addition to any trials that were aborted due to eye-tracking errors (which were repeated later in a randomized order within the same block).

Experiment 2: Static context. Figure 1B shows a sample trial timeline for Experiment 2. Unlike Experiment 1, Experiment 2 only had the one critical saccade in the middle of the trial. For a trial, the fixation cross began at one fixation location (Fixation 1) and remained there for 6000ms (matching the overall timing of Experiment 1). Stimulus 1 appeared for 500ms during this period, with the same timing as Experiment 1. Then, the fixation cross jumped to either the adjacent vertical or horizontal fixation location (Fixation 2) and stayed at the new fixation location for 3000ms. Stimulus 2 was presented for 500ms during this second period, again with the same timing in Experiment 1. There were 8 possible eye movement routes (Figure 1F).

Stimulus 2 could appear in one of four possible location conditions (25% trials for each) (Figure 1F). The two main conditions of interest were again the same absolute screen location (Same Spatiotopic Location), and the same location as Stimulus 1 relative to fixation (Same Retinotopic Location). Because there was never a saccade during the stimulus, there was no Partial Retinotopic condition in Experiment 2, so there were two control locations at an equal eccentricity from Fixation 2 (Control A Location and Control B Location). All other details were the same as Experiment 1. All conditions were counterbalanced and equally likely. Subjects completed 8 blocks with 32 trials per block, in addition to any trials that were aborted due to eye-tracking errors.

Experiment 3: Partial dynamic context with repeated eye movements only. The task was modified from Experiment 1. The timing of each trial was the same as in Experiment 1, except the onset times of the two stimuli were shifted such that they appeared during a fixation period instead of straddling a saccade (Figure 2A). In Experiment 3, ideally Stimulus 1 was shown from approximately 250ms to 750ms after the 3rd saccade completion time, and stimulus 2 from approximately 250ms to 750ms after the 8th saccade completion time. Like Experiment 1, because there was variability in saccadic reaction times across individuals and trials, we used the individualized aSRT to determine the saccade completion time and the onset of the stimulus. For example, if saccade 3 was cued at t=3000ms, and that subject's aSRT was 185ms, then Stimulus 1 would be presented at 3435ms (saccade cue onset + aSRT + 250). We utilized an eye-tracker to make sure that subjects were looking at only one fixation point when a stimulus appeared.

Stimulus 2 could appear in four possible locations, Same Spatiotopic Location, Same Retinotopic Location, Control A Location and Control B Location, similar to Experiment 2. All conditions were counterbalanced and equally likely. Subjects completed 8 blocks and 32 trials per, in addition to any trials that were aborted due to eye-tracking errors.

Experiment 4: Partial dynamic context with eye movement during stimulus only. The task was also modified from Experiment 1. In Experiment 4 the timing of the stimuli was the same as in Experiment 1 (eye movement during stimulus), but now there were fewer saccades. In order to preserve the design, we needed a minimum of three saccades per trial: One saccade during each stimulus, and the critical saccade in the middle of the trial to distinguish spatiotopic and retinotopic locations (Figure 2A). In Experiment 1, whereas subjects made four saccades

between Fixation 1 and Fixation 2 in the first part of the trial; in Experiment 4 subjects only made one saccade between Fixation 1 and Fixation 2. To best match overall timing, this first saccade occurred with the same timing as the 3rd saccade in Experiment 1, during the presentation of Stimulus 1. Similarly, subjects only made one saccade in the second part of the trial between Fixation 3 and Fixation 4, with the same timing as the 8th saccade in Experiment 1, during the presentation of Stimulus 2. The critical (middle) saccade was cued at the same time in all four experiments (Figure 2A).

Stimulus 2 could appear in four possible locations, the same as Experiment 1: Same Spatiotopic Location, Same Retinotopic Location, Partial Retinotopic Location and Control Location, similar to Experiment 1. All conditions were counterbalanced and equally likely. Subjects completed 8 blocks and 32 trials per block, in addition to any trials that were aborted due to eye-tracking errors.

Analysis. Our primary measure for all experiments was the spatial congruency bias, which is calculated as the difference in response bias for the same location versus a different location condition (Golomb et al., 2014). For each subject, we calculated hit and false alarm rates for each of the four location conditions. We defined a 'hit' as a 'Same' response when the two stimuli were actually the same (Same Identity condition), and a 'false alarm' as a 'Same' response when the two stimuli were different (Different Identity condition). Using signal detection theory, we applied the standard formula (Stanislaw & Todorov, 1999) to calculate response bias (criterion) for each subject, for each location condition:

$$\text{Response Bias} = -\frac{\text{z(hit rate)} + \text{z(false alarm rate)}}{2}$$

Note that, although it is often assumed that response bias measures reflect decision-level effects, response bias can also reflect perceptual-level processes, as in the case of the spatial congruency bias (Babu, et al., in press; Golomb et al., 2014; Shafer-Skelton et al., 2017; Witt et al., 2015).

To evaluate the spatial congruency bias (i.e., whether there was a greater bias to report two stimuli as the same identity when they appeared in the same retinotopic and//or spatiotopic location compared to a different location), we compared the response bias for the control location conditions to the response bias for the same spatiotopic and same retinotopic location conditions. For Experiments 1 and 4, the single "different" location (Control) was used for both Spatiotopic and Retinotopic comparisons; For Experiments 2 and 3, we used the average of Control A and Control B as the "different" location (Control) for both Spatiotopic and Retinotopic comparisons. We calculated the spatiotopic spatial congruency by subtracting Same Spatiotopic bias from Control bias, and the retinotopic spatial congruency bias by subtracting Same Retinotopic bias from Control bias. (Full comparisons across all pairs of conditions can also be found in Tables S3, S5, S7, and S9.)

The spatial congruency biases were calculated separately for each subject. One-sample t-tests were used to determine whether spatiotopic and retinotopic spatial congruency biases were significantly different from zero. Paired t-tests were used to determine whether spatiotopic and retinotopic congruency biases were significantly different from each other. We also report effect sizes using Cohen's d, and calculated Bayes factors of both one-sample and paired t-tests. We report both the frequentist and Bayesian statistics here.

To compare the effects between dynamic saccade and static fixation contexts, we performed a 2 × 2 ANOVA on the first two experiments with a within-subjects factor of

Reference frame (Spatiotopic or Retinotopic) and an across-subjects factor of Experiment Context factor (dynamic saccade or static fixation) for spatial congruency bias.

