

Insights into visual working memory precision at the feature- and object-level from a hemispheric encoding manipulation

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Abstract

Mnemonic precision is an important aspect of visual working memory (WM). Here, we probed mechanisms that affect precision for spatial (size) and non-spatial (colour) features of an object, and whether these features are encoded and/or stored separately in WM. We probed precision at the *feature-level*—that is, whether different features of a single object are represented separately or together in WM—and the *object-level*—that is, whether different features across a set of sequentially presented objects are represented in the same or different WM stores. By manipulating whether stimuli were encoded by the left and/or right hemisphere, we gained further insights into how objects are represented in WM. At the feature-level, we tested whether recall fidelity for the two features of an object fluctuated in tandem from trial to trial. We observed no significant coupling under either central or lateralized encoding, supporting the claim of parallel feature channels at encoding. At the level of WM storage of a set of objects, we found asymmetric feature interference under central encoding, whereby an increase in colour load led to a decrease in size precision. When objects were encoded by a single hemisphere, however, we found largely independent feature stores. Precision for size was more resistant to interference from the size of another object under right-hemisphere encoding; by contrast, precision for colour did not differ across hemispheres, suggesting a more distributed WM store. These findings suggest that distinct features of a single object are represented separately but are then partially integrated during maintenance of a set of sequentially presented objects.

Keywords

Visual working memory; precision; feature binding; encoding; hemisphere; interference

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Introduction

Working memory (WM) refers to the ability to maintain goal-relevant information over a short period of time in an active state for further processing (Baddeley & Hitch, 1974; Cowan, 1999). Cognitive resource models assume that the more resources that are allocated to an object, the less noise is present in its representation, and the more precise the recall of that object (Bays & Husain, 2008; Palmer, 1990). Mnemonic precision declines as the number of to-be-remembered objects, that is, the load, increases (e.g., Bays & Husain, 2008; W. Zhang & Luck, 2008), and is variable from trial to trial (Fougnie et al., 2012; van den Berg et al., 2012). Precision is an important aspect of visual WM capacity, and of how objects are encoded and

memorised (Bays et al., 2009; Fougnie et al., 2012; Ma et al., 2014; van den Berg et al., 2012, 2014). Precision increases during childhood (Burnett Heyes et al., 2012, 2016) and decreases in older adulthood (Peich et al., 2013; Zokaei et al., 2015).

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What are the units of visual WM? Feature-versus object-based stores

Although most behavioural and neuroimaging studies of visual WM precision have focused on memory for individual features, such as colour or orientation (for reviews see Luck & Vogel, 2013; Ma et al., 2014), features are not necessarily encoded and maintained separately in visual WM. Rather, features may be integrated to discern meaningful patterns in the stream of incoming visual information, to perceive the whole object (Gajewski & Brockmole, 2006; Luck & Vogel, 1997; Treisman & Gelade, 1980; Wheeler & Treisman, 2002; for a review see Brady et al., 2011). The question of whether visual WM maintains whole objects or separate features as basic units has long been debated, with evidence for both “object-based” (Cowan, 2001; Gajewski & Brockmole, 2006; Kahneman et al., 1992; Luck & Vogel, 1997) and “feature-based” stores (Bays et al., 2011; Fougny & Alvarez, 2011; Fougny et al., 2013; Shin & Ma, 2017; Wang et al., 2017; Wheeler & Treisman, 2002). Recently, Wang et al. (2017) demonstrated that distinct feature values for colour and orientation reduced performance for detecting changes within the same feature, but had no significant effect on detecting changes in the other feature. Moreover, a model with independent memory resources for colour and orientation fit behavioural data better than a model with fully shared capacity (Shin & Ma, 2017). These studies were based on change detection tasks in which participants viewed several objects simultaneously in a stimulus array that varied in colour and orientation, and indicated after a brief delay whether one of these objects—the probe—was the same as the one presented at the same location in the sample array (Shin & Ma, 2017; Wang et al., 2017).

