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# Independent features form integrated objects: Using a novel shape-color "conjunction task" to reconstruct memory resolution for multiple object features simultaneously<sup> $\star$ </sup>

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# ABSTRACT

Though much progress has been made to understand feature integration, debate remains regarding how objects are represented in mind based on their constituent features. Here, we advance this debate by introducing a novel shape-color "conjunction task" to reconstruct memory resolution for multiple object features simultaneously. In a first experiment, we replicate and extend a classic paradigm originally tested using a change detection task. Replicating previous work, memory resolution for individual features was reduced when the number of objects increased, regardless of the number of to-be-remembered features. Extending previous work, we found that high resolution memory near perfect in resemblance to the target was selectively impacted by the number of to-beremembered features. Applying a data-driven statistical model of stochastic dependence, we found robust evidence of integration for lower-resolution feature memories, but less evidence for integration of high-resolution feature memories. These results suggest that memory resolution for individual features can be higher than memory resolution for their integration. In a second experiment which manipulated the nature of distracting information, we examined whether object features were directly bound to each other or by virtue of shared spatial location. Feature integration was disrupted by distractors sharing visual features of target objects but not when distractors shared spatial location - suggesting that feature integration can be driven by direct binding between shape and color features in memory. Our results constrain theoretical models of object representation, providing empirical support for hierarchical representations of both integrated and independent features.

#### 1. Introduction

An ability fundamental to human experience is visual object recognition. For example, buying ingredients for a dinner party requires recognizing and purchasing multiple objects from a grocery list: apples rather than oranges, potatoes rather than onions, and eggs rather than garlic. Although these objects can have many overlapping features (e.g., apples and oranges can be spherical, apples and onions can be red), we effortlessly and correctly integrate featural information ("red", "circle") to form coherent object representations ("apple"). How the mind combines disparate multimodal features to form integrated objects is known as the *binding problem* (Riesenhuber & Poggio, 1999; Roskies, 1999; von der Malsburg, 1981), a theoretical and computational problem with a rich history in the cognitive sciences (Feldman, 2013; Garnelo & Shanahan, 2019; Treisman, 1998). Understanding how the mind solves the binding problem may be important for many real-world scenarios, such as in the design of increasingly sophisticated autonomous systems that identify complex objects from simple features (LeCun, Bengio, & Hinton, 2015). In the psychological sciences, feature integration has been a central topic of study in a variety of domains: attention (Kristjánsson & Egeth, 2020), visual search (Wolfe & Horowitz, 2017), immediate and delayed memory (Erez, Cusack, Kendall, & Barense, 2016; Horner, Bisby, Bush, Lin, & Burgess, 2015; Liang, Erez, Zhang, Cusack, & Barense, 2020; Ma, Husain, & Bays, 2014), as well as in disorders associated with binding impairments, such as Alzheimer's disease (Cecchini et al., 2017; Parra et al., 2009) and autism spectrum disorder (Simon &

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<sup>\*</sup> An earlier version of this work was presented at the Lake Ontario Visionary Establishment and the Vision Sciences Society in 2019. A preprint is available at https://psyarxiv.com/szjr3/. MATLAB code for the task, pre-generated object stimuli, and anonymized data are available at https://osf.io/976ta/.

Wallace, 2016; Stevenson et al., 2014; Stevenson et al., 2019). Though there has been much progress made in understanding feature integration, there remains no strong consensus among researchers regarding how objects are represented in the mind based on their constituent features. Below, we roughly group the models of object representation into three categories based on their representational format: objectbased, feature-based, and object+features.

Purely object-based models (Fig. 1a) hold that features such as shape and color are integrated to form representations of object identity (e.g., "grandmother-like cells", Gross, 2002; Mahon, 2015; Rey et al., 2020; Quiroga, Kreiman, Koch, & Fried, 2008; "slot models", Fukuda, Awh, & Vogel, 2010; Luck & Vogel, 1997; Zhang & Luck, 2008; "object files", Balaban, Drew, & Luria, 2019; Balaban, Assaf, Arad Meir, & Luria, 2019). Previous behavioral evidence suggests that memories are constrained by the number of objects held in mind rather than by the number of features. In classic change-detection tasks, participants can detect changes of sixteen features distributed across four objects just as well as four features distributed across four objects (Luck & Vogel, 1997), suggesting that objects may be the "building blocks" of memory. In the domain of attention, cognitive resources seem to be constrained by the number of objects rather than by the number of features (e.g., "object-based attention", Gao et al., 2017; Shen, Huang, & Gao, 2015). Not only are markers of object-based representations found in behavioral experiments, but reliable object-based markers have been observed in neuroimaging. For example, contralateral delay activity present in electroencephalography indexes the number of objects held in mind rather than the number of features (Fukuda et al., 2010; Luria, Balaban, Awh, & Vogel, 2016). Further supporting these results, both rodent neurophysiology and single-cell recording in epilepsy patients have uncovered cells in the medial temporal lobe that respond specifically to objects invariant of viewpoint (Chang & Huerta, 2012; Cohen et al., 2013; Jacklin, Cloke, Potvin, Garrett, & Winters, 2016; Quiroga, 2012; Valdez et al., 2015; Vannucci et al., 2003; Winters, Bartko, Saksida, & Bussey, 2010). This diversity of literature across many domains demonstrates robust evidence in favor of integrated object-based representations.

In contrast, purely *feature-based* models (Fig. 1b) predict that objects are formed through direct reactivations of sensory features (e.g., "embodied cognition", Barsalou, 2016; Martin, 2016; Pezzulo et al., 2013; "sensory recruitment model", Katus, Grubert, & Eimer, 2015, Sreenivasan, Curtis, & D'Esposito, 2014; Ester, Anderson, Serences, and Awh, 2014; "binding-by-synchrony"; Palanca & DeAngelis, 2005; Pina,

Bodner, & Ermentrout, 2018; Rabagliati, Doumas, & Bemis, 2017; Singer & Gray, 1995). For example, objects have been proposed to be grounded in perceptual and action systems, such that objects are linear combinations of feature-based representations (Barsalou, 2016). Behavioral evidence in favor of feature-based models include evidence of independent forgetting, whereby a single feature of an object can be successfully retrieved without access of other features (Brady, Konkle, Alvarez, & Oliva, 2013; Fougnie & Alvarez, 2011; Utochkin & Brady, 2020). Moreover, features associated within the same object can be held at different resolutions, suggesting that there is not necessarily a single all-or-nothing object representation (Bays, 2015; Fougnie & Alvarez, 2011; Ma et al., 2014; van Berg, Shin, Chou, George, & Ma, 2012). This body of work suggests that features are represented independently because separate features of the same object can be accessed at varying resolutions (e.g., one feature of an object can be remembered in perfect detail, whereas other features from the same object can be seemingly inaccessible).

Importantly, we emphasize a third class of *object* + *features* models (Fig. 1c) which posit that multiple representations of an object can be activated simultaneously in a hierarchical and distributed manner. Independent features are represented in early stages of the object processing pathway, whereas the integrated representation of the object as a cohesive whole is found at later stages of the pathway (e.g., "representational-hierarchical view"; Barense et al., 2012; Binder, 2016; Cowell, Barense, & Sadil, 2019; "binding-in-context"; Cooper & Ritchey, 2019, 2020; Diana, Yonelinas, & Ranganath, 2007; Ranganath, 2010; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019; "cognitive map"; Behrens et al., 2018; Hawkins, Lewis, Klukas, Purdy and Ahmad, 2019; Mok & Love, 2019). This viewpoint may account for both the predictions of a purely object-based (Fig. 1a) or purely feature-based (Fig. 1b) model in a single theoretical framework. In an object+features model, sensory regions represent independent features such as shape (Kourtzi & Kanwisher, 2000), sound (Feng & Wang, 2017), and color (Brouwer & Heeger, 2009), whereas anterior regions of neocortex represent featurebased information in a transformed and integrated format (Coutanche & Thompson-Schill, 2015; Erez et al., 2016; Jung, Larsen, & Walther, 2018; Liang et al., 2020; Martin, Douglas, Newsome, Man, & Barense, 2018; Rademaker, Chunharas, & Serences, 2019; Schapiro, Turk-Browne, Botvinick, & Norman, 2017). In particular, the perirhinal cortex within the medial temporal lobe is thought to contain an explicit conjunctive code for the integrated features composing an object, such that the whole is different from the sum of the parts (Erez et al., 2016;



**Fig. 1.** (*a*) Object-based models predict that features are integrated to form transformed representations of objects. In a purely object-based prediction, the fundamental "unit" of cognition is objects rather than features, such that memory and attentional resources are constrained entirely by the number of objects rather than the number of features held in mind. (*b*) Feature-based models predict that objects are reactivations of independent features. In a purely feature-based account, features are not integrated and are instead represented independently. (*c*) Object+Features models predict that objects are represented at multiple levels – both in terms of independent features and as an integrated representation of its constituent features. By this account, features are bound to form objects but are also concurrently and independently represented in sensory cortex.

Liang et al., 2020; Martin et al., 2018). Importantly, an object+features model also predicts feature independence, because each feature is represented in sensory cortex and can be susceptible to interference from competing feature-based information. For this reason, it is entirely possible to observe independent forgetting and varying resolution between features of the same object (Bays, 2015; Brady et al., 2013; Fougnie & Alvarez, 2011; Ma et al., 2014; van Berg et al., 2012), despite observed integration of those features in other task contexts. Indeed, recent evidence has increasingly favored object+features accounts which can reconcile seemingly contradictory findings of independence and integration in memory (Fig. 1c; Cowan, Saults, & Blume, 2014; Hardman & Cowan, 2015; Markov, Tiurina, & Utochkin, 2019; Markov, Utochkin, & Brady, 2021; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002; Sone, Kang, Li, Tsubomi, & Fukuda, 2021; Wheeler & Treisman, 2002).

In the present study, we adjudicate between these three models of object representation (Fig. 1) using a novel shape-color "conjunction

task" to characterize the resolution of memory for the shape and color features of an object (Fig. 2; for a previous version of this task using simpler orientation and color, see Sone et al., 2021). Critically, our shape-color conjunction task can reconstruct multiple object features simultaneously from the same behavioral response, as opposed to tasks which reconstruct each feature sequentially (Ma et al., 2014). The simultaneous property of our shape-color conjunction task is important because tasks which reconstruct features sequentially (e.g., color first and then orientation second, and vice versa) can induce independence between object features even though this information may be held in an integrated manner (Sone et al., 2021). In Experiment 1, we first replicate and then extend a classic paradigm originally tested using a change detection task (Luck & Vogel, 1997) with our shape-color conjunction task. As traditional change detection tasks are discrete (i.e., memory is often quantified through a binary "yes/no" response), the continuous nature of our shape-color conjunction task allows us to examine memory resolution in a more sensitive manner. Accounting for both higher- and



# a. Shape-Color Conjunction Task

**Fig. 2.** Shape-color conjunction task. (*a*) Circular spaces were used to capture the resolution of shape and color memory in a single response. Participants reconstructed the target by moving the cursor along the circumference (remapped from shape space) and radius (remapped from color space). An item corresponding to the position of the cursor was displayed, such that shape and color changed continuously on a 2D circle. After a mouse response, participants fine-tuned their selection. Participants were not shown the on-screen instructions during the actual task and the size of some elements have been increased for illustrative purposes. Fig. 3 and Fig. 7 depict the stimulus displays, with Fig. 3 shown approximately to scale. (*b*) Shape error was operationalized as the angular distance between the target and reconstructed shape, whereas (*c*) color error was operationalized as the radial distance between the target and reconstructed color. To equate the distributional properties between the shape and color spaces, participant responses determined the size of the response bins on circular space in a data-driven manner (see section 2.4.1. *Memory Resolution*). The 25% quantile of responses (fine-grained bin) isolated reconstructions near-perfect in resolution, whereas the 90% quantile of responses ("yes" bin) included reconstructions that ranged from higher to lower resolution. We termed 90% quantile the "yes" bin because responses here are roughly akin to "yes" responses on a discrete task such as change detection, which can include both high to lower resolution memories.

lower-resolution memories, we show that visual objects can contain both an integrated code as well as independent feature representations. Applying a data-driven statistical model of feature integration based on stochastic dependence, we then provide evidence that memory for features can be higher in resolution than memory for the integrated code, suggesting that individual and integrated features from the same object can differ in memory resolution.

Although Experiment 1 provides evidence in favor of both an integrated code and independent features underlying the object representation, we did not control for the influence of spatial location (Fig. 3). Features in the environment do not only co-occur (e.g., an apple is both spherical and red), but visual features also occupy the same spatial location (e.g., "red" and "spherical" features can be located in the same position in the environment). Indeed, previous work has highlighted the critical influence of spatial location on object identity (Cai, Sheldon, Yu, & Postle, 2019; Cai et al., 2020; Golomb, Kupitz, & Thiemann, 2014; Pertzov & Husain, 2014; Schneegans & Bays, 2017), raising the possibility that visual features may be bound to a shared spatial location rather than to each other in memory. In Experiment 2 we varied the nature of interference, examining the influence of task-irrelevant visual feature and spatial location information on the integrated object code. In this second experiment, we found that task-irrelevant feature information but not spatial location disrupted shape-color integration. Taken together, our work reveals that visual features can be bound directly to each other in a manner that cannot be entirely accounted by spatial location in memory, results which constrain models of object representation.