In addition, we conducted an across-experiments analysis across all four experiments to further explore how the two dynamic context factors (repeated eye movements and eye movements during stimulus) influence object-location binding. First, we performed a 2 × 2 × 2 ANOVA with a within-subjects factor of Reference frame (Spatiotopic or Retinotopic) and two across-subjects factors of Repeated eye movements (had or not) and Eye movement during stimulus (had or not) for spatial congruency bias. Then, we followed with two 2 (Repeated eye movements factor) × 2 (Eye movement during stimulus factor) ANOVAs to assess if there was a significant main effect or interaction for Spatiotopic and Retinotopic congruency biases respectively. For ANOVAs, effect size was calculated using partial eta-squared.

In supplementary materials, we also conducted the same analyses but assigned Control A to the Retinotopic Location and Control B to the Spatiotopic Location in Experiment 2 and 3, which was consistent with (Shafer-Skelton et al., 2017). Thus, we calculated the spatial congruency bias of spatiotopic and retinotopic conditions by subtracting Same Spatiotopic from Control B and subtracting Same Retinotopic from Control A in Experiment 2 and 3. The results are consistent with the main text reporting the average of Control A and B (Figure S1). Thus, how we choose Control doesn't affect our conclusions.

Finally, our main analyses focused on the spatial congruency bias, but we also calculated sensitivity (d') to measure possible facilitation effects. Here, we calculated d' using signal detection theory: d' = z(hit rate) – z(false alarm rate).

Before we analyzed the data, we excluded trials on which subjects responded with response times (RTs) greater than or less than 2.5 standard deviations from the subject's mean

RT for each subject. Tables S2-9 report the condition mean and statistics for all behavioral measures, including RT, accuracy, d-prime, and proportion 'Same' response.

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References

Afraz, A., & Cavanagh, P. (2009). The gender-specific face aftereffect is based in retinotopic not spatiotopic coordinates across several natural image transformations. *Journal of Vision*, *9*(10), 10–10. https://doi.org/10.1167/9.10.10

Babu, A. S., Scotti, P. S., & Golomb, J. D. (in press). The dominance of spatial information in object indentity judgements: A persistent congruency bias even amidst conflicting statistical regularities. *Journal of Experimental Psychology: Human Perception & Performance*.

Bapat, A. N., Shafer-Skelton, A., Kupitz, C. N., & Golomb, J. D. (2017). Binding object features to locations: Does the "spatial congruency bias" update with object movement? *Attention, Perception, and Psychophysics*, *79*(6), 1682–1694. https://doi.org/10.3758/S13414-017-1350-5/FIGURES/3

Bergelt, J., & Hamker, F. H. (2019). Spatial updating of attention across eye movements: A neuro-computational approach. *Journal of Vision*, *19*(7), 10–10. https://doi.org/10.1167/19.7.10

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Bridgeman, B. (2011). *Visual stability.* The Oxford Handbook of Eye Movements. https://psycnet.apa.org/record/2011-23569-028

Carlson, J. M., Foti, D., Mujica-Parodi, L. R., Harmon-Jones, E., & Hajcak, G. (2011). Ventral striatal and medial prefrontal BOLD activation is correlated with reward-related electrocortical activity: A combined ERP and fMRI study. *NeuroImage*, *57*(4), 1608–1616. https://doi.org/10.1016/J.NEUROIMAGE.2011.05.037

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153. https://doi.org/10.1016/J.TICS.2010.01.007

Cave, K. R., & Chen, Z. (2017). Two kinds of bias in visual comparison illustrate the role of location and holistic/analytic processing differences. *Attention, Perception, and Psychophysics*, *79*(8), 2354–2375. https://doi.org/10.3758/S13414-017-1405-7/TABLES/29

Chen, Z. (2009). Not all features are created equal: Processing asymmetries between location and object features. *Vision Research*, *49*(11), 1481–1491. https://doi.org/10.1016/J.VISRES.2009.03.008

Cichy, R. M., Chen, Y., & Haynes, J. D. (2011). Encoding the identity and location of objects in human LOC. *NeuroImage*, *54*(3), 2297–2307. https://doi.org/10.1016/J.NEUROIMAGE.2010.09.044

Collins, T. (2019). The perceptual continuity field is retinotopic. *Scientific Reports 2019 9:1*, *9*(1), 1–6. https://doi.org/10.1038/s41598-019-55134-6

Crespi, S., Biagi, L., d'Avossa, G., Burr, D. C., Tosetti, M., & Morrone, M. C. (2011). Spatiotopic Coding of BOLD Signal in Human Visual Cortex Depends on Spatial Attention. *PLOS ONE*, *6*(7), e21661. https://doi.org/10.1371/JOURNAL.PONE.0021661

D'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C., & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience*, *10*, 249–255. https://doi.org/10.1038/nn1824

Demeyer, M., de Graef, P., Verfaillie, K., & Wagemans, J. (2011). Perceptual Grouping of Object Contours Survives Saccades. *PLOS ONE*, *6*(6), e21257. https://doi.org/10.1371/JOURNAL.PONE.0021257

Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2009). Transsaccadic identification of highly similar artificial shapes. *Journal of Vision*, *9*(4), 28–28. https://doi.org/10.1167/9.4.28

Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2010). Parametric integration of visual form across saccades. *Vision Research*, *50*(13), 1225–1234. https://doi.org/10.1016/J.VISRES.2010.04.008

Deubel, H. (2004). Localization of targets across saccades: Role of landmark objects. *Visual Cognition*, *11*(2–3), 173–202. https://doi.org/10.1080/13506280344000284

Duhamel, J. R., Bremmer, F., BenHamed, S., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature 1997 389:6653*, *389*(6653), 845–848. https://doi.org/10.1038/39865

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The Updating of the Representation of Visual Space in Parietal Cortex by Intended Eye Movements. *Science*, *255*(5040), 90–92.

https://doi.org/10.1126/SCIENCE.1553535

Ezzati, A., Golzar, A., & Afraz, A. S. R. (2008). Topography of the motion aftereffect with and without eye movements. *Journal of Vision*, *8*(14), 23–23. https://doi.org/10.1167/8.14.23

Fairhall, S. L., Schwarzbach, J., Lingnau, A., Van Koningsbruggen, M. G., & Melcher, D. (2017). Spatiotopic updating across saccades revealed by spatially-specific fMRI adaptation. *NeuroImage*, *147*, 339–345. https://doi.org/10.1016/J.NEUROIMAGE.2016.11.071

Finlayson, N. J., & Golomb, J. D. (2016). Feature-location binding in 3D: Feature judgments are biased by 2D location but not position-in-depth. *Vision Research*, *127*, 49–56. https://doi.org/10.1016/J.VISRES.2016.07.003

Fischer, J., & Whitney, D. (2014). Serial dependence in visual perception. *Nature Neuroscience 2014 17:5*, *17*(5), 738–743. https://doi.org/10.1038/nn.3689

Gardner, J. L., Merriam, E. P., Movshon, J. A., & Heeger, D. J. (2008). Maps of Visual Space in Human Occipital Cortex Are Retinotopic, Not Spatiotopic. *Journal of Neuroscience*, *28*(15), 3988–3999. https://doi.org/10.1523/JNEUROSCI.5476-07.2008

Gao, M., Starks. M. D., Golomb, J. D., & Sloutsky, V. (under review). The development of visual cognition: The emergence of spatial congruency bias.