Some of the discrepancies in the literature regarding the degree of feature binding could be explained by the types of features that were used in the studies. For example, spatial features like bar orientation or stimulus size could be represented differentially from non-spatial ones like colour or shape (Huang, 2020), which would be consistent with neural evidence that spatial and non-spatial visual information are processed along different visual pathways (Mishkin et al., 1983). By using change detection and simultaneous stimulus presentation of coloured oriented bars or coloured shapes and by probing two features within trial (e.g., colour and shape), Huang (2020) found low degree of feature integration for colours and orientations, but high feature integration for colours and shapes. It is unclear whether these claims would also hold for size, the spatial feature examined in this study. In addition, differences in information load (Alvarez & Cavanagh, 2004), the degree of required encoding precision, and/or the temporal aspect of stimulus encoding (see below) could explain conflicting results of the degree of feature binding. These findings challenge the idea of fully object-based

WM stores, wherein WM representations are assumed to be all-or-none—that is, as one feature is lost, so are other task-relevant features, and the object has not been stored in WM (e.g., Luck & Vogel, 1997). These studies, however, do not speak directly to WM precision: with change detection and categorical items it can only be suggested that items were stored with sufficient precision to distinguish one item from a categorically different item. Studies with stimuli that are measured on a continuous feature dimension could shed additional light on this question.

Another approach to testing whether visual WM has separate stores for distinct feature dimensions has involved studies on WM precision using so-called dual-feature recall paradigms. In these studies, also involving simultaneous stimulus presentation of objects, participants were asked to recall from memory two different features (e.g., colour and orientation) of a probed object using continuous response formats (Bays et al., 2011; Fougny & Alvarez, 2011; Markov et al., 2019). Several results based on this paradigm appear to be inconsistent with a fully “feature-based” account: one reported partial overlap between features (Fougny & Alvarez, 2011), and another reported asymmetrical feature-feature relationships, whereby colour could be encoded independently into WM from orientation, whereas the reverse was not the case (Markov et al., 2019).

Specifically, Fougny and Alvarez (2011) observed that recall errors for colour and orientation were largely uncorrelated, while errors for height and width were not fully independent of each other. Markov et al. (2019) showed that when the features that were probed belonged to the same object, the precision and recall probability of colour or orientation were not affected by an increase in load in the other feature—that is, an increased number of different colours in the stimulus array did not affect precision for orientation, or vice versa—consistent with independent feature stores. However, when the two probed features belonged to objects that had appeared at different spatial locations within a stimulus array, increased colour load led to a decrease in precision of orientation WM for a given object (Markov et al., 2019). These two studies are consistent with partial, but incomplete, independence of the representation of different visual features in visual WM.

One potential explanation for incomplete independence of distinct visual features could be that features are first represented separately, but then are integrated in WM stores. It is plausible that representations in visual WM are hierarchically structured, in a manner that parallels the organisation of the visual system. Specifically, units in WM may be characterised by low-level representations with the property of independent feature stores, as well as higher level representations of integrated objects and object ensembles (Brady et al., 2011). In contrast to “slot-based” models of WM capacity, a hierarchical model takes

into account the possibility that capacity depends not only on the number of chunks encoded but also on the information contained within the chunks. Thus, there could be limits simultaneously at the level of features and the level of objects (Brady et al., 2011; Fougny et al., 2010).

Temporal aspect of stimulus encoding

An important consideration with regard to these limits could be the temporal aspect of stimulus presentation. Several prior studies of WM precision for one feature (e.g., orientation) have presented stimuli sequentially rather than simultaneously (Burnett Heyes et al., 2012; Gorgoraptis et al., 2011). This could be an important distinction, as the encoding of one object at a time may be less influenced by the level of attention allocated to each object than the encoding of multiple objects at a time (e.g., Oberauer, 2002). Thus, sequential stimulus presentation could clarify whether the partial interdependence of feature representations in prior work (Markov et al., 2019) was related to the simultaneous encoding of multiple objects, and/or whether there is still a memory advantage for spatial features when objects are encoded one at a time (cf. Huang, 2020).

By presenting stimuli sequentially, we aimed to examine visual WM precision at two levels of the proposed hierarchy of memory representations (Brady et al., 2011). We probed precision at (1) the *feature-level*—that is, whether different features of a single object are encoded separately or together in WM—and (2) the *object-level*—that is, whether different features across a set of sequentially presented objects are represented in the same WM store or in different stores. Moreover, sequential stimulus presentation enabled us to employ a novel *hemispheric manipulation* to test how interference between objects affect WM precision when two objects are presented to the LH, both to the RH, or one to each.