**Fig. 3.** Experiment 1 task design. We varied the number of objects and to-be-remembered features in each condition. (*a*) In the single-feature shape condition, participants remembered shape and ignored color. In the single-feature color condition, participants remembered color and ignored shape. In the both-features condition, participants remembered both shape and color. Each of the three conditions was presented in two blocks of 120 trials, with blocks presented in an interleaved order. (*b*) An example of a set size 2 trial in the both-features condition. Each box indicates a possible location that an object could appear in. No boxes were actually displayed. During the test phase, the shape-color conjunction task appeared at the location of the target object, with the reconstructed object appearing in the middle of the computer monitor.

# 2. Experiment 1

#### 2.1. Participants

Thirty participants were recruited from the undergraduate student pool at the University of Toronto and from the community. One participant was excluded without further data analysis as they did not complete all trials of the experiment. The final sample contained 29 individuals ( $M_{age} = 20.93$  years,  $SD_{age} = 1.22$  years, *Females* = 24). Participants recruited from the undergraduate student pool received course credit whereas individuals recruited from the community received \$20 CAD as compensation. REB approval was received from the University of Toronto (Protocol 38,856).

#### 2.2. Apparatus and Stimuli

The experiment was developed in MATLAB using psychoolbox-3 (Kleiner, 2007). Participants were tested on a Latitude 3460 Dell laptop, with a screen resolution of  $1920 \times 1080$  and a frame refresh rate of 60 Hz. Participants responded using a Dell mouse and keyboard to task instructions.

Shape stimuli were sampled from the *Validated Circular Shape Space* (VCS space, available on the Open Science Framework at https://osf. io/d9gyf/; Li, Liang, Lee, and Barense, 2020), a shape space comparable to circular color space. Color stimuli were sampled from a circle defined on CIELAB color space with luminance held constant (L = 70, a = 20, b = 38, radius = 60 units; Zhang & Luck, 2008). Stimuli were approximately 3.5 cm × 3.5 cm on the monitor and participants were seated approximately 60 cm away from the monitor, with each stimulus subtending approximately 3.34 degrees of visual angle.

We used the properties of circular shape and color space to quantify memory resolution, defined as the detail of the representation held in mind (Yonelinas, 2013; Ekstrom and Yonelinas, 2020). Angular distance approximated the magnitude of visual similarity on circular space, meaning that items sampled from closer distances tended to be more visually similar compared to items sampled from further distances. For example, stimuli sampled from 60 degrees apart are more visually similar compared to stimuli sampled from 120 degrees apart, a property that is true anywhere on circular space. The magnitude of visual similarity was therefore used as a proxy for the resolution of memory (described in the next section), as reconstructions high in similarity was nearly identical to the target, whereas reconstructions lower in similarity was less similar to and therefore lower in detail relative to the target.

#### 2.2.1. Shape-color conjunction task

We developed a novel shape-color task which can be used to reconstruct the resolution of multiple object features in a single behavioral response. Circular spaces for shape and color features were displayed together on a 2D circle (Fig. 2a), with circular shape space remapped along the circumference and circular color space remapped along the radius. Each degree corresponded to a unique shape sampled from VCS space, whereas each radial position corresponded to a unique color sampled from circular color space, creating a series of concentric color rings. As the mouse cursor moved along x and y coordinates on the shape-color conjunction task, the shape and color transitioned along each respective feature dimension. The reconstructed object was displayed at the center of the computer monitor, and this reconstructed shape-color object dynamically changed with the mouse movement. During the test portion of each trial, participants freely explored the shape-color feature space using the mouse cursor to reconstruct the target object (middle Fig. 2a). Participants made their response using the left mouse button, after which they could fine-tune their response using the keyboard arrow keys (Fig. 2a). The left-right arrow keys incrementally sampled shapes whereas the up-down arrow keys incrementally sampled colors from circular space (see a visual example on the Open Science Framework: https://osf.io/976ta/).

The x and y coordinates on the shape-color conjunction task corresponded to two types of information: angular position ( $\theta$ ), reflecting shape identity, and radial position (r), reflecting color identity (Fig. 2). As visual similarity was precisely defined on shape and color space (Li, Liang, Lee, and Barense, 2020), reconstructions closer in distance to the target item reflect higher resolution memories of the target. The resolution of the memory trace, termed error, was defined as the angular distance for shape responses (i.e.,  $\theta$ ; Fig. 2b) and radial distance for color responses (i.e., r; Fig. 2c) of a reconstructed shape-color object from the target shape-color object, with higher resolution memories being closer to the target (lower error) and lower resolution memories being farther from the target (higher error). Importantly, our shape-color conjunction task can be used to reconstruct multiple features simultaneously, in contrast to existing continuous tasks which are used to reconstruct features sequentially. In particular, sequential tasks favor feature-based strategies which can promote independence between features in memory (Sone et al., 2021). Our task also allows for the investigation of shape-color conjunctive objects that are more complex than the simpler orientation and color stimuli commonly studied using continuous retrieval tasks (for a review, see Ma et al., 2014), while also reducing the contribution of well-established categorical labels as the shape-color object stimuli are unfamiliar to participants (Bae, Olkkonen, Allred, & Flombaum, 2015; Hardman, Vergauwe, & Ricker, 2017; Pratte, Park, Rademaker, & Tong, 2017; Souza, Overkott, & Matyja, 2021).

A small empty circle was included at the center of the shape-color conjunction task to ensure that the displayed colors at this central position were visually differentiable (Fig. 2a). Color was remapped differently on the shape-color conjunction task for each trial, such that there were never any systematic mappings between particular colors and locations. In contrast, eight shapes sampled from equidistant positions from VCS space were displayed along the cardinal axes of the conjunction task (i.e., every 45 degrees). These eight shapes served as visual anchors as all shapes from VCS space could not be displayed due to space limitations (i.e., it is impossible to depict all 360 shapes at a decipherable size). These anchor shapes could be used by participants to learn and infer the organization of all the shapes from VCS space. To ensure that there were never any systematic mappings between particular stimuli and spatial coordinates on the conjunction task across participants, the positions of shapes were remapped differently for each participant. These shape mappings were not randomized every trial because we reasoned that doing so would generate large amounts of undesired interference from trial to trial (as observed in previous work; Li, Fukuda, Lee, and Barense, 2020). Critically, the difference in location-feature mappings between shape and color on the shape-color conjunction task could not drive observed results, as the experiment was conducted using a within-subject design. Moreover, the mappings between shape and color on our conjunction task were directly comparable to our previous work on an orientation-color conjunction task (Sone et al., 2021).

# 2.3. Procedure

Experiment 1 was based on a classic paradigm originally tested using a change detection task (Luck & Vogel, 1997). At the beginning of every trial, a fixation dot appeared for 500 ms at the center of the screen. Objects could appear at six possible locations every trial (Fig. 3b). After a 1000 ms retention interval, participants were cued to report a target object. Each participant completed three conditions (Fig. 3a). In the *single-feature shape* condition, only the shape of the target shape-color object was task-relevant, and participants were instructed to attend to shape and to ignore color. In the *single-feature color* condition, only the color of the target shape-color object was task-relevant, and participants were instructed to attend to color and to ignore shape. In the *both-feature condition*, both the shape and color of the target shape-color object were task-relevant, and participants were instructed to attend to features. Each of the single-feature shape, single-feature color, and bothfeature conditions were presented in separate blocks of 120 trials. Within each block, 60 trials displayed a single object (set size 1) and 60 trials displayed two objects (set size 2). The presentation order of set size 1 and set size 2 trials was randomized within each block, with the presentation order of blocks was randomized for each participant. In total, the experiment comprised 720 trials and participants were allotted an optional break between every block of 60 trials. Participants were explicitly asked to avoid verbal strategies and were to guess if they could not remember. A set of practice trials ensured that participants correctly followed task instructions.

The task-irrelevant feature in each single-feature condition was identical (i.e., either the same shape or the same color) during set size 2 trials. For example, when the task-relevant feature was shape (i.e., single-feature shape condition), the task-irrelevant color might be the same shade of blue for both objects (Fig. 3a). Likewise, when the taskrelevant feature was color (i.e., single-feature color condition), the task-irrelevant shape was identical for both objects. This manipulation directly constrained the number of to-be-remembered features within each condition. In each single-feature condition, a set size 1 trial would include one to-be-remembered feature, whereas a set size 2 trial would include two to-be-remembered features. In contrast, the both-feature condition would include two to-be-remembered features in a set size 1 trial, whereas a set size 2 trial would include four to-be-remembered features. In this way, the number of to-be-remembered features and the number of objects could be experimentally manipulated as was done in previous work (Luck & Vogel, 1997). The critical difference between the present and previous work was the implementation of our novel shape-color conjunction task, which allowed us to examine with a single behavioral response how memory resolution was affected by increasing the features to-be-remembered within each object compared with increasing the number of objects. As described below (Section 2.4.1. Memory Resolution), we examined memory resolution by binning shape and color responses in a data-driven manner based on quantiles.

#### 2.4. Statistical analysis

Shape resolution was operationalized as the angular distance between a reconstructed and target shape. Color resolution was operationalized as the radial distance between a reconstructed and target color (Fig. 2). See *Fig. S1* in the *Supplemental Material* for raw error distributions.

# 2.4.1. Memory resolution

As angular distance is a proxy for visual similarity on a circular stimulus space (Li, Liang, Lee, and Barense, 2020), we directly captured the resolution of the memory trace by quantifying the distance between a reconstructed object with the target object (i.e., error).

To characterize responses, we first equated the distributional properties between the shape and color spaces. Responses were binned by varying the cut of circular space derived from participant responses in the single-feature condition at set-size 1 (i.e., the condition with 1 to-beremembered feature displayed in 1 object). In this data-driven approach, we determined the size of circular space for shape and color individually at the 25%, 50%, 75%, and 90% quantiles (Fig. 2). For example, if 25% of all trial-wise shape responses fell within circular space at  $4^{\circ}$  error on either side of the target across all participants in the single-feature condition for set size 1, we would use 4° error as the cut-off for all subsequent conditions (e.g., the both-feature condition). Thus, this 25% quantile captures the size of circular space corresponding to the 25% highest resolution responses and was termed *fine-grained*, because these responses were nearly identical in similarity with respect to the target (validated in separate experiments; see Li, Liang, Lee, and Barense, 2020; Schurgin, Wixted, & Brady, 2020). The bins corresponding to the 50%, 75%, and 90% quantiles contained increasingly lower resolution responses, because the shape-color reconstruction could range from

nearly identical to incrementally less similar with respect to the target. Overall, this approach resulted in the following cuts of circular space: 25% quantile (fine-grained responses) for shape at  $4^{\circ}$  error and color at  $6^{\circ}$  error; 50% quantile for shape at  $10^{\circ}$  error and color at  $14^{\circ}$  error; 75% quantile for shape at  $20^{\circ}$  error and color at  $30^{\circ}$  error; and 90% quantile ("yes" responses) for shape at  $47^{\circ}$  error and color at  $60^{\circ}$  error.

We used the term "yes" responses (90% quantile) because responses in this bin roughly reflect "yes" responses on a discrete task such as change detection. Importantly, a "yes" response on a discrete task includes responses that range from higher to lower memory resolution and can reflect the existence of a memory that varies from a near-perfect match to a lower-resolution coarse-grained match to the target. For example, even if a participant's memory is not an exact match to the specific shade of blue or red, participants can succeed on a change detection task so long as the foils are visually distinct (e.g., Awh, Barton, & Vogel, 2007). Thus, yes/no responses on a discrete task like change detection does not explicitly distinguish between higher and lower resolution representations, and the "yes" response bin in our experiment approximates this property of discrete tasks. Importantly, the continuous nature of our shape-color conjunction task can also isolate responses reflecting the highest memory resolution near-perfect in resemblance to the target (fine-grained: 25% quantile, Fig. 2).

We assumed that memories can range from high to low resolution, an assumption supported by behavioral, computational, and neuroimaging evidence (Bays, Catalao and Husain, 2009; Berens, Richards and Horner, 2020; Brunec, Moscovitch, & Barense, 2018; Greene and Naveh-Benjamin, 2020; Korkki, Richter, Jeyarathnarajah and Simons, 2020; Ma et al., 2014; Richter, Cooper, Bays and Simons, 2016; Yonelinas, 2013; Schurgin et al., 2020; Zhang & Luck, 2008; 2009). Fine-grained responses (25% quantile) included reconstructions that were identical or a near-perfect match to the target (i.e., because these responses are highly similar to the target on perceptually uniform space), whereas the response bins corresponding to the 50%, 75%, and 90% quantile contained responses that were a near-perfect match to the target as well as responses that reflected increasingly lower-resolution memory for the target (i.e., because these responses could range from high to low similarity to the target on perceptually uniform space). Notably, this analysis approach is different from the analysis approaches typical in the visual short-term memory literature (Ma et al., 2014). Previous studies have analyzed responses from a continuous retrieval task in terms of the mean absolute error across all trials of a condition or have fit errors with mixture models to delineate specific states in memory (e.g., a "guessing" state; Zhang & Luck, 2008). In contrast, we were specifically interested in isolating the resolution of memories without assuming any difference in memory states (i.e., a difference between precision and guessing; Schurgin et al., 2020). Our approach captures memory across high to lower resolution, without assumptions of guessing. See Supplemental Material for an analysis of the raw distributions and an analysis using mean absolute errors. Critically, the analysis based on mean absolute error was insufficient for our purposes, as this analysis was not sensitive to fine-grained representations of the target (Fig. S3a, b). The response bin approach based on quantiles was furthermore critical for the modelbased stochastic dependence analyses (see next section), and we discuss the implications of these response bins on the interpretation of the results in section 4. Interim Discussion and 7. General Discussion.