Golomb, J. D. (2019). Remapping locations and features across saccades: a dual-spotlight theory of attentional updating. *Current Opinion in Psychology*, *29*, 211–218. https://doi.org/10.1016/J.COPSYC.2019.03.018

Golomb, J. D., Albrecht, A. R., Park, S., & Chun, M. M. (2011). Eye Movements Help Link Different Views in Scene-Selective Cortex. *Cerebral Cortex*, *21*(9), 2094–2102.

https://doi.org/10.1093/CERCOR/BHQ292

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The Native Coordinate System of Spatial Attention Is Retinotopic. *Journal of Neuroscience*, *28*(42), 10654–10662. https://doi.org/10.1523/JNEUROSCI.2525-08.2008

Golomb, J. D., & Kanwisher, N. (2012a). Retinotopic memory is more precise than spatiotopic memory. *Proceedings of the National Academy of Sciences*, *109*(5), 1796–1801. https://doi.org/10.1073/PNAS.1113168109

Golomb, J. D., & Kanwisher, N. (2012b). Higher Level Visual Cortex Represents Retinotopic, Not Spatiotopic, Object Location. *Cerebral Cortex*, *22*(12), 2794–2810. https://doi.org/10.1093/CERCOR/BHR357

Golomb, J. D., Kupitz, C. N., & Thiemann, C. T. (2014). The influence of object location on identity: A "spatial congruency bias". *Journal of Experimental Psychology: General*, *143*(6), 2262. https://doi.org/10.1037/XGE0000017

Golomb, J. D., & Mazer, J. A. (2021). Visual Remapping. *Annual Review of Vision Science*, *7*, 257–277. https://doi.org/10.1146/ANNUREV-VISION-032321-100012

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. In *Trends in Neurosciences* (pp. 20–25). https://doi.org/10.1016/0166-2236(92)90344-8

Gronau, N., Neta, M., & Bar, M. (2008). Integrated Contextual Representation for Objects' Identities and Their Locations. *Journal of Cognitive Neuroscience*, *20*(3), 371–388. https://doi.org/10.1162/JOCN.2008.20027

Harris, I. M., Harris, J. A., & Corballis, M. C. (2020). Binding identity and orientation in object recognition. *Attention, Perception, and Psychophysics*, *82*(1), 153–167.

https://doi.org/10.3758/S13414-019-01677-9/FIGURES/4

Harrison, W. J., & Bex, P. J. (2014). Integrating Retinotopic Features in Spatiotopic Coordinates. *Journal of Neuroscience*, *34*(21), 7351–7360. https://doi.org/10.1523/JNEUROSCI.5252-13.2014

Hartmann, T. S., Zirnsak, M., Marquis, M., Hamker, F. H., & Moore, T. (2017). Two types of receptive field dynamics in area v4 at the time of eye movements? *Frontiers in Systems Neuroscience*, *11*, 13. https://doi.org/10.3389/FNSYS.2017.00013/BIBTEX

Hayhoe, M., Lachter, J., & Feldman, J. (1991). Integration of form across saccadic eye movements. *Perception*, *20*(3), 393–402. https://doi.org/10.1068/p200393

Hui, J., Wang, Y., Zhang, P., Tse, P. U., & Cavanagh, P. (2020). Apparent Motion Is Computed in Perceptual Coordinates. *I-Perception*, *11*(4). https://doi.org/10.1177/2041669520933309/ASSET/IMAGES/LARGE/10.1177_2041669520933309-FIG2.JPEG

Kovacs, O., & Harris, I. M. (2019). The role of location in visual feature binding. *Attention, Perception, and Psychophysics*, *81*(5), 1551–1563. https://doi.org/10.3758/S13414-018-01638-8/FIGURES/9

Lappi, O. (2016). Eye movements in the wild: Oculomotor control, gaze behavior & frames of reference. *Neuroscience & Biobehavioral Reviews*, *69*, 49–68. https://doi.org/10.1016/J.NEUBIOREV.2016.06.006

Lescroart, M. D., Kanwisher, N., & Golomb, J. D. (2016). No evidence for automatic remapping of stimulus features or location found with fMRI. *Frontiers in Systems Neuroscience*, *10*(JUN), 53. https://doi.org/10.3389/FNSYS.2016.00053/ABSTRACT

Lu, Z., Shafer-Skelton, A., & Golomb, J. (2022). Gaze-centered spatial representations in human hippocampus. *2022 Conference on Cognitive Computational Neuroscience*, 614–616. https://doi.org/10.32470/ccn.2022.1088-0

Majima, K., Sukhanov, P., Horikawa, T., & Kamitani, Y. (2017). Position Information Encoded by Population Activity in Hierarchical Visual Areas. *ENeuro*, *4*(2). https://doi.org/10.1523/ENEURO.0268-16.2017

Marino, A. C., & Mazer, J. A. (2016). Perisaccadic updating of visual representations and attentional states: Linking behavior and neurophysiology. *Frontiers in Systems Neuroscience*, *10*(FEB), 3. https://doi.org/10.3389/FNSYS.2016.00003/BIBTEX

McConkie, G. W., & Currie, C. B. (1996). Visual Stability Across Saccades while Viewing Complex Pictures. *Journal of Experimental Psychology: Human Perception and Performance*, *22*(3), 563–581. https://doi.org/10.1037/0096-1523.22.3.563

McKyton, A., Pertzov, Y., & Zohary, E. (2009). Pattern matching is assessed in retinotopic coordinates. *Journal of Vision*, *9*(13), 19–19. https://doi.org/10.1167/9.13.19

McKyton, A., & Zohary, E. (2007). Beyond Retinotopic Mapping: The Spatial Representation of Objects in the Human Lateral Occipital Complex. *Cerebral Cortex*, *17*(5), 1164–1172. https://doi.org/10.1093/CERCOR/BHL027

Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, *10*(7), 903–907. https://doi.org/10.1038/nn1917