Probing feature- and object-based visual WM with a hemispheric encoding manipulation

To further investigate how objects are represented, we manipulated which hemisphere encodes objects into WM, via lateralized stimulus presentation (Bourne, 2006; Young & Bion, 1980). It has been proposed that there are independent, but limited, WM resource pools for right versus left visual hemifields (Buschman et al., 2011). In this prior study, macaques were trained to indicate whether one of the objects in a stimulus array changed colour. Neurophysiological recording from neurons in parietal and frontal cortices revealed that the information the animal had about the full stimulus array could be decomposed into the sum of the two hemifields. It is an open question as to whether humans would exhibit the same degree of independence in memory capacity across the two hemispheres, given a greater degree of hemispheric

asymmetry than in non-human primates (Hervé et al., 2013). However, there is evidence that attentional tracking capacity for moving objects is independently limited in the left and right visual fields in humans, lending credence to this idea (Alvarez & Cavanagh, 2005). To date, however, we have limited understanding of how WM precision for multiple features of an object, or a set of objects, emerges from within- versus between-hemispheric processing.

In neurologically healthy participants, there is robust communication between hemispheres. Visual information is separated into the left and right visual hemifields from the earliest stages, each initially encoded by the opposite or contralateral hemisphere, but is rapidly transferred between hemispheres. Thus, lateralized stimulus presentation affects only which hemisphere initially encodes the information (Bourne, 2006; Gazzaniga, 2000; Sperry et al., 1969). As a result, differences in cognitive performance as a result of a hemispheric encoding manipulation are typically subtle. Nonetheless, as reviewed below, there is some evidence that this type of manipulation affects performance on measures of attention and WM.

Hemispheric asymmetries in attention and WM

Hemispheric lateralization, or the tendency of a cognitive or neurophysiological process to be dominant in one of the two hemispheres, is assumed to enhance cognitive processing (Marinsek et al., 2014). Thus, one hemisphere could show an advantage for feature encoding over the other hemisphere, such that precision would be highest under encoding by the dominant hemisphere. In particular, the right-hemisphere (RH) dominance theory of attention proposes that the right parietal lobe controls the deployment of attention to both visual hemifields, whereas the left parietal lobe does so only on the contralateral (right) hemifield (Mesulam, 1981). There is also some evidence for RH dominance in visual WM (Sheremata et al., 2010; Sheremata & Shomstein, 2014), in addition to attention (Bowers & Heilman, 1980; De Schotten et al., 2011; Mesulam, 1981), but the results have been mixed (Sheremata et al., 2010; Sheremata & Shomstein, 2014; Umemoto et al., 2010; Y. Zhang et al., 2017). Sheremata and colleagues (2010) demonstrated asymmetric processing in human intraparietal sulcus (IPS) during visual WM, such that left hemisphere IPS exhibited load effects for contralateral objects, while right-hemisphere IPS responded to objects presented in either visual hemifield. Behavioural studies demonstrated higher WM capacity in terms of the number of objects remembered (Delvenne, 2005; Holt & Delvenne, 2014; Umemoto et al., 2010), as well as higher precision (Y. Zhang et al., 2017), when stimuli were presented across the two hemifields (i.e., bilaterally) as opposed to only one hemifield (i.e., unilaterally).

In sum, there may be RH dominance for visual WM, although the literature is mixed (Buschman et al., 2011; Delvenne, 2005; Delvenne & Holt, 2012; Holt & Delvenne, 2014; Sheremata & Shomstein, 2014, 2017; Sheremata et al., 2010; Umemoto et al., 2010; Y. Zhang et al., 2017). Here, we sought to test for a hemispheric asymmetry in WM precision for one or both features, and/or an asymmetry in the degree to which the two features are integrated in WM.