Inferential statistics were conducted with linear mixed models using the *lme4* package (Bates, Kliegl, Vasishth, & Baayen, 2015) in R version 2.6.1 (R Core Team, 2019). Effect sizes were estimated using Cohen's *d*, measured by the difference between condition means divided by the pooled standard deviation across conditions (Lakens, 2013). Number of objects (set size 1 or 2) and number of to-be-remembered features (single-feature or both-feature condition) were modelled as fixed effects whereas participants were modelled as random intercepts to account for the within-subject design. This analysis was conducted for shape and color independently and was repeated for each quantile. In this way, we examined how the number of to-be-remembered features and number of objects influenced the resolution of reconstructed shape and color memories. For the benefits of applying linear mixed models over repeated-measures ANOVA in within-subject designs, see Magezi (2015). Linear mixed models are commonly applied in psychology and other disciplines (for previous applications in the visual short-term memory literature, see Bartsch, Singmann, & Oberauer, 2018; Kliegl, Masson, & Richter, 2010; Mitchell & Cusack, 2018).

#### 2.4.2. Stochastic dependence model of feature integration

The above analyses of memory resolution assessed the relationship between shape and color by examining how each condition impacted shape and color memory independently (i.e., how the number of objects and number of to-be-remembered features impacted memory resolution for shape and color separately). Here, we developed a data-driven statistical model of feature integration using stochastic dependence (Hicks & Starns, 2015; Horner & Burgess, 2013; Joensen, Gaskell, & Horner, 2020; Meiser & Bröder, 2002), extending previous stochastic dependence models to our continuous shape-color conjunction task. As an example of how this model works, imagine a scenario where you are asked to determine whether flipping one coin can influence the results of a second coin (Fig. 4a). We can conduct an experiment by flipping two coins every trial for many trials (i.e., "Coin A" and "Coin B"), recording on each trial whether Coin A and Coin B landed on heads or tails. After each trial, we can then record instances when both coins landed on heads, both coins landed on tails, and when one coin landed on heads and the other on tails. If Coin A and Coin B do not influence each other (i.



**Fig. 4.** Data-driven stochastic dependence model. (*a*) The probability of observing two heads when flipping two fair coins is the probability of observing heads in one coin (50%) multiplied by the probability of observing heads in the other coin (50%). In this case, the joint probability (50% \* 50% = 25%) is equivalent to the observed probability of obtaining two heads (25%) because each coin toss is independent (e.g., 25% - 25% = 0%; numerator in the observed dependence formula above). (*c*) Because the maximum possible dependence observable in the data is 25% for two fair coins (e.g., 50% - 25%; denominator in the observed dependence formula above), the observed dependence is 0% (e.g., observed dependence = 0% / 25% = 0%). (*b*) Using this same logic, we can examine whether the observed probability of reconstructing shape and color within the same quantile is greater than the joint probability of reconstructing shape and color. On the example above for the 90% quantile ("yes" responses), the observed probability of reconstructing shape and color. On the observed dependence formula above). Because the maximum observable dependence in one example above of probability of reconstructing shape and color. On the example above for the 90% quantile ("yes" responses), the observed probability of reconstructing shape and color. On the example above of 90% - (90% \* 90%) = 9%; numerator in the observed dependence formula above). Because the maximum observable dependence in our example is also 9% (90% - 81%; denominator in the observed dependence formula above), the (*c*) observed dependence is 100% (e.g., observed dependence = 9%/9% = 100%). In other words, our example of fair coins was completely independent (i.e., the outcome of one coin does not predict the outcome of another: observed dependence = 0%), whereas our example of "yes" responses was completely dependent (i.e., shape and color perfectly covaried in their resolution: observed dependence = 100%).

e., statistical independence), we know that the probability of observing two heads in our experiment ( $P_{observed(A\&B)} = 25\%$ ) is equivalent to the probability of heads in one coin ( $P_A = 50\%$ ) multiplied by the probability of heads in the other coin ( $P_B = 50\%$ ). By comparing the observed probability of two heads ( $P_{observed(A\&B)} = 25\%$ ) with the predicted joint probability assuming independence ( $P_A \times P_B = 50 \% \times 50\% = 25\%$ ), we can examine whether our recorded data about the coin tosses matches our prediction of independence. If the observed probability of obtaining two heads is equal to the joint probability of obtaining two heads ( $P_{ob}$ - $_{served}(A\&B) = P_A \times P_B$ ), we know that the coins are independent because our observations did not differ from a predicted model positing complete independence. On the other hand, if the observed probability of obtaining two heads is greater than the joint probability of obtaining two heads, we know that the coin tosses can influence each other (i.e., not independent) because two heads occur together more often than would be possible given complete independence.

We extend the coin-toss logic described above to the both-feature condition on our shape-color conjunction task (Fig. 4b). This analysis was repeated at each bin, with the 25% quantile reflecting dependence for fine-grained memory (containing high-resolution reconstructions near-identical to the target), and 90% quantile reflecting dependence for "yes" responses (containing both higher and lower resolution reconstructions). Critically, object memory was defined as the observed proportion of responses whereby both shape and color were reconstructed within a given response bin, akin to identifying the likelihood of observing two heads in our coin-flipping example. Below, we provide an example using the "yes" response bin (90% quantile):

#### Object Memory = $P_{observed(A\&B)}$

A data-driven *independent model* positing no dependency between shape and color was created by multiplying the proportion of trials with "yes" shape  $(P_A)$  and color responses  $(P_B)$ . Multiplication results in the joint probability of reconstructing both features as a "yes" response, assuming complete independence.

#### Independent Model = $P_A \times P_B$

Next, the observed proportion of "yes" shape-color responses were subtracted by the independent model to obtain a dependence score:

# Dependence Score = $P_{observed(A\&B)} - (P_A \times P_B)$

This dependence score captures the degree to which shape and color was reconstructed together compared to a model positing complete independence. If shape and color are reconstructed together at a probability that is not different than the independent model, then we know that these features tend to be reconstructed independently (i.e., the resolution of one feature does not covary with the resolution of another feature in the same quantile). However, if the observed probability of reconstructing "yes" shape and color responses together is greater than the independent model, we know that "yes" shape and color responses are reconstructed together more often than would be predicted by independence (i.e., the resolution of one feature covaries with the resolution of another feature). Thus, a dependence score above zero indicates feature integration.

The dependence score described above characterizes how different the observed shape-color responses are from *complete independence* (i.e., how much dependence is present in the shape-color responses produced by the participant). However, it would also be useful to know how different the observed shape-color responses are from *complete dependence* (i.e., how much independence is present in the shape-color responses produced by the participant). To quantify how different the participant shape-color responses are from complete dependence and complete independence within a single measure, we can divide the dependence score by the maximum possible dependence observable in the data (Fig. 4c). In this context, 0% observed dependence means that participant responses captured none of the possible dependence that could be observable in the data (i.e., complete independence). In contrast, 100% observed dependence means that participant responses captured all of the possible dependence that could be observable in the data (i.e., complete dependence).

$$Observed \ Dependence : \frac{\left[P_{observed(A\&B)} - (P_A \times P_B)\right]}{\left[min(P_A, P_B) - (P_A \times P_B)\right]}$$

Using observed dependence (Fig. 4c), we can determine not only whether two coins are fair or not, but also how different our coin flips are from two hypothetical coins that are always fair (observed dependence = 0%) or always unfair (observed dependence = 100%). In other words, we can characterize how dependence changes as response bins increasingly contain lower resolution responses (e.g., the 25%, 50%, 75%, and 90% quantiles). If the resolution of shape and color were completely independent (i.e., the resolution of shape does not predict the resolution of color), then the observed dependence will equal to 0%. On the other hand, if the resolution of shape and color were completely dependent (i.e., when shape is reconstructed in high-resolution, color is also reconstructed in high-resolution), then the observed dependence will equal to 100%.

Bayesian one-sample *t*-tests assessed whether the observed dependence produced by participants was greater than 0% (complete independence) and was less than 100% (complete dependence) using JASP 0.9.1.0 (JASP Team, 2019). In all cases, the Cauchy distribution was used as the prior and the Bayes factor was interpreted using established guidelines (Gelman, Jakulin, Pittau, & Su, 2008; Lee & Wagenmakers, 2013). Importantly, the use of Bayesian tests can reduce concerns with multiple comparisons (see Kruschke, 2010). For readers more familiar with null-significance hypothesis testing, we include the probabilities associated with the Bayes factors.

#### 2.5. Predictions

We adjudicated between three models of object representation based on the resolution of memory as a function of the number of objects (i.e., set size 1 compared to set size 2) and the number of to-be-remembered features within each object (i.e., single-feature compared to both-feature conditions).

#### 2.5.1. Object-based models

According to these models, the features composing objects are thought to be integrated (Fig. 1a). A purely object-based model predicts that memory resolution is entirely constrained by the number of objects rather than by the number of to-be-remembered features (Fig. 5a). Thus, memory resolution should not differ between the single-feature and both-feature conditions for the same set size, as these conditions differed only by the number of to-be-remembered features (and did not differ by the number of objects). Instead, memory performance should be reduced only when comparing memory resolution for one object (i.e., set size 1) compared to two objects (i.e., set size 2).

#### 2.5.2. Feature-based models

According to these models, the features composing objects are thought to be independent (Fig. 1b). A purely feature-based model predicts that memory resolution is entirely constrained by the number of features held in memory, rather than by the number of objects (Fig. 5b). Thus, memory resolution should be highest when one feature is taskrelevant (e.g., set size 1, single-feature condition), followed by when two features are task-relevant (e.g., set size 2, single-feature condition and set size 1, both-feature condition), followed by when four features are task-relevant (e.g., set size 2, both-feature condition).

#### 2.5.3. Object + Features models

According to these models, the features composing objects are thought to be represented both as an integrated code and as independent



**Fig. 5.** (*a-c*) Predictions of the different models. (*a*) A purely object-based account predicts reduced memory as the number of objects increase, regardless of the number of to-be-remembered features within each object. (*b*) In contrast, a purely feature-based account predicts reduced memory as the number of to-be-remembered features increase. (*c*) An Object+Features account predicts reduced memory as both the number of objects and to-be-remembered features increase. (*d*) Based on participant responses in the single-feature condition at set size 1, cuts on circular space were defined to create quantiles which include 25% (fine-grained responses) and 90% ("yes") of all responses. Critically, the "yes" bin (90% quantile) includes responses that range from higher to lower resolution, akin to discrete yes/no metrics such as accuracy on a change detection task. (*e*, *f*) Experiment 1 results. Fine-grained (*e*) shape and (*f*) color responses were reduced by both the number of objects presented (set size 1 vs. set size 2) and the number of to-be-remembered features (single- vs. both-feature condition) – supporting an Object+Features account that posits the presence of both object- and feature-based representations. In contrast, "yes" shape and color responses were reduced only by the number of objects presented, not the number of to-be-remembered features – supporting a purely object-based account that posits integrated object-based representations. Error bars reflect the 95% CI for the condition mean.

features. Here, memory resolution is constrained both by the number of objects and by the number of to-be-remembered features (Fig. 5c). Thus, resolution should be highest when only one feature is task-relevant within one object (e.g., set size 1, single-feature condition). Increasing the number of task-relevant features within an object should reduce resolution (e.g., set size 1, both-feature condition). However, resolution should be further reduced when two objects are displayed within two features (e.g., set size 2, single-feature condition), with the lowest resolution observed when four features are displayed within two objects (e.g., set size 2, both-feature condition).

#### 2.5.4. Stochastic dependence model of feature integration

In a purely object-based account, shapes and colors are completely dependent (Fig. 6a). In an example of purely object-based memory, shape and color would be reconstructed together in an entirely all-ornothing manner, such that the resolution of both features perfectly covary (i.e., when shape is reconstructed in high-resolution, color is also reconstructed in high-resolution).

In a purely feature-based account, shapes and colors are completely independent (Fig. 6b). In an example of purely feature-based memory, shape and color reconstructions would not influence each other (i.e., one feature can be reconstructed in high resolution with no influence on the resolution of the other feature).

Finally, evidence of both independence and dependence would

support Object+Features models (Fig. 6c). In an example of an integrated code and independent features, the resolution of shape and color reconstructions covary more often than chance (i.e., evidence of dependence), but the resolution of individual features can nevertheless differ from each other (i.e., evidence of independence).

#### 3. Results

Anonymized data and commented code are available on the Open Science Framework: https://osf.io/976ta/.

#### 3.1. Memory resolution

Shape and color responses were binned in a data-driven manner by varying the cut of circular space four ways (Fig. 5d), ranging from *fine-grained* (i.e., 25% quantile; responses near-perfect in resolution to the target) to "*yes*" responses (i.e., 90% quantile; roughly corresponding to "yes" responses on a discrete accuracy measure, which include memories that range from higher to lower resolution to the target). Linear mixed models examined the proportion of responses within each bin as a function of the number of objects (i.e., set size 1 and set size 2) and the number of to-be-remembered features (i.e., single-feature and both-feature conditions). For raw error distributions and mean absolute error analyses, see *Supplemental Material*. Importantly, the analysis





# d. Stochastic Dependence Model Results



**Fig. 6.** Stochastic dependence model predictions and results. (*a*) In a purely object-based prediction, shape and color reconstructions perfectly covary in their resolution (i.e., completely dependent: observed dependence = 100%). (*b*) In a purely feature-based prediction, shape and color reconstructions are completely independent (i.e., the resolution of shape has no influence on the resolution of color, and vice versa: observed dependence = 0%). (*c*) In an object+features prediction, shape and color reconstructions are both independent and integrated (e.g., observed dependence = 50%). (*d*) Critically, we found more evidence of dependence as the bin contained increasingly lower resolution responses (e.g., 25%, 50%, 75%, and 90% quantiles). For example, there was primarily independence for fine-grained responses (25% quantile), as observed dependence was close to 0%. Although we found more evidence of dependence for "yes" responses (90% quantile), the resolution of shape and color was not completely dependent (i.e., observed dependence was substantially lower than 100%). These results suggest that feature-based representations can be higher in resolution than the integrated code, because we found more evidence of independence for fine-grained responses. Error bars reflect the 95% confidence interval for the condition mean.

based on mean absolute error was not sensitive to differences between conditions at the highest memory resolution, supporting the usefulness of our analytical approach (*Fig. S3a, b*).