Melcher, D., & Morrone, M. C. (2003). Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nature Neuroscience 2003 6:8*, *6*(8), 877–881. https://doi.org/10.1038/nn1098

Mikellidou, K., Cicchini, G. M., & Burr, D. C. (2021). Perceptual History Acts in World-Centred Coordinates. *I-Perception*, *12*(5). https://doi.org/10.1177/20416695211029301/ASSET/IMAGES/LARGE/10.1177_20416695211029301-FIG2.JPEG

Mishkin, M., & Ungerleider, L. G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behavioural Brain Research*, *6*(1), 57–77. https://doi.org/10.1016/0166-4328(82)90081-X

Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(6), 4026–4031. https://doi.org/10.1073/PNAS.052379899/SUPPL_FILE/3798FIG9LEGEND.HTML

Neupane, S., Guitton, D., & Pack, C. C. (2016). Two distinct types of remapping in primate cortical area V4. *Nature Communications 2016 7:1*, *7*(1), 1–11. https://doi.org/10.1038/ncomms10402

O'Herron, P., & von der Heydt, R. (2013). Remapping of Border Ownership in the Visual Cortex. *Journal of Neuroscience*, *33*(5), 1964–1974. https://doi.org/10.1523/JNEUROSCI.2797-12.2013

Op, H., & Vogels, R. (2000). Spatial Sensitivity of Macaque Inferior Temporal Neurons. *J. Comp. Neurol*, *426*, 505–518. https://doi.org/10.1002/1096-9861

Prime, S. L., Niemeier, M., & Crawford, J. D. (2006). Transsaccadic integration of visual features in a line intersection task. *Experimental Brain Research*, *169*(4), 532–548. https://doi.org/10.1007/S00221-005-0164-1/FIGURES/9

Raffone, A., & Wolters, G. (2001). A Cortical Mechanism for Binding in Visual Working Memory. *Journal of Cognitive Neuroscience*, *13*(6), 766–785. https://doi.org/10.1162/08989290152541430

Rao, H. M., Mayo, J. P., & Sommer, M. A. (2016). Circuits for presaccadic visual remapping. *Journal of Neurophysiology*, *116*(6), 2624–2636. https://doi.org/10.1152/JN.00182.2016/ASSET/IMAGES/LARGE/Z9K0121639080005.JPEG

Rao, S. C., Rainer, G., & Miller, E. K. (1997). Integration of What and Where in the Primate Prefrontal Cortex. *Science*, *276*(5313), 821–824. https://doi.org/10.1126/SCIENCE.276.5313.821

Reynolds, J. H., & Desimone, R. (1999). The Role of Neural Mechanisms of Attention in Solving the Binding Problem. *Neuron*, *24*(1), 19–29. https://doi.org/10.1016/S0896-6273(00)80819-3

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience 1999 2:11*, *2*(11), 1019–1025. https://doi.org/10.1038/14819

Ross, J., & Ma-Wyatt, A. (2003). Saccades actively maintain perceptual continuity. *Nature Neuroscience 2003 7:1*, *7*(1), 65–69. https://doi.org/10.1038/nn1163

Schneegans, S., & Bays, P. M. (2017). Neural Architecture for Feature Binding in Visual Working Memory. *Journal of Neuroscience*, *37*(14), 3913–3925. https://doi.org/10.1523/JNEUROSCI.3493-16.2017

Schwarzlose, R. F., Swisher, J. D., Dang, S., & Kanwisher, N. (2008). The distribution of category and location information across object-selective regions in human visual cortex.

Proceedings of the National Academy of Sciences of the United States of America, *105*(11), 4447–4452. https://doi.org/10.1073/PNAS.0800431105/SUPPL_FILE/00431FIG7.JPG

Shafer-Skelton, A., & Golomb, J. D. (2018). Memory for retinotopic locations is more accurate than memory for spatiotopic locations, even for visually guided reaching. *Psychonomic Bulletin and Review*, *25*(4), 1388–1398. https://doi.org/10.3758/S13423-017-1401-X/FIGURES/3

Shafer-Skelton, A., Kupitz, C. N., & Golomb, J. D. (2017). Object-location binding across a saccade: A retinotopic spatial congruency bias. *Attention, Perception, and Psychophysics*, *79*(3), 765–781. https://doi.org/10.3758/S13414-016-1263-8/TABLES/5

Sheremata, S., Malcolm, G. L., & Shomstein, S. (2023). Behavioral asymmetries in visual short-term memory occur in retinotopic coordinates. *Attention, Perception, and Psychophysics*, *85*(1), 113–119. https://doi.org/10.3758/S13414-022-02610-3/FIGURES/3

Snyder, L. H., Grieve, K. L., Brotchie, P., & Andersen, R. A. (1998). Separate body- and world-referenced representations of visual space in parietal cortex. *Nature 1998 394:6696*, *394*(6696), 887–891. https://doi.org/10.1038/29777

So, N. Y., & Shadlen, M. N. (2022). Decision formation in parietal cortex transcends a fixed frame of reference. *Neuron*, *110*(19), 3206-3215.e5. https://doi.org/10.1016/J.NEURON.2022.07.019

Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature 2006 444:7117*, *444*(7117), 374–377. https://doi.org/10.1038/nature05279

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior*

Research Methods, Instruments, & Computers 1999 31:1, *31*(1), 137–149. https://doi.org/10.3758/BF03207704

Starks, M. D., Shafer-Skelton, A., Paradiso, M., Martinez, A. M., & Golomb, J. D. (2020). The influence of spatial location on same-different judgments of facial identity and expression. *Journal of Experimental Psychology: Human Perception and Performance*, *46*(12), 1538–1552. https://doi.org/10.1037/XHP0000872

Steinberg, N. J., Roth, Z. N., & Merriam, E. P. (2022). Spatiotopic and retinotopic memory in the context of natural images. *Journal of Vision*, *22*(4), 11–11. https://doi.org/10.1167/JOV.22.4.11

Subramanian, J., & Colby, C. L. (2014). Shape selectivity and remapping in dorsal stream visual area LIP. *Journal of Neurophysiology*, *111*(3), 613–627. https://doi.org/10.1152/JN.00841.2011/ASSET/IMAGES/LARGE/Z9K0031422860010.JPEG

Sun, L. D., & Goldberg, M. E. (2016). Corollary Discharge and Oculomotor Proprioception: Cortical Mechanisms for Spatially Accurate Vision. *Annual Review of Vision Science*, *2*, 61–84. https://doi.org/10.1146/ANNUREV-VISION-082114-035407