The present study

In the present set of experiments, we designed a new paradigm to test three questions: (1) how representations of two features of a single object (i.e., colour and size) are stored in WM, (2) the extent to which increased load within the same versus the other feature dimension across a set of objects affects WM precision, and (3) how a hemispheric encoding manipulation affects WM precision at the feature- and object-level. Our paradigm's unique constellation of features distinguished it from prior studies examining how different features of visual stimuli are represented in WM. These design choices and their affordances are summarised here and discussed in detail below: (1) along with other studies of WM precision, we used *continuous* rather than categorical response formats so that we could examine WM in a more nuanced way; (2) unlike most other studies of WM precision, we presented objects *sequentially* rather than simultaneously, addressing the concern that encoding multiple objects at a time affects the level of attention allocated to each object (e.g., Oberauer, 2002). Presenting objects one at a time also made it possible, in our second experiment, to limit the encoding of each one to a single hemisphere; (3) unlike many prior studies, we measured precision for *two features* of a stimulus. We focused on two salient properties of real-world objects: their colour—a non-spatial feature commonly used in the literature—and their *size*—a spatial feature that has not been studied previously in dual-feature recall tasks but that can also be measured on a continuous dimension; (4) we examined whether these visual features were represented separately or jointly at the *feature-level* by testing whether WM precision for the two features covaried across trials. In addition, we tested whether the features overlapped in WM stores at the *object-level* by examining whether WM precision for one feature varied as a function of WM load for the other feature across a set of objects; and (5) unlike prior studies of WM precision, we manipulated *encoding hemisphere* to gain further insights into how two visual features are encoded and stored in WM. As discussed below, these aspects of our task design could yield new insights.

In Experiment 1, we probed visual WM precision for colour and size features after sequential presentation of three objects that varied in the number of distinct colour

and/or size feature values—that is, feature load. We measured mnemonic fidelity separately for colour and size features on each trial with a measure of recall error: the difference between the actual and the reported feature of the probe item (Wilken & Ma, 2004) (Experiment 1). In Experiment 2, we adapted this task for a visual half-field paradigm, employing eyetracking to ensure that stimuli were encoded by a single hemisphere (Bourne, 2006). We examined feature-based WM within each hemifield by measuring precision for colour and size features belonging to one object. We further assessed the degree to which these features were segregated or integrated within each hemisphere, based on whether manipulating feature load would affect WM precision for a given object depending on whether a second object was encoded by the same or opposite hemisphere. Presenting one stimulus to each hemisphere provides a strong test of whether distinct features can interfere with each other in WM despite having been encoded separately.

We evaluated representational precision at the *feature-level* by testing whether the absolute magnitude in recall error for the two features of a single object covaried across trials (Bays et al., 2011). Negative coupling between size and colour fidelity across trials would be consistent with a limited resource for WM precision, whereby higher precision for one feature necessarily entails lower precision for the other. By contrast, no evidence of coupling would suggest that the features are processed independently. Finally, positive coupling would indicate that they rise and fall together. Positive coupling would be compatible with the hypothesis that the features are encoded together, with precision varying from trial to trial as a result of attentional fluctuations (e.g., Palmer, 1990; van den Berg et al., 2012).

Furthermore, we assessed WM precision at the *object-level* by varying colour and size feature load across a set of objects. Specifically, we estimated colour and size response precision for each participant and condition using a model-free approach based on individual distributions of errors in recall (Bays et al., 2009). Within each feature, feature load was variable (i.e., differentially sized or coloured circles) or was held constant across objects (i.e., same sized or coloured circles). Objects could have the same colour and size, the same colour but different sizes, the same size but different colours, or different colours and sizes. By varying one feature while holding the other constant, and by probing both colour and size within a trial, we tested whether load-related changes in the same versus other feature affected WM colour and size precision at the object-level.