For fine-grained shape responses (25% quantile, Fig. 5e), a linear mixed model found a main effect of the number of objects ( $F_{1, 84} =$ 141.83, p < 0.001, *partial*  $r^2 = 0.63$ ) and a main effect of the number of to-be-remembered features ( $F_{1, 84} = 12.34, p < 0.001, partial r^2 = 0.13$ ), with no interaction ( $F_{1, 84} = 3.47$ , p = 0.066). For fine-grained color responses (25% quantile, Fig. 5f), a linear mixed model found a main effect of number of objects ( $F_{1, 84} = 61.13$ , p < 0.001, partial  $r^2 = 0.42$ ) and a main effect of the number of to-be-remembered features ( $F_{1, 84} =$ 25.24, p < 0.001, partial  $r^2 = 0.23$ ), with no interaction ( $F_{1, 84} = 0.013$ , p = 0.91). For both fine-grained shape and color (25% quantile), increasing the number of objects (from set size 1 to set size 2) and the number of to-be-remembered features (from single-feature to bothfeature conditions) decreased the proportion of responses. These results were replicated for the bins corresponding to 50% and 75% quantiles, which contained increasingly lower resolution responses (see Fig. S2 in Supplemental Material for statistical analyses).

For "yes" shape responses (90% quantile, Fig. 5e), a linear mixed model found a main effect of the number of objects ( $F_{1, 84} = 167.99, p < 0.001$ , *partial*  $r^2 = 0.67$ ), with no main effect of the number of to-beremembered features ( $F_{1, 84} = 0.74, p = 0.39$ ) or interaction ( $F_{1, 84} = 0.74, p = 0.39$ ) 1.01, p = 0.32). For "yes" color responses (90% quantile, Fig. 5f), a linear mixed model found a main effect of the number of objects ( $F_{1, 84} = 62.00, p < 0.001, partial r^2 = 0.42$ ), with no main effect of the number of to-be-remembered features ( $F_{1, 84} = 0.78, p = 0.38$ ) or interaction ( $F_{1, 84} = 0.53, p = 0.47$ ). Taken together, these results indicate that increasing the number of objects (from set size 1 to set size 2) decreased the proportion of both "yes" shape and color responses, whereas increasing the number of to-be-remembered features (from single feature to both-feature conditions) did not.

#### 3.2. Summary of memory resolution

The proportion of responses in all bins decreased as the number of objects increased (i.e., controlling for the number of to-be-remembered features, we observed a main effect of number of objects). Moreover, the proportion of responses decreased in all bins except for "yes" responses as the number of features increased (i.e., controlling for the number of objects, we observed a main effect of number of to-be-remembered features). In other words, memory resolution was reduced when participants remembered two objects with one feature each (i.e., two objects, two features total) compared to when participants remembered one object with two features (i.e., one object, two features total): fine-grained responses (25% quantile) for shape:  $t_{28} = 5.92$ , p < 0.001,

*Cohen's* D = 0.87, and color:  $t_{28} = 1.97$ , p = 0.059, *Cohen's* D = 0.27, "yes" responses (90% quantile) for shape:  $t_{28} = 6.83$ , p < 0.001, *Cohen's* D = 0.89, and color:  $t_{28} = 3.90$ , p < 0.001, *Cohen's* D = 0.60. In contrast, fine-grained but not "yes" responses were reduced when participants remembered one object with two features (i.e., one object, two features total) compared to one object with one feature (i.e., one object, one feature total): fine-grained responses (25% quantile) for shape:  $t_{28} = 3.24$ , p = 0.003, *Cohen's* D = 0.49, and color:  $t_{28} = 3.12$ , p = 0.0042, *Cohen's* D = 0.45, "yes" responses (90% quantile) for shape:  $t_{28} = 0.17$ , p = 0.87, and color:  $t_{28} = 0.16$ , p = 0.87).

Overall, these results support an *Object* + *Features* model (Fig. 1c), because memory resolution was reduced both when the number of objects and the number of to-be-remembered features increased. Intriguingly, we found evidence that memory resolution for integrated and independent features can differ, as "yes" responses which included the lowest resolution responses of all bins were not influenced by the number of to-be-remembered features (see section *4. Interim Discussion* and *7. General Discussion* for elaboration on this point).

# 3.3. Stochastic dependence model of feature integration

We next examined the stochastic dependence between shape and color across all four response bins (Fig. 3). This analysis was conducted only for the both-feature condition (Fig. 3a), as it is only this condition that participants were instructed to accurately reconstruct both shape and color (see section 1.3. *Procedure*). Bayesian one-sample *t*-tests determined whether the observed dependence differed from complete independence (0%) and complete dependence (100%). For brevity, we report here the statistical results for fine-grained (25% quantile) and "yes" responses (90% quantile), whereas statistical results for the bins corresponding to 50% and 75% quantiles are reported in the *Supplemental Material (Fig. S4*). Data from all results is displayed in Fig. 6.

There was no evidence that the observed dependence for finegrained responses (25% quantile) was greater than 0% for trials with a single object (set size 1),  $BF_{10} = 0.27$ , P(p > 0) = 0.21, or trials with two objects (set size 2),  $BF_{10} = 0.98$ , P(p > 0) = 0.49, suggesting that shapecolor responses highest in resolution were primarily independent. Critically, we found more evidence of dependence as the bins increasingly contained lower-resolution responses (Fig. 6). For "yes" responses (90% quantile), there was decisive evidence that the observed dependence was greater than 0% for trials with a single object (set size 1),  $BF_{10} =$ 165.78, P(p > 0) = 0.99, and decisive evidence that the observed dependence was greater than 0% for trials with two objects (set size 2),  $BF_{10} > 2000$ , P(p > 0) = 1.00.

Although we found more evidence of dependence as quantiles increasingly contained low-resolution responses, responses in all quantiles differed from the maximum dependence observable in the data for trials with one object,  $BF_{10} > 2000$ , P(p < 1) = 1.00, or trials with two objects (set size 2),  $BF_{10} > 2000$ , P(p < 1) = 1.00. In other words, although there was robust evidence of dependence (i.e., the observed dependence differed from 0% as quantiles increasingly contained lower-resolution responses, Fig. 6d), shape and color responses did not perfectly covary (i.e., the observed dependence differed considerably from 100% in all quantiles, Fig. 6d).

#### 3.4. Summary of stochastic dependence

Converging stochastic dependence (Fig. 6) and memory resolution (Fig. 5) analyses revealed that object representations contain both an integrated code as well as independent features. We found primarily evidence of independence for fine-grained responses (25% quantile) and increasing evidence of dependence as response bins contained lower-resolution information (50%, 75%, and 90% quantile). Critically, we found the greatest evidence of dependence for "yes" responses (90% quantile) which contained the lowest resolution reconstructions of all bins (Fig. 6d).

# 4. Interim discussion

We developed a novel shape-color conjunction task to capture memory resolution for objects containing multiple component features (shape and color). We found evidence for both integrated object-level representations as well as independent feature-level representations. Consistent with an object-based account, increasing the number of objects (set size 1 to set size 2) reduced both fine-grained responses that were near-perfect in resolution to the target, as well as "yes" responses that contained both higher and lower resolution representations. Consistent with a feature-based account, increasing the number of to-beremembered features within a single object (i.e., single-feature compared to both-feature condition within the same set size) reduced fine-grained responses. Importantly, the same manipulation did not impact "yes" responses - when the response type included both higherand lower- resolution representations (i.e., the "yes" bin), there was no additional cost to remembering both features of objects (i.e., singlefeature compared to both-feature condition). On the other hand, remembering both features of an object in high resolution (i.e., the finegrained response bin) reduced the proportion of responses compared to remembering one feature in high resolution. These findings not only extend previous behavioral experiments that have found evidence of integrated object-based representations (Balaban, Drew, & Luria, 2019; Fukuda et al., 2010; Luck & Vogel, 1997; Zhang & Luck, 2008), but also support neuroimaging-based models positing the hierarchical and distributed organization of objects and their component features (Barense et al., 2012; Cowell et al., 2019; Erez et al., 2016; Lee et al., 2012; Liang et al., 2020). Our results are most consistent with an Object+Features model rather than a purely object- or feature-based model (Fig. 1), as our results reveal that object representations contain both an integrated code as well as independent features (Figs. 5, 6).

Using our shape-color conjunction task, we replicate an influential paradigm originally tested using a change detection task which found that memory capacity was constrained by the number of objects held in mind rather than by the number of features (Luck & Vogel, 1997). Extending this work, however, we found that high resolution memory was also influenced by the number of individual features. What might explain these seemingly contradictory results? Past work finding integrated object representations primarily use discrete accuracy metrics (e. g., yes/no, same/different, old/new). These discrete tasks do not necessarily distinguish between a high- or low-resolution memory; that is, a participant may be able to succeed on these discrete tasks with a coarse-grained memory of a target object. For example, if the foils on a change detection task are categorically dissimilar, a participant can succeed on this task with only coarse-grained information (e.g., memory for a shade of blue that did not exactly match the target blue). Indeed, we replicated the original finding that memory was constrained by the number of objects when we analyzed responses using the "yes" response bin (Fig. 5 g, k). Notably, this "yes" response bin was designed to mimic "yes" responses on a discrete task, which include both higher to lower resolution memories (Fig. 2). In contrast, when we analyzed responses using the fine-grained response bin, we found that memory was now also constrained by the number of to-be-remembered features. Importantly, these response bins were derived in a data-driven manner by varying the cut of circular space based on participant responses, allowing us to equate the distributional properties between the shape and color stimulus spaces. Furthermore, an analysis of mean absolute error was found to be insensitive to representations at the highest resolution (Fig. S3a, b in Supplemental Material). Thus, our results suggest that whether objectbased or feature-based representations are observed in an experiment may be contingent upon whether the task itself requires high- or lowerresolution memory of the target. Continuous tasks like the one employed here may be better placed to investigate memory at multiple levels of resolution (e.g., as with the present study, comparisons using the finegrained and "yes" response bins).

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In Experiment 1, memory resolution was reduced when participants remembered one object with two features compared to two objects with one feature each (i.e., the number of objects differed while the number of features were held constant), which we interpret as evidence of integrated object representations in memory (Fig. 5). However, this difference in memory resolution could have been instead driven by the number of spatial locations rather than by the number of objects. That is, trials with one object always included one task-relevant spatial location whereas trials with two objects always included two task-relevant spatial locations (Fig. 3a). The number of objects and the number of spatial locations was therefore conflated in Experiment 1, leading to the possibility that shapes and colors were bound to a shared spatial location rather than to each other in memory. Indeed, previous experiments have found evidence not only that spatial location influences memory for object identity (Cai et al., 2019; 2020; Golomb et al., 2014; Oberauer and Lin, 2017), but some experiments have suggested that object features are bound entirely by virtue of their shared spatial location (Kovacs & Harris, 2019; Pertzov & Husain, 2014; Schneegans & Bays, 2017). In Experiment 2, we applied our shape-color conjunction task to test whether shape and color can be bound directly to each other or bound by virtue of a shared spatial location in memory. Manipulating the nature of distracting information, feature integration was disrupted when distractors shared the same visual features as target objects but was not influenced when distractors shared the same spatial location -

suggesting that visual object features can be directly bound to each other in a manner not entirely accounted by shared spatial location.

# 5. Experiment 2

# 5.1. Participants

Thirty participants were recruited from the undergraduate participant pool at the University of Toronto and from the community. Participants from the undergraduate pool received course credit whereas participants from the community received \$20 CAD. One participant was excluded prior to data analysis as they did not complete all trials of the experiment. Two participants performed at chance and were excluded. The final sample size contained 27 individuals (Mean age = 19.85 years, SD = 2.25 years, Females = 20).

# 5.2. Procedure

During the study phase of every trial, a target shape-color object was presented. Objects were drawn from a random position from circular shape and color space (Fig. 7). This target object was randomly displayed either on the left or right side of the monitor for 1000 ms. After a 250 ms ISI, a colored mask was displayed for 350 ms to prevent visual afterimages. Five distractor objects were then sequentially displayed for



# **b.** Distractor Selection

Fig. 7. Experiment 2 task design. (a) We manipulated the feature overlap (shape and spatial location) between irrelevant distractors and the target object in order to infer whether shapes and color where bound directly to each other or bound only to a shared spatial location. During the study phase, the target shape-color object was shown on either the left or right side of the monitor. Next, distractors were sequentially displayed during an n-back task in four possible conditions. During the test phase, the shape-color conjunction task appeared at the location that had contained the target object during the study phase. An item corresponding to the position of the cursor was displayed, such that shape and color changed continuously on a 2D circle. After a mouse response, participants fine-tuned their selection. For illustrative clarity, we have enlarged the target object and kept it consistent across all conditions. Dashed line boxes were not shown during the actual experiment. (b) Distractor shapes were either identical or dissimilar relative to the target shape (sampled from the opposite side of circular shape space, shown in teal). Distractor colors were always dissimilar relative to the target color, such that color information was equated across conditions (sampled from the opposite side of circular color space). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

350 ms each, interleaved with a 250 ms ISI. One of the distractors repeated (i.e., n-back task) and participants were instructed to respond with the spacebar key when a repeat was detected. We emphasized that there could be multiple repeats each trial but in reality, only one object was ever repeated; this instruction was given to ensure that all distractor objects were attended. Participants were instructed to remember only the target shape-color object and not the distractor objects, as well as to guess if they could not remember.