Treisman, A. M. (1996). The binding problem. *Current Opinion in Neurobiology*, *6*(2), 171–178. https://doi.org/10.1016/S0959-4388(96)80070-5

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136. https://doi.org/10.1016/0010-0285(80)90005-5

Treisman, A. M., & Zhang, W. (2006). Location and binding in visual working memory. *Memory & Cognition 2006 34:8*, *34*(8), 1704–1719. https://doi.org/10.3758/BF03195932

Tsal, Y., & Lavie, N. (1988). Attending to color and shape: The special role of location in selective visual processing. *Perception & Psychophysics 1988 44:1*, *44*(1), 15–21. https://doi.org/10.3758/BF03207469

Turi, M., & Burr, D. (2012). Spatiotopic perceptual maps in humans: evidence from motion adaptation. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1740), 3091–3097. https://doi.org/10.1098/RSPB.2012.0637

Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology*, *78*(3), 1373–1383. https://doi.org/10.1152/JN.1997.78.3.1373/ASSET/IMAGES/LARGE/JNP.SE10F10.JPEG

Umeno, M. M., & Goldberg, M. E. (2001). Spatial processing in the monkey frontal eye field. II. Memory responses. *Journal of Neurophysiology*, *86*(5), 2344–2352. https://doi.org/10.1152/JN.2001.86.5.2344/ASSET/IMAGES/LARGE/9K1111984013.JPEG

Van Eccelpoel, C., Germeys, F., De Graef, P., & Verfaillie, K. (2008). Coding of identity-diagnostic information in transsaccadic object perception. *Journal of Vision*, *8*(14), 29–29. https://doi.org/10.1167/8.14.29

Vaziri-Pashkam, M., & Xu, Y. (2019). An information-driven 2-pathway characterization of occipitotemporal and posterior parietal visual object representations. *Cerebral Cortex*, *29*(4), 1704. https://doi.org/10.1093/CERCOR/BHY343

Verfaillie, K. (1997). Transsaccadic memory for the egocentric and allocentric position of a biological-motion walker. *Journal of Experimental Psychology: Learning Memory and Cognition*, *23*(3), 739–760. https://doi.org/10.1037/0278-7393.23.3.739

Von Der Malsburg, C. (1999). The What and Why of Binding: The Modeler's Perspective. *Neuron*, *24*(1), 95–104. https://doi.org/10.1016/S0896-6273(00)80825-9

Wexler, M., & Van Boxtel, J. J. A. (2005). Depth perception by the active observer. *Trends in Cognitive Sciences*, *9*(9), 431–438. https://doi.org/10.1016/J.TICS.2005.06.018

Wijdenes, L. O., Marshall, L., & Bays, P. M. (2015). Evidence for Optimal Integration of Visual Feature Representations across Saccades. *Journal of Neuroscience*, *35*(28), 10146–10153. https://doi.org/10.1523/JNEUROSCI.1040-15.2015

Witt, J. K., Taylor, J. E. T., Sugovic, M., & Wixted, J. T. (2015). Signal Detection Measures Cannot Distinguish Perceptual Biases from Response Biases. *Perception*, *44*(3), 289–300. https://doi.org/10.1068/P7908

Wittenberg, M., Bremmer, F., & Wachtler, T. (2008). Perceptual evidence for saccadic updating of color stimuli. *Journal of Vision*, *8*(14), 9–9. https://doi.org/10.1167/8.14.9

Wolfe, B. A., & Whitney, D. (2015). Saccadic remapping of object-selective information. *Attention, Perception, and Psychophysics*, *77*(7), 2260–2269. https://doi.org/10.3758/S13414-015-0944-Z/FIGURES/4

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089. https://doi.org/10.1016/J.VISRES.2008.03.021

Zhang, X., Jones, C. M., & Golomb, J. D. (2020). Decoding 3D spatial location across saccades in human visual cortex. *BioRxiv*, 2020.07.05.188458. https://doi.org/10.1101/2020.07.05.188458

Zimmermann, E., Morrone, M. C., Fink, G. R., & Burr, D. (2013). Spatiotopic neural representations develop slowly across saccades. *Current Biology*, *23*(5), R193–R194.

https://doi.org/10.1016/J.CUB.2013.01.065

Supplementary materials

Sensitivity effects for all experiments

Table S1. Sensitivity effects for spatiotopic and retinotopic conditions (Spatiotopic sensitivity effect = Same Spatiotopic d-prime minus Control d-prime; Retinotopic sensitivity effect = Same Retinotopic d-prime minus Control d-prime; Control conditions defined as in main text).

Sensitivity Effect	Spatiotopic	Retinotopic
Expt 1	t=-0.1973, p=0.8463, d=-0.0390, BF=0.260	t=1.5730, p=0.1366, d=0.3088, BF=0.710
Expt 2	t=-1.3346, p=0.2019, d=-0.2558, BF=0.541	t=1.6148, p=0.1272, d=0.4073, BF=0.747
Expt 3	t=1.4076, p=0.1796, d=0.3181, BF=0.586	**t=3.1428, p=0.0067, d=0.5066, BF=7.619**
Expt 4	t=-0.8300, p=0.4195, d=-0.1700, BF=0.345	t=-0.3086, p=0.7619, d=-0.0868, BF=0.266

Tables with full results for all behavioral measures and conditions

Table S2. Means (and standard deviations) for all behavioral measures and conditions in Experiment 1 (dynamic saccade context condition). *SS = Same Spatiotopic; SR = Same Retinotopic; PR = Partial Retinotopic; C = Control*

Expt 1	Same/Different Identity	SS	SR	PR	C
RT(s)	Same Identity	0.6771(0.2741)	0.6870(0.2935)	0.6526(0.2875)	0.6649(0.2752)
	Different Identity	0.6769(0.2924)	0.6810(0.2912)	0.6827(0.2818)	0.6784(0.3087)
Accuracy	Same Identity	0.7452(0.1244)	0.7644(0.1069)	0.7578(0.0988)	0.6702(0.1203)
	Different Identity	0.6218(0.1246)	0.6667(0.1658)	0.6863(0.1360)	0.7105(0.1334)
P('Same')	Same Identity	0.7452(0.1243)	0.7644(0.1069)	0.7578(0.0988)	0.6702(0.1203)
	Different Identity	0.3782(0.1246)	0.3333(0.1658)	0.3137(0.1360)	0.2895(0.1334)
d-prime		1.0520(0.5891)	1.2446(0.5464)	1.2762(0.6252)	1.0743(0.5566)
Response Bias		-0.1916(0.2694)	-0.1362(0.3348)	-0.0934(0.2565)	0.0679(0.2845)

Table S3. Statistical comparisons, p-values (and BF10), for measures between different location conditions in Experiment 1 (dynamic saccade context condition).