If colour and size features across a set of objects are represented in the same object-based WM store, precision of a given feature should be reduced not only for a load increase in the same feature but also for a load increase in the other feature. By contrast, if features are represented in different stores, precision should depend on load-related increases in the same feature but not the other feature. That

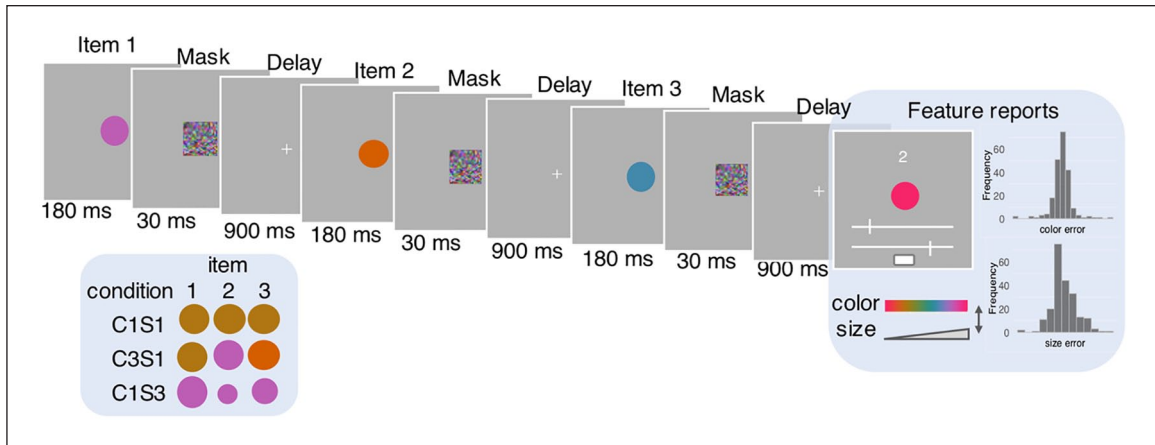


Figure 1. Visual working memory task, featuring a “C3S1” trial. Sample stimulus sets for each condition are shown in the bottom left panel. Participants were asked to encode both the colour and size of three sequentially presented objects, and to reproduce colour and size of one randomly chosen probe item using sliders. The probe item was indicated by the respective number in the sequential sample array (i.e., 1, 2, or 3). Distributions of errors were obtained for each participant and feature load manipulation (i.e., C1S1, C1S3, and C3S1) by measuring the colour and size error on a given trial as the difference between presented and reported feature value.

is, colour precision should be reduced under higher colour but not size load, and vice versa for size precision. However, it is possible that the colour and size of an individual object could be represented by segregated WM stores in one hemisphere, and an integrated store in the other hemisphere. If such a difference does exist, it might take the form of a RH advantage, based on evidence of a RH bias in visual attention (Bowers & Heilman, 1980; De Schotten et al., 2011) and visual WM (Sheremata et al., 2010). We sought to test for hemispheric differences in the degree of feature integration by evaluating colour and size response coupling within an individual object under LH versus RH encoding.

Finally, we evaluated hemispheric differences at the object-level by assessing within- versus cross-feature interference with WM precision as a function of hemispheric encoding (LH, mixed, RH). If we were to observe little or no interference in the extreme test case when one object is encoded in each hemisphere, this would imply a lower cognitive load when stimuli can be stored by different hemispheres. Less interference in one hemisphere over the other would imply a hemispheric asymmetry for storing objects in WM, while no differences would suggest that sets of objects are stored equally well across hemispheres.

Experiment 1

Methods

Participants. A total of 32 undergraduate students at the University of California at Berkeley (UC Berkeley) completed the experiment for course credit in a Psychology class. Although this was a convenience sample, the undergraduate population at UC Berkeley is diverse in terms of

socioeconomic background and ethnicity. Participants had self-reported normal or corrected to normal visual acuity, no history of neurological or psychiatric disorder, were fluent in English, and had normal colour vision. One participant had to be removed from the sample due to left-handedness, and another participant due to extreme low performance on the colour WM task (>3 standard deviation [SD] from the sample mean in all conditions). The final sample consisted of 30 right-handed participants, mean age 21.07 (± 2.64) years, range 18–31 years, 50% females.

Experimental protocol. Informed consent was obtained in accordance with a protocol approved by the local institutional review board. All participants were tested individually in a quiet room in a single session lasting approximately 60 min. Experimenters explained the WM task by reading computerised instructions to the participants. Participants performed 12 practice trials and then completed the WM task. Afterwards, they completed neuropsychological assessments including a standardised test of fluid reasoning (Matrix Reasoning subtest of Wechsler Abbreviated Scale of Intelligence [WASI]; Wechsler, 1999) and a colour vision test (Ishihara, 1917). They filled out a handedness inventory (Oldfield, 1971) and answered demographic questions at the end of the session.