The color of distractor objects was always visually dissimilar relative to the target color. For this reason, distractor colors were sampled from the opposite side of circular color space relative to the position of the target color (Fig. 7). The shape of the distractor objects was either the same as the target or visually dissimilar (sampled from the opposite side of circular shape space). In addition, we varied whether spatial location was the same as the target or dissimilar (on the opposite side of the display). These parameters led to four experimental conditions (Fig. 7b): 1) same shape & same location, 2) different shape & same location, 3) same shape & different location, 4) different shape & different location.

Critically, we controlled for several potential confounding factors in this design. First, the amount of color information in each condition was equated because target colors were always sampled from a random position on circular color space and distractor colors were always visually dissimilar relative to the target object. Second, the amount of information present at the study and test phases was equated across conditions. Participants always studied a single target object during the study phase and reconstructed this target object using the shape-color conjunction task during test, ensuring that only a single object was task-relevant in all conditions. Third, we only analyzed trials in which the *n*-back task was correct, ensuring that participants paid attention in all analyzed trials. We examined how integration for the target shape-color object – whereby the amount of color information was equated across all conditions – was impacted by whether the shape and spatial location of irrelevant distractors overlapped with the target.

#### 5.3. Statistical analysis

We determined the size of circular space for shape and color individually at the 25%, 50%, 75%, and 90% quantiles, using all trial-wise participant responses from the same shape & same location condition. Overall, this approach resulted in the following cuts of circular space: 25% quantile (fine-grained responses) for shape at 4° error and color at 8° error; 50% quantile for shape at 9° error and color at 20° error; 75% quantile for shape at 17° error and color at 42° error; and 90% quantile ("yes" responses) for shape at 33° error and color at 110° error. Notably, the size of bins differed for shape and color because participants were reminded by the distractor shapes, whereas color memory was disrupted by dissimilar interference.

Here, we specifically interpreted our stochastic dependence model which provides the strongest evidence of feature integration (Fig. 4c). In other words, we examined how the nature of distracting information



**Fig. 8.** Experiment 2 stochastic dependence predictions and results. (a) If shape and color are directly bound to each other, the observed dependence between shape and color will be disrupted when the shape of distractor objects is identical to the shape of the target. (b) If shape and color are bound to a shared spatial location, the observed dependence between shape and color will be disrupted when the spatial location of distractors are identical to the spatial location of the target. (c) If shape and color will be disrupted both when the shape and color are both bound to each other and to spatial location, the observed dependence between shape and color will be disrupted both when the shape and the spatial location of distractor objects are identical to the target. (*d*, *e*) Experiment 2 stochastic dependence results. Distractors sharing the same shape as the target disrupted the observed dependence between the target shape-color pairing. In contrast, there was no evidence that showing interfering material at the same spatial location as the target object influenced the observed dependence between the target shape-color pairing. These data are consistent with the notion that shape and color can be bound to each other in a manner not entirely accounted by their shared spatial location. Error bars reflect the 95% confidence interval for the condition mean.

influenced the observed dependence between features of a target object (see Andermane, Joensen, & Horner, 2021).

# 5.4. Predictions

# 5.4.1. Shape-color binding

If shapes and colors are directly bound to each other, then the observed dependence between shape and color should be decreased by distractors sharing the same shape as the target object (Fig. 8a). For example, remembering the color of a target apple would be more difficult due to competing interference from other apples of different colors.

#### 5.4.2. Spatial binding

If the shape and color features are bound to a shared spatial location, then the observed dependence between shape and color should be decreased by distractors sharing the same spatial location as the target object (Fig. 8b). For example, remembering the color of a target apple would be more difficult due to competing interference from other fruit in the same location as the target apple.

#### 5.4.3. Shape-color-spatial binding

A final possibility is that shapes and colors are both directly bound to each other as well as to their shared spatial location. In this prediction, the observed dependence between the target shape-color object should be decreased by both the shape and the spatial location of distractor objects (Fig. 8c). For example, remembering the color of a target apple would be more difficult due to competing interference from apples that differ in their color in the same spatial location as the target apple.

#### 6. Results

Anonymized data are available on the Open Science Framework: htt ps://osf.io/976ta/.

#### 6.1. Stochastic dependence

Irrelevant distractor shape but not irrelevant distractor location decreased the observed dependence between participant shape-color responses. For fine-grained responses (25% quantile), there was a main effect of distractor shape ( $F_{1, 78} = 4.76$ , p = 0.032, partial  $r^2 = 0.057$ ), no main effect of distractor location ( $F_{1, 78} = 0.0023$ , p = 0.96), and no interaction between distractor shape and location ( $F_{1, 78} = 0.99$ , p = 0.32), such that observed dependence between shape and color decreased when irrelevant distractors overlapped in their shape but not their spatial location with the target (Fig. 8d). Similarly, for "yes" responses (90% quantile), there was a main effect of distractor location ( $F_{1, 78} = 0.82$ , p = 0.37), and no interaction between distractor shape and location ( $F_{1, 78} = 0.82$ , p = 0.37), and no interaction between distractor shape and location ( $F_{1, 78} = 0.10$ , p = 0.75) on observed dependence (Fig. 8e). See Fig. S5 in the Supplemental Material for detailed statistics for the bins corresponding to 50% and 75% quantiles.

Replicating Experiment 1 (Fig. 6d), we found primarily evidence of independence for fine-grained responses (25% Quantile) near-perfect in resolution. There was no evidence that observed dependence was greater than 0% for the same shape & same location condition ( $BF_{10} = 0.18$ , P(p > 0) = 0.15) or the same shape & different location condition ( $BF_{10} = 0.11$ , P(p > 0) = 0.099). There was also no evidence that observed dependence was greater than 0% for the different shape & same location condition ( $BF_{10} = 0.57$ , P(p > 0) = 0.36), and anecdotal evidence that observed dependence was greater than 0% for the different shape & different location ( $BF_{10} = 1.85$ , P(p > 0) = 0.65).

Also replicating Experiment 1 (Fig. 6d), we found robust evidence of dependence for "yes" responses (90% Quantile) which included responses ranging from high- to lower-resolution. There was decisive evidence that observed dependence was greater than 0% for the same

shape & same location condition ( $BF_{10} = 229.97$ , P(p > 0) = 1.00) and strong evidence for the same shape & same location condition ( $BF_{10} = 21.44$ , P(p > 0) = 0.96). There was also decisive evidence that observed dependence was greater than 0% for the different shape & same location condition ( $BF_{10} = 820.43$ , P(p > 0) = 1.00) and decisive evidence for the different shape & same location condition ( $BF_{10} = 117.79$ , P(p > 0) = 0.99). Although the resolution of shape and color covaried more often than chance, the observed dependence differed substantially from 100% in all quantiles and conditions ( $BF_{10} >$ 2000, P(p < 1) = 1.00), suggesting that the resolution of shape and color did not perfectly covary.

Overall, the dependence between shape and color was disrupted when distractors shared the same shape as the target object. In contrast, we found no evidence that distractors overlapping in spatial location disrupted dependence in any stochastic dependence analysis. These results suggest that shape and color can be directly bound to each other in a manner that cannot be entirely accounted by their shared spatial location. That is, distractors sharing the same *shape* as the target disrupted dependence between the target shape and color memory, whereas distractors sharing the same *spatial location* as the target did not influence dependence between the target shape and color. See *Supplemental Material* for the memory resolution analyses (*Fig. S6, S7*), results which were consistent with our interpretation of direct binding between shape and color that could not be entirely accounted by the shared location of features.

# 7. General discussion

In two experiments, we sought to understand how constituent visual features are integrated to form objects in memory. We developed a novel shape-color "conjunction task" to reconstruct the memory resolution of object features simultaneously in a single response (Fig. 2). Relative to traditional discrete tasks (e.g., change detection), our task allows for more precise quantification of both high- and low-resolution memories. Furthermore, our task assessed the resolution of multiple object features simultaneously in a single response. Depending on the research question, simultaneous tasks may offer an advantage relative to established sequential continuous tasks that may underestimate the possible dependence between object features. In a first experiment, we replicate and extend a paradigm originally tested using a change detection task by experimentally manipulating the number of objects and to-beremembered features (Luck & Vogel, 1997). We found that memory was impacted both by the number of objects and to-be-remembered features, consistent with Object + Features models that posit a hierarchical and distributed code underlying the representation of objects and their component features (Fig. 1c). To delineate whether features were bound directly to each other or by virtue of shared spatial location, a second experiment manipulated the type of task-irrelevant distracting information. In this second experiment, distracting feature information disrupted integration regardless of its spatial location, providing evidence that shapes and colors can be directly bound to each other in a manner not entirely accounted by their shared location (also see Sone et al., 2021).

Although we found evidence of integration and independence between object features, the finding that shared spatial location did not drive feature integration may be surprising, as previous studies have suggested that object features may be bound entirely by virtue of their spatial location (Pertzov & Husain, 2014; Schneegans & Bays, 2017), as well as evidence suggesting that spatial location can play an important role for binding an object to a position within the environment (i.e., object-in-place memory; Cai, Fulvio, Yu, Sheldon, & Postle, 2020; Golomb et al., 2014; Hollingworth, 2007; Kovacs & Harris, 2019; Reagh & Yassa, 2014; Tsao, Moser, & Moser, 2013; Yeung et al., 2019; Yonelinas, Ranganath, Ekstrom, and Wiltgen, 2019). One important difference between our task in the second experiment (Fig. 7) and previous literature is that we neither tested memory for spatial location nor made spatial location task-relevant. In other words, although participants were required to remember both shape and color at study and were required to reconstruct both shape and color at test, participants did not need to remember spatial location at any time during our task. By deemphasizing the role of spatial location, we provide an explicit demonstration that the shape and color features of an object can be bound directly to each other in memory in a manner that could not be entirely accounted by shared spatial location. Following this logic, spatial location can likely become a more important property for feature binding in tasks that emphasize spatial location through a response at test (Schneegans & Bays, 2017) or through multiple study positions during the study phase of an experiment (Golomb et al., 2014; Kovacs & Harris, 2019; Pertzov & Husain, 2014).

As we have found robust evidence of independence between features, could a purely feature-based model account for our findings of integration (Fig. 1b)? For example, could it be the case that on some trials cognitive resources are flexibly directed towards features, such that participants represent one feature in high resolution at the expense of another object feature (potentially accounting for independence in the fine-grained response bin; Fig. 6d), whereas on other trials, participants direct cognitive resources towards both object features, resulting in a seemingly integrated but lower resolution response (accounting for dependence in the "yes" response bin; Fig. 6d)? We argue that this possibility is unlikely for two reasons. First, Experiment 1 manipulated the number of objects and number of to-be-remembered features. If objects were represented in an entirely feature-based manner, then there should be no difference between the condition with 1 feature displayed in 2 objects (2 features total) compared to the condition with 2 features displayed in 1 object (2 features total). Yet, we observed a robust drop in memory resolution where the number of to-be-remembered features were equated but the number of objects varied (Fig. 5), suggesting the presence of an integrated code. Second, if participants adopted a particular strategy whereby cognitive resources are directed towards a single object feature at the expense of another, then we should observe anti-dependence in our stochastic dependence model (Fig. 4). For example, if participants only represented shape in high resolution on 50% of trials (and not color), or color in high resolution on 50% of trials (and not shape), then the probability of reconstructing shape and color together would be 0% even though the predicted independence would be 25%, resulting in a negative value in the model. The observed shapecolor data did not differ from the predicted independence (i.e., observed dependence did not differ from 0%, Fig. 6d), suggesting that participants did not preferentially direct cognitive resources towards single features in high resolution at the expense of the other feature.

Conversely, could a purely object-based theory of memory account for our findings (Fig. 1a)? For example, influential "slot" models of visual short-term memory predict that features are integrated when present in memory and thus, object features would perfectly covary in resolution. Our results do not support extreme versions of this perspective. For example, shape and color exhibited dependence for "yes" responses but not fine-grained responses, suggesting that when one object feature is represented at high resolution, the other object feature can be represented at a lower resolution in a dependent manner (Fig. 6). Relatedly, how might our results compare to findings based on an influential mixture model separating "precision" from "guessing" (Zhang & Luck, 2008)? Although this previous study did not manipulate the number of features within the same object, Zhang and Luck (2008) found evidence that there was a fundamental capacity limit to the number of high-resolution items held in mind. Here, perhaps our findings of independence and integration can be reconciled with slot models by characterizing multiple representational levels. For example, we can consider an architecture whereby integrated object representations are present in addition to representations of the individual features comprising that object, such that there may be different capacity limits for multiple representational levels concurrently held in mind. This perspective would be consistent with behavioral evidence of features

and their integration (Cowan, Saults and Blume, 2014; Hardman & Cowan, 2015; Markov et al., 2019; Markov et al., 2021; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002; Sone et al., 2021; Wheeler & Treisman, 2002) and well-supported by neuroimaging work characterizing multiple levels of object representation (Coutanche & Thompson-Schill, 2015; Erez et al., 2016; Jung et al., 2018; Liang et al., 2020; Martin et al., 2018). For this reason, better understanding how measurement models of short-term memory (such as the mixture model) relate to simultaneous continuous tasks may be a fruitful avenue of future investigation (Oberauer, 2021).