Expt 1	Same/Different Identity	SS vs. SR	SS vs. PR	SS vs. C	SR vs. PR	SR vs. C	PR vs. C
RT(s)	Same Identity	p=0.4834 BF=0.320	p=0.2765 BF=0.441	p=0.5002 BF=0.315	p=0.0645 BF=1.237	p=0.1852 BF=0.574	p=0.2829 BF=0.435
	Different Identity	p=0.8705 BF=0.259	p=0.7845 BF=0.264	p=0.9547 BF=0.256	p=0.9154 BF=0.257	p=0.8951 BF=0.257	p=0.7806 BF=0.265
Accuracy	Same Identity	p=0.5461 BF=0.302	p=0.6595 BF=0.279	p=0.0174 BF=3.479	p=0.7923 BF=0.264	**p=0.0119** **BF=4.728**	**p=0.0002** **BF=148.2**
	Different Identity	p=0.1335 BF=0.722	**p=0.0324** **BF=2.111**	**p=0.0096** **BF=5.660**	p=0.5770 BF=0.295	p=0.1801 BF=0.585	p=0.1594 BF=0.637
P('Same')	Same Identity	p=0.5461 BF=0.302	p=0.6595 BF=0.279	**p=0.0174** **BF=3.479**	p=0.7923 BF=0.264	**p=0.0119** **BF=4.728**	**p=0.0002** **BF=148.2**
	Different Identity	p=0.1335 BF=0.722	p=0.0324 BF=2.111	p=0.0096 BF=5.660	p=0.5770 BF=0.295	p=0.1801 BF=0.585	p=0.1594 BF=0.637
d-prime		p=0.1050 BF=0.858	p=0.0794 BF=1.056	p=0.8463 BF=0.260	p=0.7967 BF=0.263	p=0.1366 BF=0.710	**p=0.02889** **BF=2.313**
Response Bias		p=0.5139 BF=0.311	p=0.1689 BF=0.611	**p=0.0026** **BF=16.94**	p=0.5735 BF=0.296	**p=0.0196** **BF=3.152**	**p=0.0020** **BF=21.29**

Table S4. Means (and standard deviations) for all behavioral measures and conditions in Experiment 2 (static context condition). *SS = Same Spatiotopic; SR = Same Retinotopic; CA = Control A; CB = Control B.*

Expt 2	Same/Different Identity	SS	CB	SR	CA
RT(s)	Same Identity	0.5596(0.1912)	0.5750(0.2012)	0.5658(0.1999)	0.5796(0.1963)
	Different Identity	0.5631(0.1900)	0.5665(0.2056)	0.5844(0.2023)	0.5873(0.2152)
Accuracy	Same Identity	0.6952(0.1124)	0.7541(0.0893)	0. 8459(0.0711)	0.6603(0.1147)
	Different Identity	0.6645(0.1442)	0.6928(0.0946)	0.6017(0.1527)	0.7076(0.1054)
P('Same')	Same Identity	0.6952(0.1124)	0.7541(0.0893)	0. 8459(0.0711)	0.6603(0.1147)
	Different Identity	0.3355(0.1442)	0.3072(0.0946)	0.3983(0.1527)	0.2924(0.1054)
d-prime		1.0017(0.5335)	1.2364(0.4042)	1.3735(0.7590)	1.0118(0.5106)
Response Bias		-0.0387(0.2816)	-0.0982(0.2002)	-0.3884(0.1677)	0.0738(0.2127)

Table S5. Statistical comparisons, p-values (and BF10), for measures between different location conditions in Experiment 2 (static context condition).

Expt 2	Same/Different Identity	SS vs. CB	SS vs. SR	SS vs. CA	CB vs. SR	CB vs.CA	SR vs. CA
RT(s)	Same Identity	p=0.6050 BF=0.289	p=0.7869 BF=0.264	p=0.2363 BF=0.488	p=0.6845 BF=0.276	p=0.8543 BF=0.259	p=0.4498 BF=0.332
	Different Identity	p=0.8953 BF=0.257	p=0.3608 BF=0.375	p=0.4053 BF=0.352	p=0.2702 BF=0.447	p=0.2547 BF=0.465	p=0.8629 BF=0.259
Accuracy	Same Identity	**p=0.0132** **BF=4.343**	**p<0.0001** **BF=415.5**	p=0.1026 BF=0.873	**p=0.0003** **BF=115.3**	**p=0.0015** **BF=26.87**	**p<0.0001** **BF=4013**
	Different Identity	p=0.4500 BF=0.332	p=0.0516 BF=1.466	p=0.1788 BF=0.588	**p=0.0283** **BF=2.349**	p=0.4901 BF=0.318	**p=0.0055** **BF=8.926**
P('Same')	Same Identity	**p=0.0132** **BF=4.343**	**p<0.0001** **BF=415.5**	p=0.1026 BF=0.873	**p=0.0003** **BF=115.3**	p=0.0015 BF=26.87	**p<0.0001** **BF=4013**
	Different Identity	p=0.4500 BF=0.722	p=0.0516 BF=2.111	p=0.1788 BF=5.660	p=0.5770 BF=0.295	p=0.1801 BF=0.585	p=0.1594 BF=0.637
d-prime		p=0.0588 BF=1.327	**p=0.0182** **BF=3.351**	p=0.9140 BF=0.257	p=0.3995 BF=0.354	p=0.0367 BF=1.915	**p=0.0456** **BF=1.615**
Response Bias		p=0.3913 BF=0.358	**p<0.0001** **BF= 502.5**	p=0.0572 BF=1.355	**p<0.0001** **BF=511.4**	**p=0.0019** **BF=22.46**	**p<0.0001** **BF=482600**

Table S6. Means (and standard deviations) for all behavioral measures and conditions in Experiment 3 (repeated eye movements only context condition). SS = Same Spatiotopic; SR = Same Retinotopic; CA = Control A; CB = Control B.