During the WM task (see Figure 1), participants briefly viewed and were instructed to memorise sets of three sequentially presented objects consisting of circles that varied in colour and size. The two distinguishing features of these objects, colour and size, varied along continuous quantitative dimensions, enabling direct measures of mnemonic quality (adapted from Gorgoraptis et al., 2011; Wilken & Ma, 2004). Participants were instructed at the outset of the experiment to memorise the colour and size of

each object as precisely as possible. The instructions emphasised that participants should not prioritise one feature over the other, because both features were probed at the end of each trial. After a delay of 900 ms, they were cued with the number 1, 2, or 3, and had to reproduce the colour and size of the first, second, or third object, accordingly. They responded by adjusting the remembered colour and size with a slider for each feature, thereby yielding continuous WM performance measures. Sliders were presented below the probe item. When participants moved the bar to the remembered colour and size, the item visibly changed in the respective feature dimension. Because we anticipated that participants might respond more frequently with the upper slider first and then with the lower slider, and that this might influence their precision on the second response, we counterbalanced across participants which of the two sliders appeared on top. We measured the recall error on each trial as the Cartesian distance between the presented and reported feature of the probe item (Wilken & Ma, 2004) separately for colour and size features.

Stimuli were generated in Python (v2.7) using the PsychoPy (v1.90.1) software package (Peirce, 2009). Objects were circles of varying colours and sizes presented at the centre of the screen and at a viewing distance of 60 cm by a Dell monitor (1680 × 1050 pixels resolution). The colour dimension consisted of 360 isoluminant, equally spaced colours that were drawn from the CIE 1976 (L^* , a^* , b^*) circular colour space, centred at $L=54$, $a=18$, $b=-8$ (Fougnie et al., 2012). Each item was pseudorandomly assigned one of 360 colours and one of 100 sizes, with a minimal difference of colours between items constrained to 36° so as to reduce potential influences of similarity between memory items within trial (Kahana & Sekuler, 2002; W. Zhang & Luck, 2009). Similarly, the minimal difference of sizes between items was fixed to 0.51 visual degrees (21 pixels). Colour errors could range from -180 to 180 arc degrees (max. $SD=180$ arc degrees). The size dimension encompassed 100 circles with different diameters, drawn from a Cartesian size space ranging from 0.37 to 7.77 visual degrees (here 15 to 315 pixels; 1 pixel = ~ 0.025 visual degrees) with increments of 0.07 visual degrees (3 pixels). Size errors could range from -7.43 to 7.43 visual degrees (here -300 to 300 pixels) (max. $SD=7.43$ visual degrees).

Each trial started with a sequential presentation of the sample items (see Figure 1). Items were presented for 180 ms each, followed by a visual pattern mask to reduce any after-image perceptual influences. The mask, consisting of a pixelated square shape with a random colour pattern, appeared for 30 ms in the same location as the previous item. The mask was followed by a 900-ms delay period, during which a fixation cross was displayed at the centre of the screen.

After the final delay period, participants were asked to report the colour and size of one randomly chosen target item that was cued by the respective number in the

sequential sample array. Participants responded using a linear slider for each feature dimension. Each slider consisted of a horizontal line with a vertical small bar that could be moved along the line using a mouse device. Size is a non-circular bounded feature; sizes were arranged in ascending order on the slider with the smallest size on the most left. As colour is a circular feature, colours were wrapped around the slider line, such that both colour values on the most left and most right covered the same colour spectrum. We used a slider to report colour as opposed to a colour wheel (e.g., W. Zhang & Luck, 2008), so as to make motor response conditions comparable between colour and size dimensions. Colour and size values were not directly visible on the respective sliders; rather, the probed stimulus changed gradually on a given dimension as participants moved the corresponding slider. A visible colour wheel as response condition might have increased guessing behaviour, as shown in a previous study comparing a scrolling condition through a visible versus invisible colour wheel (van den Berg et al., 2012). To minimise within-person variance due to variability other than WM recall error (e.g., task difficulty, motor behaviour), the colour and size values along the points on the sliders were the same across trials. Participants, all of whom were right-handed, used their right hand to operate the mouse.