Finally, could idiosyncratic properties of our simultaneous conjunction task or extraneous factors such as noise explain the findings of integration and independence? For example, perhaps shape and color perfectly covary in their resolution as predicted by a purely object-based model (Fig. 1a, Fig. 6a), but noise at test due to properties of our task or differences in attention across trials artificially induce independence between features at the highest memory resolution. This explanation is unlikely for both theoretical and methodological reasons. Theoretically, if the resolution of object features perfectly covary within an integrated representation and were only influenced by noise or fluctuations in attention, then noise should be correlated between both object features (i.e., both features tend to be represented in high-resolution during low noise, or both features tend to be represented in low-resolution during high noise, as noise would influence a single integrated representation). Contrary to this prediction, shape responses in the fine-grained bin could be reconstructed in high-resolution whereas color could not (and vice versa; see Fig. 6d). Critically, the independence between high-resolution shape and color suggests that either features can differ in resolution from the integrated code or that noise can impact features individually - here, both cases imply the existence of independent feature-based representations. Methodologically, we selected our response bins in a data-driven manner based on quantiles (Fig. 2). Memory resolution for shape and color did not perfectly covary in any quantile, with "yes" responses (90% quantile) accounting for only approximately 30% of the maximum observable dependence in the data (Fig. 6d). It would be challenging to account for the low observed dependence based on noise alone, because we found robust evidence of independence even in a condition where participants reconstruct a single shape-color object. In Experiment 2, we equated differences in attentional demand because the study and test phases were identical across conditions and only n-back correct trials were analyzed. Nevertheless, we find explicit evidence of integration and independence in Experiment 2 that was modulated by the type of distracting information, even when differences in attentional demand between conditions were equated (Fig. 8). These data suggest that feature integration can be modulated by the nature of interference, such that shape-color object responses can appear more feature-like after irrelevant shape interference rather than irrelevant spatial location interference. For these reasons, we suggest that our data are best supported by an Object+Features perspective, rather than by purely objector feature-based accounts.

Taken together, we find integration and independence between features of a shape-color object that is broadly consistent with our previous work on a simultaneous conjunction task with simpler orientation-color stimuli (Sone et al., 2021). In three experiments, we previously found that the resolution of orientation-color objects exhibited dependence across both simultaneous conditions (both features reconstructed at the same time at test) and sequential conditions (one feature reconstructed then the other at test). However, our previous study (Sone et al., 2021) found that the sequential version of the orientation-color conjunction task induced more independence between features at test compared to the simultaneous version of the task, suggesting that object representations can appear more or less independent depending on task requirements. In the current study, we advance this work with two experiments that employed novel measures of memory resolution based on data-driven quantiles. Furthermore, we applied a data-driven statistical model of stochastic dependence, finding that a

framework which incorporates both integration and independence between features is most consistent with the format of how objects are represented in mind.

Critically, we also provide new evidence showing that the resolution of independent features can differ from the resolution of the integrated code. In Experiment 1, the number of to-be-remembered features influenced memories near-perfect in resolution (i.e., the fine-grained response bin) but not "ves" responses which included both higher and lower resolution memories (Figs. 3, 5). This finding implies that memory for individual features can be held in higher resolution than memory for their integration. Had the resolution of the integrated code been equivalent to memory resolution for the individual features, we should not have observed any differences in memory resolution between conditions with the same number of objects but a different number of to-beremembered features (e.g., the condition with one feature displayed in one object compared to the condition with two features displayed in one object; Fig. 5). In other words, features from the same object should perfectly covary if the integrated code is higher in resolution than the individual features. However, our data-driven statistical model of stochastic dependence (Figs. 4, 6) found the strongest evidence of integration for responses that included low resolution reconstructions, suggesting that individual features can be represented at a higher resolution than the integrated code. Results from the stochastic dependence analysis were replicated in Experiment 2 (Fig. 8), again suggesting that feature-based representations can be higher in resolution compared to the integrated code.

Why might the resolution of the integrated code differ from the resolution of independent features? Integrated representations are necessary for object invariance (Rolls, 2012), whereby we can correctly recognize an object despite variation in lighting, visibility, or viewpoint. For example, we can recognize our blue umbrella on the beach, even if the umbrella's color changes due to a shadow cast by an overhead cloud. Despite subtle changes in fine-grained appearance, we can nevertheless recognize our blue umbrella. In this scenario, it may be that memories held at a lower resolution are more flexible in accommodating these variations in appearance while supporting accurate object recognition. In contrast, object memories held in very high resolution may be intolerant to subtle changes in appearance and thus lead to an object being falsely recognized as a different entity. Indeed, it is well established that featural information can be represented in a highly detailed manner in sensory cortex (e.g., Ester, Anderson, Serences, & Awh, 2013; Katus et al., 2015; Rabagliati et al., 2017; Sreenivasan et al., 2014) and it may be advantageous to combine these high-resolution feature representations with a lower resolution integrated code in anterior regions of the neocortex. Such an architecture could represent information in high resolution and retain invariance without requiring a combinatorially explosive number of representations unique to each object viewpoint. This perspective is supported by one previous neuroimaging study which found dependence between "gist" memory of object color and spatial context operationalized using a mixture model, which may be comparable to the results of our "yes" response bin (Cooper & Ritchey, 2019). Importantly, this previous study provides initial neural evidence that more integrated representations may be lower in resolution than less integrated representations (but see perspectives by Yonelinas, 2013; Ekstrom & Yonelinas, 2020).

Although researchers have found dependence between lowerresolution object color representations bound to spatial context (Cooper & Ritchey, 2019), to our knowledge no neuroimaging studies have yet examined how the brain supports memory resolution for integrated and independent features for multiple features associated within the same object (e.g., shape and color). Instead, existing neuroimaging work have found that the integrated code itself can differ in several ways from the representation of independent features. Beginning with seminal investigations by Hubel and Wiesel (1969), the sensory cortex has been known to represent independent object features such as oriented line (Kamitani & Tong, 2005), color (Brouwer & Heeger, 2009), shape (Kourtzi & Kanwisher, 2000), and texture (Lieber & Bensmaia, 2019). In addition to these posterior regions which represent featurebased information, anterior regions represent information about conjunctions of object features in a hierarchical manner (Cowell et al., 2019). For example, the parietal cortex seems to represent simple conjunctions located in the environment (Cai et al., 2020; Todd & Marois, 2004), and other regions such as the perirhinal cortex and hippocampus represent complex conjunctions containing multiple features bound to spatial and temporal context (Ekstrom & Yonelinas, 2020; Erez et al., 2016; Martin et al., 2018; Robin, Buchsbaum, & Moscovitch, 2018; Yonelinas et al., 2019). Directly supporting an integrated code, experimenters have found evidence of object representations that are not the simple sum of constituent features (Erez et al., 2016; Liang et al., 2020). Furthermore, the specific characteristics of the integrated code and feature-based representations can differ with expertise, such that object features change in their representational similarity in parallel to changes at the level of the conjunction (Liang et al., 2020).

Despite the wealth of neuroimaging and behavioral evidence supporting feature-based representations in memory, some experiments have found evidence for only object-based representations in memory. For example, an influential change detection task found that remembering 16 features distributed across four objects were as accurate as remembering four features displayed in four objects (Luck & Vogel, 1997). These results have been used to support "slot models" (Fukuda, Awh, & Vogel, 2011; Zhang & Luck, 2008), extreme versions of which predict that memory resolution is entirely constrained by objects rather than their constituent features, and thus, object features perfectly covary in their resolution. However, this work was challenged by researchers finding evidence of feature-based representations when using continuous tasks which assess memory resolution (Fougnie & Alvarez, 2011; Ma et al., 2014). Critically, when we interpret our results from Experiment 1 using a "yes" response bin designed to mimic accuracy on a discrete change detection task, we replicate the original pattern of entirely object-based representations in memory. In other words, when we analyze our data using a response metric which included memories of both higher and lower resolution, we find no evidence of featurebased representations in our memory resolution analysis. However, when we isolated representations at the highest resolution using the fine-grained response bin on our continuous shape-color conjunction task, we then found explicit evidence of feature-based representations in memory. These analyses reveal that the type of response used to assess memory may have led to seemingly contradictory findings in the literature. Indeed, we were able to replicate both traditional discrete change detection tasks finding object-based representations and more recent continuous tasks finding feature-based representations, depending on the response type used to assess memory performance (i.e., fine-grained vs. "yes" responses for memory resolution analyses in Experiment 1, Fig. 5).

Whereas discrete tasks such as change detection with very discriminable stimuli may find evidence of only object-based representations, we suggest that continuous tasks are more sensitive to feature-based representations at the highest memory resolution. In the present study, we have designed a continuous shape-color task to simultaneously reconstruct multiple object features in a single response. Not only is our task potentially useful for studying the resolution of the integrated code and component features in future work, but the specific nature of the shape-color stimuli can be usefully adapted to study a range of phenomena. Given that recent models have proposed that subjective similarity may be especially important for understanding visual short-term memory (Schurgin et al., 2020), our task combines two well-controlled feature spaces validated on the basis of similarity. Indeed, both shape space (VCS space; Li, Liang, Lee, and Barense, 2020) and color space (CIELAB color space; Robertson, 1977) are explicitly defined such that distance along the stimulus space corresponds to subjective distance in visual similarity. Furthermore, the shape-color objects are unfamiliar to participants, allowing experimenters the

ability to isolate memory responses without the contribution of wellestablished object labels acquired over a lifetime of experiences (Souza et al., 2021).

In conclusion, replicating and extending a classic paradigm using our novel continuous shape-color conjunction task, we find evidence for *both* integrated and independent feature representations in memory. Moreover, we found that shape and color can be directly bound to each other in a manner not entirely accounted by their shared spatial location. Finally, we provide new evidence that independent features from the same object can be represented in higher resolution than when those features are integrated, suggesting a resolution trade-off between high resolution individual features and lower resolution integrated objects. These results constrain models of feature integration, advancing the ageold question of how objects are represented in mind based on their constituent features.

# CRediT authorship contribution statement

Aedan Y. Li: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. Keisuke Fukuda: Conceptualization, Methodology, Writing – review & editing, Supervision. Morgan D. Barense: Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

# **Declaration of Competing Interest**

None.

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# Supplementary data

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#### References

- Andermane, N., Joensen, B. H., & Horner, A. J. (2021). Forgetting across a hierarchy of episodic representations. *Neurobiology*, 67, 50–57. https://doi.org/10.1016/j. conb.2020.08.004
- Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological Science*, 18(7), 622–628. https://doi.org/10.1111/j.1467-9280.2007.01949.x
- Bae, G.-Y., Olkkonen, M., Allred, S. R., & Flombaum, J. I. (2015). Why some colors appear more memorable than others: A model combining categories and particulars in color working memory. *Journal of Experimental Psychology. General*, 144(4), 744–763. https://doi.org/10.1037/xge0000076
- Balaban, H., Assaf, D., Arad Meir, M., & Luria, R. (2019). Different features of real-world objects are represented in a dependent manner in long-term memory. *Journal of Experimental Psychology*. https://doi.org/10.1037/xge0000716. General, No Pagination Specified-No Pagination Specified.
- Balaban, H., Drew, T., & Luria, R. (2019). Neural evidence for an object-based pointer system underlying working memory. *Cortex*, 119, 362–372. https://doi.org/ 10.1016/j.cortex.2019.05.008
- Barense, M. D., Groen, I. I. A., Lee, A. C. H., Yeung, L.-K., Brady, S. M., Gregori, M., Kapur, N., Bussey, T. J., Saksida, L. M., & Henson, R. N. A. (2012). Intact memory for irrelevant information impairs perception in amnesia. *Neuron*, 75(1), 157–167. https://doi.org/10.1016/j.neuron.2012.05.014