Expt 3	Same/Different Identity	SS	CB	SR	CA
RT(s)	Same Identity	0.7753(0.2380)	0.7476(0.2126)	0.7776(0.2819)	0.7672(0.2206)
	Different Identity	0.7272(0.1921)	0.7250(0.1637)	0.7940(0.2939)	0.7559(0.2243)
Accuracy	Same Identity	0.6739(0.1744)	0.6886(0.1041)	0.7904(0.1046)	0.6516(0.1290)
	Different Identity	0.7519(0.1193)	0.7073(0.1331)	0.6637(0.1346)	0.7002(0.1245)
P('Same')	Same Identity	0.6739(0.1744)	0.6886(0.1041)	0.7904(0.1046)	0.6516(0.1290)
	Different Identity	0.2481(0.1193)	0.2927(0.1331)	0.3363(0.1346)	0.2998(0.1245)
d-prime		1.2350(0.7708)	1.0991 (0.4625)	1.3120(0.6401)	0.9757(0.5637)
Response Bias		0.1270(0.2715)	0.0371(0.2797)	-0.2054(0.2038)	0.0699(0.2477)

Table S7. Statistical comparisons, p-values (and BF10), for measures between different location conditions in Experiment 3 (repeated eye movements only context condition).

Expt 3	Same/Different Identity	SS vs. CB	SS vs. SR	SS vs. CA	CB vs. SR	CB vs.CA	SR vs. CA
RT(s)	Same Identity	p=0.1274 BF=0.746	p=0.9312 BF=0.256	p=0.5291 BF=0.307	p=0.3162 BF=0.406	p=0.1832 BF=0.578	p=0.6994 BF=0.274
	Different Identity	p=0.9098 BF=0.257	p=0.0714 BF=1.144	0.1374 BF=0.707	p=0.1220 BF=0.769	p=0.2320 BF=0.494	p=0.1932 BF=0.558
Accuracy	Same Identity	p=0.7128 BF=0.272	**p=0.0114** **BF=4.896**	0.3975 BF=0.355	**p=0.0115** **BF=4.858**	p=02811 BF=0.436	**p=0.0001** **BF=220.3**
	Different Identity	p=0.1747 BF=0.597	**p=0.0007** **BF=49.06**	p=0.0658 BF=1.210	p=0.1671 BF=0.616	p=0.8142 BF=0.262	p=0.2452 BF=0.476
P('Same')	Same Identity	p=0.7128 BF=0.272	**p=0.0114** **BF=4.896**	p=0.3975 BF=0.355	**p=0.0115** **BF=4.858**	p=0.2811 BF=0.436	**p=0.0001** **BF=220.3**
	Different Identity	p=0.1747 BF=0.597	**p=0.0007** **BF=49.06**	p=0.0658 BF=1.218	p=0.1671 BF=0.616	p=0.8142 BF=0.262	p=0.2452 BF=0.476
d-prime		p=0.4569 BF=0.330	p=0.6276 BF=0.285	**p=0.0775** **BF=1.075**	p=0.1629 BF=0.627	p=0.4182 BF=0.346	**p=0.0003** **BF=106.1**
Response Bias		p=0.1043 BF=0.862	**p<0.0001** **BF=655.6**	p=0.2572 BF=0.462	**p=0.0039** **BF=11.93**	p=0.5727 BF=0.296	**p=0.0022** **BF=19.15**

Table S8. Means (and standard deviations) for all behavioral measures and conditions in Experiment 3 (eye movement during stimulus only context condition). SS = Same Spatiotopic; SR = Same Retinotopic; PR = Partial Retinotopic; C = Control.

Expt 4	Same/Different Identity	SS	SR	PR	C
RT(s)	Same Identity	0.6893(0.2914)	0.7230(0.2874)	0.6933(0.2923)	0.7022(0.2792)
	Different Identity	0.7022(0.2786)	0.6777(0.2593)	0.6985(0.2617)	0.7171(0.2763)
Accuracy	Same Identity	0.7145(0.1091)	0.7913(0.0881)	0.7410(0.1496)	0.6859(0.1236)
	Different Identity	0.7460(0.1260)	0.6986(0.1002)	0.7669(0.1043)	0.8045(0.0917)
P('Same')	Same Identity	0.7145(0.1091)	0.7913(0.0881)	0.7410(0.1496)	0.6859(0.1236)
	Different Identity	0.2540(0.1260)	0.3014(0.1002)	0.2331(0.1043)	0.1955(0.0917)
d-prime		1.3327(0.6266)	1.3892(0.4389)	1.5103(0.7482)	1.4316(0.5337)
Response Bias		0.0680(0.2685)	-0.1543(0.2100)	0.0182(0.2682)	0.2042(0.2647)

Table S9. Statistical comparisons, p-values (and BF10), for measures between different location conditions in Experiment 4 (eye movement during stimulus context condition).

Expt 4	Same/Different Identity	SS vs. SR	SS vs. PR	SS vs. C	SR vs. PR	SR vs. C	PR vs. C
RT(s)	Same Identity	p=0.1676 BF=0.615	p=0.9072 BF=0.257	p=0.7134 BF=0.272	p=0.3694 BF=0.370	p=0.5414 BF=0.303	p=0.8465 BF=0.260
	Different Identity	p=0.2879 BF=0.430	p=0.9099 BF=0.257	p=0.5936 BF=0.291	p=0.4661 BF=0.326	p=0.0739 BF=1.115	p=0.4914 BF=0.318
Accuracy	Same Identity	**p=0.0285** **BF=2.337**	p=0.3206 BF=0.403	p=0.3576 BF=0.377	p=0.1699 BF=0.609	**p=0.0012** **BF=32.92**	**p=0.0414** **BF=1.740**
	Different Identity	p=0.1397 BF=0.698	p=0.3459 BF=0.385	**p=0.0216** **BF=2.917**	**p=0.0308** **BF=2.197**	**p=0.0016** **BF=25.00**	p=0.1277 BF=0.745
P('Same')	Same Identity	**p=0.0285** **BF=2.337**	p=0.3206 BF=0.403	p=0.3576 BF=0.377	p=0.1699 BF=0.609	**p=0.0012** **BF=32.92**	**p=0.0414** **BF=1.740**
	Different Identity	p=0.1397 BF=0.698	p=0.3459 BF=0.385	**p=0.0216** **BF=2.917**	**p=0.0308** **BF=2.197**	**p=0.0016** **BF=25.00**	p=0.1277 BF=0.745
d-prime		p=0.7098 BF=0.272	p=0.1883 BF=0.568	p=0.4195 BF=0.345	p=0.4913 BF=0.318	p=0.7619 BF=0.266	p=0.5265 BF=0.307
Response Bias		p=0.0138 BF=4.201	p=0.4655 BF=0.327	p=0.0564 BF=1.370	**p=0.0280** **BF=2.372**	**p<0.0001** **BF=1024**	**p=0.0179** **BF=3.395**

Analysis with different assignment of control conditions in Experiment 2 and 3

In the main text, we calculated the spatial congruency bias of spatiotopic and retinotopic conditions using a common Control condition baseline. (In Experiments 1 and 4, there was just a single Control location; in Experiments 2 and 3, we averaged Control A and Control B). However, there are other potential ways to assign the control conditions for Experiments 2-3, as discussed in Shafer-Skelton et al (2017). As a supplemental analysis, we tested whether our results would differ if we used a different control assignment. Following Shafer-Skelton et al (2017), we recalculated the spatial congruency bises by subtracting Same Spatiotopic from Control B and subtracting Same Retinotopic from Control A in Experiment 2 and 3. (Spatiotopic and retinotopic spatial congruency biases in Experiment 1 and 4 remain the same.) The pattern of results reported in the main text did not change (see Figure S1, followed by detailed results).

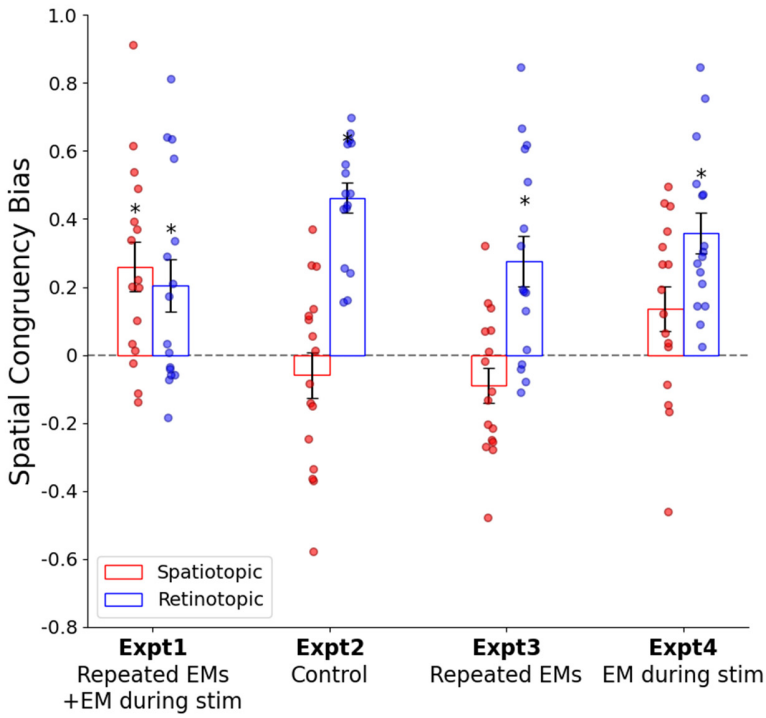

Figure S1. (Compare to main text Figure 2B.) Spatial congruency bias on the identity task re-plotted for spatiotopic and retinotopic conditions based on alternative Control condition assignment (In Experiment 1 and 4: spatiotopic congruency bias: Control bias minus Same Spatiotopic bias; retinotopic congruency bias: Control bias minus Same Retinotopic bias; In Experiment 2 and 3: spatiotopic congruency bias: Control B bias minus Same Spatiotopic bias; retinotopic congruency bias: Control A bias minus Same Retinotopic bias). Error bars are standard error of the mean. Asterisk indicates p<.05 (one-sample t-test for each condition). Spatio = Spatiotopic; Retino = Retinotopic; EM = eye movement, stim = stimulus.

In Experiment 2 (static context), we only found a significant retinotopic SCB ($t(15) = 10.4888$, $p < 0.001$, $d = 2.4131$, $BF_{10} = 482600$) with no significant spatiotopic SCB ($t(15) = -0.8827$, $p = 0.3913$, $d = -0.2433$, $BF_{10} = 0.358$), and a significantly greater retinotopic than spatiotopic bias ($t(15) = 5.5787$, $p < 0.001$, $d = 1.5088$, $BF_{10} = 503$). In Experiment 3, we also only found a significant retinotopic SCB ($t(15) = 3.8460$, $p = 0.0016$, $d = 0.9615$, $BF_{10} = 25.739$), but no significant spatiotopic SCB ($t(15) = -1.7728$, $p = 0.0966$, $d = -0.4432$, $BF_{10} = 0.913$), and the retinotopic congruency bias was significantly stronger than the spatiotopic congruency bias ($t(15) = 4.2042$, $p = 0.0022$, $d = 1.4864$, $BF_{10} = 109.615$).

The 2 × 2 × 2 ANOVA with a within-subjects factor of Reference frame (Spatiotopic or Retinotopic) and across-subjects factors of Repeated eye movements factor (present or not) and Eye movement during stimulus factor (present or not) revealed a significant main effect for reference frame ($F(1, 60) = 40.385$, $p < 0.001$, $\eta^2 = 0.402$). The main effects of repeated eye movements factor and eye movement during stimulus factor were not significant (repeated eye movements factor: $F(1, 60) = 1.527$, $p = 0.221$, $\eta^2 = 0.025$; eye movement during stimulus factor: $F(1, 60) = 3.390$, $p = 0.0710$, $\eta^2 = 0.053$), but there were significant interactions between reference frame and repeated eye movements factor ($F(1, 60) = 6.851$, $p = 0.0110$, $\eta^2 = 0.102$), and reference frame and eye movement during stimulus factor ($F(1, 60) = 18.852$, $p < 0.001$, $\eta^2 = 0.239$). However, the interaction between the two factors was not significant ($F(1, 60) = 0.859$, $p = 0.358$, $\eta^2 = 0.014$), nor was the 3-way interaction ($F(1, 60) = 0.534$, $p = 0.468$, $\eta^2 = 0.009$).

For spatiotopic 2 (Repeated eye movements factor) × 2 (Eye movement during stimulus factor) ANOVA, a significant main effect was found for the eye movement during stimulus factor ($F(1, 60) = 17.727$, $p < 0.001$, $\eta^2 = 0.228$), but not for the repeated eye movements factor ($F(1, 60) = 0.513$, $p = 0.476$, $\eta^2 = 0.008$). For retinotopic 2 × 2 ANOVA, a significant main effect was found for the repeated eye movements factor ($F(1, 60) = 6.767$, $p = 0.012$, $\eta^2 = 0.101$) but not for the eye movement during stimulus factor ($F(1, 60) = 1.776$, $p = 0.188$, $\eta^2 = 0.029$). There was no significant interaction between the two factors for either case (spatiotopic congruency bias: $F(1, 60) = 1.411$, $p = 0.240$, $\eta^2 = 0.023$, retinotopic congruency bias: $F(1, 60) = 0.062$, $p = 0.8048$, $\eta^2 = 0.001$).