- Barsalou, L. W. (2016). On staying grounded and avoiding quixotic dead ends. Psychonomic Bulletin & Review, 23(4), 1122–1142. https://doi.org/10.3758/s13423-016-1028-3
- Bartsch, L. M., Singmann, H., & Oberauer, K. (2018). The effects of refreshing and elaboration on working memory performance, and their contributions to long-term memory formation. *Memory and Cognition*, 46, 796–808. https://doi.org/10.3758/ s13421-018-0805-9
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1–48. https://doi.org/ 10.18637/jss.v067.i01
- Bays, P. M. (2015). Spikes not slots: Noise in neural populations limits working memory. Trends in Cognitive Sciences, 19(8), 431–438. https://doi.org/10.1016/j. tics.2015.06.004
- Bays, P. M., Catalao, R. F., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. J Vis, 9(10), 7.1-11. https://doi.org/ 10.1167/9.10.7
- Behrens, T. E. J., Muller, T. H., Whittington, J. C. R., Mark, S., Baram, A. B., Stachenfeld, K. L., & Kurth-Nelson, Z. (2018). What is a cognitive map? Organizing Knowledge for Flexible Behavior. *Neuron*, 100(2), 490–509. https://doi.org/ 10.1016/j.neuron.2018.10.002
- Berens, S. C., Richards, B. A., & Horner, A. J. (2020). Dissociating memory accessibility and precision in forgetting. *Nat Hum Behav*, 4(8), 866–877. https://doi.org/ 10.1038/s41562-020-0888-8
- van den Berg, R., Shin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences*, 109(22), 8780–8785. https://doi.org/10.1073/ pnas.1117465109
- Binder, J. R. (2016). In defense of abstract conceptual representations. Psychonomic Bulletin & Review, 23(4), 1096–1108. https://doi.org/10.3758/s13423-015-0909-1
- Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2013). Real-world objects are not represented as bound units: Independent forgetting of different object details from visual memory. *Journal of Experimental Psychology: General*, 142(3), 791–808. https://doi.org/10.1037/a0029649
- Brouwer, G. J., & Heeger, D. J. (2009). Decoding and reconstructing color from responses in human visual cortex. *The Journal of Neuroscience*, 29(44), 13992–14003. https:// doi.org/10.1523/JNEUROSCI.3577-09.2009
- Brunec, I. K., Moscovitch, M., & Barense, M. D. (2018). Boundaries shape cognitive representations of spaces and events. *Trends in Cognitive Sciences*, 22(7), 637–650. https://doi.org/10.1016/j.tics.2018.03.013
- Cai, Y., Fulvio, J. M., Yu, Q., Sheldon, A. D., & Postle, B. R. (2020). The role of locationcontext binding in nonspatial visual working memory. *ENeuro*, 7(6). https://doi.org/ 10.1523/ENEURO.0430-20.2020
- Cai, Y., Sheldon, A. D., Yu, Q., & Postle, B. R. (2019). Overlapping and distinct contributions of stimulus location and of spatial context to nonspatial visual shortterm memory. *Journal of Neurophysiology*, 121(4), 1222–1231. https://doi.org/ 10.1152/jn.00062.2019
- Cecchini, M. A., Yassuda, M. S., Bahia, V. S., de Souza, L. C., Guimarães, H. C., Caramelli, P., Carthery-Goulart, M. T., Patrocínio, F., Foss, M. P., Tumas, V., Lima-Silva, T. B., Brucki, S. M. D., Nitrini, R., Della Sala, S., & Parra, M. A. (2017). Recalling feature bindings differentiates Alzheimer's disease from frontotemporal dementia. *Journal of Neurology, 264*(10), 2162–2169. https://doi.org/10.1007/ s00415-017-8614-9
- Chang, E. H., & Huerta, P. T. (2012). Neurophysiological correlates of object recognition in the dorsal subiculum. Frontiers in Behavioral Neuroscience, 6. https://doi.org/ 10.3389/fnbeh.2012.00046
- Cohen, S. J., Munchow, A. H., Rios, L. M., Zhang, G., Ásgeirsdóttir, H. N., & Stackman, R. W. (2013). The rodent hippocampus is essential for nonspatial object memory. *Current Biology*, 23(17), 1685–1690. https://doi.org/10.1016/j. cub.2013.07.002
- Cooper, R. A., & Ritchey, M. (2019). Cortico-hippocampal network connections support the multidimensional quality of episodic memory. *ELife*, 8, Article e45591. https:// doi.org/10.7554/eLife.45591
- Cooper, R. A., & Ritchey, M. (2020). Progression from feature-specific brain activity to hippocampal binding during episodic encoding. *Journal of Neuroscience*, 40(8), 1701–1709. https://doi.org/10.1523/JNEUROSCI.1971-19.2019
- Coutanche, M. N., & Thompson-Schill, S. L. (2015). Creating concepts from converging features in human cortex. *Cerebral Cortex*, 25(9), 2584–2593. https://doi.org/ 10.1093/cercor/bhu057
- Cowan, N., Saults, J.S., & Blume, C.L. (2014). Central and peripheral components of working memory storage. Journal of Experimental Psychology: General, 143(5), 1806–1836. https://doi.org/10.1037/a0036814.
- Cowan, N., Saults, J. S., & Blume, C. L. (2014). Central and peripheral components of working memory storage. *Journal of Experimental Psychology. General*, 143(5), 1806–1836. https://doi.org/10.1037/a0036814
- Cowell, R. A., Barense, M. D., & Sadil, P. S. (2019). A roadmap for understanding memory: Decomposing cognitive processes into operations and representations. *ENeuro*, 6(4). https://doi.org/10.1523/ENEURO.0122-19.2019
- Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, 11(9), 379–386. https://doi.org/10.1016/j.tics.2007.08.001
- Ekstrom, A. D., & Yonelinas, A. P. (2020). Precision, binding, and the hippocampus: Precisely what are we talking about? *Neuropsychologia*, 138, Article 107341. https:// doi.org/10.1016/j.neuropsychologia.2020.107341
- Erez, J., Cusack, R., Kendall, W., & Barense, M. D. (2016). Conjunctive coding of complex object features. *Cerebral Cortex*, 26(5), 2271–2282. https://doi.org/10.1093/cercor/ bhv081

Ester, E. F., Anderson, D. E., Serences, J. T., & Awh, E. (2013). A neural measure of precision in visual working memory. *Journal of Cognitive Neuroscience*, 25(5), 754–761. https://doi.org/10.1162/jocn.a.00357

Ester, E.F., Ho, T.C., Brown, S.D., & Serences, J.T. (2014). Variability in visual working memory ability limits the efficiency of perceptual decision making. Journal of Vision, 14(4), 2. https://doi.org/https://doi.org/10.1167/14.4.2.

- Feldman, J. (2013). The neural binding problem(s). Cognitive Neurodynamics, 7(1), 1–11. https://doi.org/10.1007/s11571-012-9219-8
- Feng, L., & Wang, X. (2017). Harmonic template neurons in primate auditory cortex underlying complex sound processing. *Proceedings of the National Academy of Sciences*, 114(5), E840–E848. https://doi.org/10.1073/pnas.1607519114
- Fougnie, D., & Alvarez, G. A. (2011). Object features fail independently in visual working memory: Evidence for a probabilistic feature-store model. *Journal of Vision*, 11(12). https://doi.org/10.1167/11.12.3
- Fukuda, K., Awh, E., & Vogel, E. K. (2010). Discrete capacity limits in visual working memory. Current Opinion in Neurobiology, 20(2), 177–182. https://doi.org/10.1016/ j.conb.2010.03.005
- Gao, Z., Wu, F., Qiu, F., He, K., Yang, Y., & Shen, M. (2017). Bindings in working memory: The role of object-based attention. Attention, Perception, & Psychophysics, 79 (2), 533–552. https://doi.org/10.3758/s13414-016-1227-z
- Garnelo, M., & Shanahan, M. (2019). Reconciling deep learning with symbolic artificial intelligence: Representing objects and relations. *Current Opinion in Behavioral Sciences*, 29, 17–23. https://doi.org/10.1016/j.cobeha.2018.12.010
- Gelman, A., Jakulin, A., Pittau, M. G., & Su, Y.-S. (2008). A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics*, 2(4), 1360–1383. https://doi.org/10.1214/08-AOAS191
- 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), 2262–2278. https://doi.org/10.1037/xge0000017
- Greene, N. R., & Naveh-Benjamin, M. (2020). A specificity principle of memory: Evidence from aging and associative memory. *Psychological Science*, 31(3), 316–331. https:// doi.org/10.1177/0956797620901760
- Gross, C. G. (2002). Genealogy of the "Grandmother Cell". *The Neuroscientist*, 8(5), 512–518. https://doi.org/10.1177/107385802237175
- Hardman, K. O., & Cowan, N. (2015). Remembering complex objects in visual working memory: Do capacity limits restrict objects or features? *Journal of Experimental Psychology. Learning, Memory, and Cognition,* 41(2), 325–347. https://doi.org/ 10.1037/xlm0000031
- Hardman, K. O., Vergauwe, E., & Ricker, T. J. (2017). Categorical working memory representations are used in delayed estimation of continuous colors. *Journal of Experimental Psychology. Human Perception and Performance*, 43(1), 30–54. https:// doi.org/10.1037/xhp0000290
- Hawkins, J., Lewis, M., Klukas, M., Purdy, S., & Ahmad, S. (2019). A framework for intelligence and cortical function based on grid cells in the neocortex. *Frontiers in Neural Circuits*, 12. https://doi.org/10.3389/fncir.2018.00121
- Hicks, J. L., & Starns, J. J. (2015). Chapter four—Using multidimensional encoding and retrieval contexts to enhance our understanding of stochastic dependence in source memory. In B. H. Ross (Ed.), Vol. 62. Psychology of learning and motivation (pp. 101–140). Academic Press. https://doi.org/10.1016/bs.plm.2014.09.004.
- 101–140). Academic Press. https://doi.org/10.1016/bs.plm.2014.09.004.
   Hollingworth, A. (2007). Object-position binding in visual memory for natural scenes and object arrays. Journal of Experimental Psychology: Human Perception and Performance, 33(1), 31–47. https://doi.org/https://doi.org/10.103 7/00966-1523-33-1-31
- Horner, A. J., Bisby, J. A., Bush, D., Lin, W.-J., & Burgess, N. (2015). Evidence for holistic episodic recollection via hippocampal pattern completion. *Nature Communications*, 6 (1), 1–11. https://doi.org/10.1038/ncomms8462
- Horner, A. J., & Burgess, N. (2013). The associative structure of memory for multielement events. *Journal of Experimental Psychology. General*, 142(4), 1370–1383. https://doi.org/10.1037/a0033626
- Hubel, D. H., & Wiesel, T. N. (1969). Anatomical demonstration of columns in the monkey striate cortex. *Nature*, 221(5182), 747–750. https://doi.org/10.1038/ 221747a0
- JASP Team (2019). JASP (Version 0.9)[Computer software].
- Jacklin, D. L., Cloke, J. M., Potvin, A., Garrett, I., & Winters, B. D. (2016). The dynamic multisensory engram: Neural circuitry underlying crossmodal object recognition in rats changes with the nature of object experience. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 36*(4), 1273–1289. https://doi.org/ 10.1523/JNEUROSCI.3043-15.2016
- Joensen, B. H., Gaskell, M. G., & Horner, A. J. (2020). United we fall: All-or-none forgetting of complex episodic events. *Journal of Experimental Psychology. General*, 149(2), 230–248. https://doi.org/10.1037/xge0000648
- Jung, Y., Larsen, B., & Walther, D. B. (2018). Modality-independent coding of scene categories in prefrontal cortex. *Journal of Neuroscience*, 38(26), 5969–5981. https:// doi.org/10.1523/JNEUROSCI.0272-18.2018
- Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. Nature Neuroscience, 8(5), 679–685. https://doi.org/10.1038/nn1444
- Katus, T., Grubert, A., & Eimer, M. (2015). Electrophysiological evidence for a sensory recruitment model of somatosensory working memory. *Cerebral Cortex*, 25(12), 4697–4703. https://doi.org/10.1093/cercor/bhu153
  Kleiner, M. (2007). *What's new in Psychtoolbox-37. 89*.
- Kliegl, R., Masson, M. E. J., & Richter, E. M. (2010). A linear mixed model analysis of masked repetition priming. *Visual Cognition*, 18(5), 655–681. https://doi.org/ 10.1080/13506280902986058
- Korkki, S. M., Richter, F. R., Jeyarathnarajah, P., & Simons, J. S. (2020). Healthy ageing reduces the precision of episodic memory retrieval. Psychology and Aging, 35(1), 124–142. https://doi.org/https://doi.org/10.1037/pag0000432.

- Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. Journal of Neuroscience, 20(9), 3310–3318. https://doi.org/10.1523/ JNEUROSCI.20-09-03310.2000
- Kovacs, O., & Harris, I. M. (2019). The role of location in visual feature binding. Attention, Perception, & Psychophysics, 81(5), 1551–1563. https://doi.org/10.3758/ s13414-018-01638-8
- Kristjánsson, Á., & Egeth, H. (2020). How feature integration theory integrated cognitive psychology, neurophysiology, and psychophysics. *Attention, Perception, & Psychophysics*, 82(1), 7–23. https://doi.org/10.3758/s13414-019-01803-7
- Kruschke, J. K. (2010). What to believe: Bayesian methods for data analysis. Trends in Cognitive Sciences, 14(7), 293–300. https://doi.org/10.1016/j.tics.2010.05.001
- Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. Frontiers in Psychology, 4, 863.
  LeCun, Y., Bengio, Y., & Hinton, G. (2015). Deep learning. Nature, 521(7553), 436–444.
- https://doi.org/10.1038/nature14539
  Lee, A. C. H., Yeung, L.-K., & Barense, M. D. (2012). The hippocampus and visual perception. Frontiers in Human Neuroscience, 6. https://doi.org/10.3389/fnhum.2012.00091
- Lee, M. D., & Wagenmakers, E.-J. (2013). Bayesian cognitive modeling: A practical course. Cambridge University Press. https://doi.org/10.1017/CB09781139087759
- Li, A.Y., Fukuda, K., Lee, A.C.H., & Barense, M.D. (2020). Visual interference can help and hinder memory: Capturing representational detail using the Validated Circular Shape Space. bioRxiv, 535922. doi: https://doi.org/https://doi.org/10.1101 /535922.
- Li, A. Y., Liang, J. C., Lee, A. C. H., & Barense, M. D. (2020). The validated circular shape space: Quantifying the visual similarity of shape. *Journal of Experimental Psychology. General.*, https://doi.org/10.1037/xge0000693
- Li, A. Y., Liang, J. C., Lee, A. C. H., & Barense, M. D. (2020). The validated circular shape space: Quantifying the visual similarity of shape. Journal of Experimental Psychology. General. https://doi.org/https://doi.org/10.1037/xge0000693.
- Liang, J. C., Erez, J., Zhang, F., Cusack, R., & Barense, M. D. (2020). Experience transforms conjunctive object representations: Neural evidence for unitization after visual expertise. *Cerebral Cortex*, 30(5), 2721–2739. https://doi.org/10.1093/ cercor/bhz250
- Lieber, J. D., & Bensmaia, S. J. (2019). High-dimensional representation of texture in somatosensory cortex of primates. *Proceedings of the National Academy of Sciences*, 116(8), 3268–3277. https://doi.org/10.1073/pnas.1818501116
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390(6657), 279–281. https://doi.org/10.1038/36846
- Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience & Biobehavioral Reviews*, 62, 100–108. https://doi.org/10.1016/j.neubiorev.2016.01.003
- Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. Nature Neuroscience, 17(3), 347–356. https://doi.org/10.1038/nn.3655
- Magezi, D. A. (2015). Linear mixed-effects models for within-participant psychology experiments: An introductory tutorial and free, graphical user interface (LMMgui). *Frontiers in Psychology*, 6. https://doi.org/10.3389/fpsyg.2015.00002
- Mahon, B. Z. (2015). The burden of embodied cognition. Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 69(2), 172–178. https://doi.org/10.1037/cep0000060
- von der Malsburg, C. (1981). The correlation theory of brain function. In E. Domany, J. L. van Hemmen, & K. Schulten (Eds.), Models of neural networks: Temporal aspects of coding and information processing in biological systems (pp. 95–119). Springer. https:// doi.org/10.1007/978-1-4612-4320-5\_2.
- Markov, Y. A., Tiurina, N. A., & Utochkin, I. S. (2019). Different features are stored independently in visual working memory but mediated by object-based representations. *Acta Psychologica*, 197, 52–63. https://doi.org/10.1016/j. actpsy.2019.05.003
- Markov, Y. A., Utochkin, I. S., & Brady, T. F. (2021). Real-world objects are not stored in holistic representations in visual working memory. *Journal of Vision*, *21*(3), 18. https://doi.org/10.1167/jov.21.3.18
   Martin, A. (2016). GRAPES—Grounding representations in action, perception, and
- Martin, A. (2016). GRAPES—Grounding representations in action, perception, and emotion systems: How object properties and categories are represented in the human brain. *Psychonomic Bulletin & Review*, 23(4), 979–990. https://doi.org/10.3758/ s13423-015-0842-3
- Martin, C. B., Douglas, D., Newsome, R. N., Man, L. L., & Barense, M. D. (2018). Integrative and distinctive coding of visual and conceptual object features in the ventral visual stream. *ELife*, 7, Article e31873. https://doi.org/10.7554/eLife.31873
- Meiser, T., & Bröder, A. (2002). Memory for multidimensional source information. Journal of Experimental Psychology: Learning, Memory, and Cognition, 28, 116–137. https://doi.org/10.1037/0278-7393.28.1.116
- Mitchell, D. J., & Cusack, R. (2018). Visual short-term memory through the lifespan: Preserved benefits of context and metacognition. *Psychology and Aging*, 33(5), 841–854. https://doi.org/10.1037/pag0000265
- Mok, R. M., & Love, B. C. (2019). A non-spatial account of place and grid cells based on clustering models of concept learning. *Nature Communications*, 10(1), 5685. https:// doi.org/10.1038/s41467-019-13760-8
- Oberauer, K. (2021). Measurement models for visual working memory—A factorial model comparison. *Psychological Review*. https://doi.org/10.1037/rev0000328. Advance online publication.
- Oberauer, K., & Eichenberger, S. (2013). Visual working memory declines when more features must be remembered for each object. *Memory & Cognition*, 41(8), 1212–1227. https://doi.org/10.3758/s13421-013-0333-6
- Oberauer, K., & Lin, H.-Y. (2017). An interference model of visual working memory. Psychological Review, 124(1), 21–59. https://doi.org/https://doi.org/10.1037/r ev0000044.

Olson, I. R., & Jiang, Y. (2002). Is visual short-term memory object based? Rejection of the "strong-object" hypothesis. *Perception & Psychophysics*, 64(7), 1055–1067. https://doi.org/10.3758/BF03194756

- Palanca, B. J. A., & DeAngelis, G. C. (2005). Does neuronal synchrony underlie visual feature grouping? *Neuron*, 46(2), 333–346. https://doi.org/10.1016/j. neuron.2005.03.002
- Parra, M. A., Abrahams, S., Fabi, K., Logie, R., Luzzi, S., & Della Sala, S. (2009). Shortterm memory binding deficits in Alzheimer's disease. *Brain: A Journal of Neurology*, 132(Pt 4), 1057–1066. https://doi.org/10.1093/brain/awp036
- Pertzov, Y., & Husain, M. (2014). The privileged role of location in visual working memory. Attention, Perception, & Psychophysics, 76(7), 1914–1924. https://doi.org/ 10.3758/s13414-013-0541-y
- Pezzulo, G., Barsalou, L. W., Cangelosi, A., Fischer, M. H., McRae, K., & Spivey, M. J. (2013). Computational grounded cognition: A new alliance between grounded cognition and computational modeling. *Frontiers in Psychology*, 3. https://doi.org/ 10.3389/fpsyg.2012.00612
- Pina, J. E., Bodner, M., & Ermentrout, B. (2018). Oscillations in working memory and neural binding: A mechanism for multiple memories and their interactions. *PLoS Computational Biology*, 14(11), Article e1006517. https://doi.org/10.1371/journal. pcbi.1006517
- Pratte, M. S., Park, Y. E., Rademaker, R. L., & Tong, F. (2017). Accounting for stimulusspecific variation in precision reveals a discrete capacity limit in visual working memory. *Journal of Experimental Psychology. Human Perception and Performance*, 43 (1), 6–17. https://doi.org/10.1037/xhp0000302
- Quiroga, R. Q., Kreiman, G., Koch, C., & Fried, I. (2008). Sparse but not 'grandmothercell' coding in the medial temporal lobe. *Trends in Cognitive Sciences*, 12(3), 87–91. https://doi.org/10.1016/j.tics.2007.12.003
- Quiroga, R. Q. (2012). Concept cells: The building blocks of declarative memory functions. Nature Reviews Neuroscience, 13(8), 587–597. https://doi.org/10.1038/ nrn3251
- Rabagliati, H., Doumas, L. A. A., & Bemis, D. K. (2017). Representing composed meanings through temporal binding. *Cognition*, 162, 61–72. https://doi.org/ 10.1016/j.cognition.2017.01.013
- Rademaker, R. L., Chunharas, C., & Serences, J. T. (2019). Coexisting representations of sensory and mnemonic information in human visual cortex. *Nature Neuroscience*, 22 (8), 1336–1344. https://doi.org/10.1038/s41593-019-0428-x
- Ranganath, C. (2010). Binding items and contexts: The cognitive neuroscience of episodic memory. *Current Directions in Psychological Science*, 19(3), 131–137. https:// doi.org/10.1177/0963721410368805
- Reagh, Z. M., & Yassa, M. A. (2014). Object and spatial mnemonic interference differentially engage lateral and medial entorhinal cortex in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 111(40), E4264–E4273. https://doi.org/10.1073/pnas.1411250111
- Rey, H. G., Gori, B., Chaure, F. J., Collavini, S., Blenkmann, A. O., Seoane, P., Seoane, E., Kochen, S., & Quiroga, R. Q. (2020). Single neuron coding of identity in the human hippocampal formation. *Current Biology*, 0(0). https://doi.org/10.1016/j. cub.2020.01.035
- Richter, F. R., Cooper, R. A., Bays, P. M., & Simons, J. S. (2016). Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory., eLife, 5: e18260. https://doi.org/10.7554/eLife.18260
- Riesenhuber, M., & Poggio, T. (1999). Are cortical models really bound by the "binding problem"? Neuron, 24(1), 87–93. https://doi.org/10.1016/S0896-6273(00)80824-7
- Robertson, A. R. (1977). The CIE 1976 color-difference formulae. Color Research & Application, 2(1), 7–11. https://doi.org/10.1002/j.1520-6378.1977.tb00104.x
- Robin, J., Buchsbaum, B. R., & Moscovitch, M. (2018). The primacy of spatial context in the neural representation of events. *Journal of Neuroscience*, 38(11), 2755–2765. https://doi.org/10.1523/JNEUROSCI.1638-17.2018
- Rolls, E. T. (2012). Invariant visual object and face recognition: neural and computational bases, and a model. VisNet. Frontiers in Computational Neuroscience, 6. https://doi.org/10.3389/fncom.2012.00035
- Roskies, A. L. (1999). The binding problem. Neuron, 24(1), 7–9. https://doi.org/ 10.1016/S0896-6273(00)80817-X
- Schapiro, A. C., Turk-Browne, N. B., Botvinick, M. M., & Norman, K. A. (2017). Complementary learning systems within the hippocampus: A neural network modelling approach to reconciling episodic memory with statistical learning. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1711). https://doi.org/10.1098/rstb.2016.0049
- Schneegans, S., & Bays, P. M. (2017). Neural architecture for feature binding in visual working memory. *The Journal of Neuroscience*, 37(14), 3913–3925. https://doi.org/ 10.1523/JNEUROSCI.3493-16.2017

- Schurgin, M. W., Wixted, J. T., & Brady, T. F. (2020). Psychophysical scaling reveals a unified theory of visual memory strength. *Nature Human Behaviour*, 4(11), 1156–1172. https://doi.org/10.1038/s41562-020-00938-0
- Shen, M., Huang, X., & Gao, Z. (2015). Object-based attention underlies the rehearsal of feature binding in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 41(2), 479–493. https://doi.org/10.1037/ xhp0000018
- Simon, D. M., & Wallace, M. T. (2016). Dysfunction of sensory oscillations in autism Spectrum disorder. Neuroscience & Biobehavioral Reviews, 68, 848–861. https://doi. org/10.1016/j.neubiorev.2016.07.016
- Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. Annual Review of Neuroscience, 18, 555–586. https://doi.org/10.1146/ annurev.ne.18.030195.003011
- Sone, H., Kang, M.-S., Li, A. Y., Tsubomi, H., & Fukuda, K. (2021). Simultaneous estimation procedure reveals the object-based, but not space-based, dependence of visual working memory representations. *Cognition, 209*, Article 104579. https://doi. org/10.1016/j.cognition.2020.104579
- Souza, A. S., Overkott, C., & Matyja, M. (2021). Categorical distinctiveness constrains the labeling benefit in visual working memory. *Journal of Memory and Language, 119*, Article 104242. https://doi.org/10.1016/j.jml.2021.104242
- Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in Cognitive Sciences*, 18(2), 82–89. https://doi.org/10.1016/j.tics.2013.12.001
- Stevenson, R. A., Philipp-Muller, A., Hazlett, N., Wang, Z. Y., Luk, J., Lee, J., Black, K. R., Yeung, L.-K., Shafai, F., Segers, M., Feber, S., & Barense, M. D. (2019). Conjunctive visual processing appears abnormal in autism. *Frontiers in Psychology*, 9. https://doi. org/10.3389/fpsyg.2018.02668
- Stevenson, R. A., Siemann, J. K., Schneider, B. C., Eberly, H. E., Woynaroski, T. G., Camarata, S. M., & Wallace, M. T. (2014). Multisensory temporal integration in autism spectrum disorders. *The Journal of Neuroscience*, 34(3), 691–697. https://doi. org/10.1523/JNEUROSCI.3615-13.2014
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428(6984), 751–754. https://doi.org/10.1038/ nature02466
- Treisman, A. (1998). Feature binding, attention and object perception. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 353(1373), 1295–1306.
- Tsao, A., Moser, M.-B., & Moser, E. I. (2013). Traces of experience in the lateral entorhinal cortex. *Current Biology: CB*, 23(5), 399–405. https://doi.org/10.1016/j. cub.2013.01.036
- Utochkin, I. S., & Brady, T. F. (2020). Independent storage of different features of realworld objects in long-term memory. *Journal of Experimental Psychology. General*, 149 (3), 530–549. https://doi.org/10.1037/xge0000664
- Valdez, A. B., Papesh, M. H., Treiman, D. M., Smith, K. A., Goldinger, S. D., & Steinmetz, P. N. (2015). Distributed representation of visual objects by single neurons in the human brain. *Journal of Neuroscience*, 35(13), 5180–5186. https:// doi.org/10.1523/JNEUROSCI.1958-14.2015
- Vannucci, M., Dietl, T., Pezer, N., Viggiano, M. P., Helmstaedter, C., Schaller, C., Elger, C. E., & Grunwald, T. (2003). Hippocampal function and visual object processing in temporal lobe epilepsy. *NeuroReport*, 14(11), 1489–1492.
- Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. Journal of Experimental Psychology. General, 131(1), 48–64. https://doi.org/10.1037//0096-3445.131.1.48
- Winters, B. D., Bartko, S. J., Saksida, L. M., & Bussey, T. J. (2010). Muscimol, AP5, or scopolamine infused into perirhinal cortex impairs two-choice visual discrimination learning in rats. *Neurobiology of Learning and Memory*, 93(2), 221–228. https://doi. org/10.1016/j.nlm.2009.10.002
- Wolfe, J. M., & Horowitz, T. S. (2017). Five factors that guide attention in visual search. Nature Human Behaviour, 1(3), 1–8. https://doi.org/10.1038/s41562-017-0058
- Yeung, L.-K., Olsen, R. K., Hong, B., Mihajlovic, V., D'Angelo, M. C., Kacollja, A., Ryan, J. D., & Barense, M. D. (2019). Object-in-place memory predicted by anterolateral entorhinal cortex and Parahippocampal cortex volume in older adults. *Journal of Cognitive Neuroscience*, 31(5), 711–729. https://doi.org/10.1162/jocn\_a\_ 01385
- Yonelinas, A. P. (2013). The hippocampus supports high-resolution binding in the service of perception, working memory and long-term memory. *Behavioural Brain Research*, 254, 34–44. https://doi.org/10.1016/j.bbr.2013.05.030
- Yonelinas, A. P., Ranganath, C., Ekstrom, A. D., & Wiltgen, B. J. (2019). A contextual binding theory of episodic memory: Systems consolidation reconsidered. *Nature Reviews Neuroscience*, 20(6), 364–375. https://doi.org/10.1038/s41583-019-0150-4
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453(7192), 233–235. https://doi.org/10.1038/ nature06860