After participants had selected a value on both sliders, they pressed a “Done” button to receive feedback. The feedback consisted of two rows, each showing five stars that varied in fill depending on the colour and size errors, respectively. Stars varied from one half-star (error $\geq 63\%$; lowest performance) to five full stars (error $< 7\%$; best performance), with steps of half-stars (increases in 7% error). Participants were always given at least one half-star as a reward for having performed the trial. An intertrial interval, during which a fixation cross was presented centrally on a grey background, followed the feedback at the end of each trial; the timing of this interval was jittered with an interval of 600–900 ms.

WM demands were manipulated by varying the feature load for colour and size features. The three objects could all have the same colour, or three different colours: that is, a given trial could have a colour WM load of 1 or 3 (C1 or C3), and a size load of 1 or 3 (S1 or S3). In all, there were three conditions: C1S3, wherein the three objects had the same colour but differed in size, C3S1, wherein all objects differed in colour but had the same size, and C1S1, wherein all objects had the same colour and the same size. We did not include C3S3 trials, so as to measure mnemonic precision under load conditions that did not exceed participants’ WM capacity. On average across participants this limit is suggested to be four chunks of information (Cowan, 2001). Given that we sought to keep the task duration below 40 min, omitting C3S3 trials allowed us to present a larger number of C1S1, C1S3, and C3S1 trials.

C3S1, C1S3, and C1S1 were presented in a random order from trial to trial. To reduce effects of serial position of sequential item presentation, we randomised the position of the item that was probed during retrieval phase (i.e., first, second, or third item) within each feature load condition. Participants performed 12 practice trials, followed by 6 blocks of 27 trials per block. They were allowed to rest as long as needed between breaks. The total number of trials per participants was 162 (51–58 per feature load combination).

Data analysis. Behavioural data were analysed in R-statistics (<http://www.r-project.org>, R Core Team, 2016). Object responses were measured in terms of the recall error, a continuous measure of WM performance (Bays et al., 2009; Wilken & Ma, 2004). For colour, error magnitude corresponds to the angular difference between the presented and reported colour, within a circular parameter space. For size, error magnitude corresponds to the Cartesian distance between the presented and reported size, within a Euclidean parameter space. Size errors were normalised ($\text{error} = [\text{reported size} - \text{correct size}] / \text{correct size}$) to account for the fact that differences in smaller sizes might be perceived with higher sensitivity than those with larger sizes, as predicted by Weber's law (Fechner, 1966). We simultaneously measured colour and size error for a given object to assess (1) the trial-to-trial relationship between absolute magnitude of colour and size error (colour-size precision coupling) and (2) trial-to-trial variability in error magnitude as a function of the load of the same feature and the other feature.

Response precision. We selected a measure for precision that it would be appropriate for both colour and size feature dimensions. To this end, colour precision was formalised as the inverse of the circular *SD* of colour error distributions using Fisher's definition given a circular response space by incorporating a correction that ensures that the expected precision value under uniform response errors P_0 is zero ($= [1 / SD] - P_0$) (Bays et al., 2009). The expected precision under uniform responses was computed by simulating 1000 precision values, each calculated with 50 response values that were randomly sampled from the feature response range. For the sake of continuity with prior research on colour precision, we also estimated P_0 using the method of Bays et al. (2009); our key findings did not change (cf. Supplementary Material, 1A).

For the estimation of size precision, reversed scores of normalised size errors were log-transformed to approach normally distributed size errors, which was required for reliable estimates of response precision. Size precision was formalised as the inverse of the *SD* corrected for chance given a Cartesian non-circular response space. We applied a simulation to estimate expected size

precision under uniform responses in the same way as for colour precision. Colour and size response precision were computed separately for each participant and feature load condition.

Response precision of both colour and size features measures the trial-to-trial variability in response error, corrected for chance. This non-parametric approach has the advantage that it makes no assumption about the shape of the error distribution (Bays et al., 2009). We applied a model-free rather than a modelling approach (e.g., mixture modelling; W. Zhang & Luck, 2008) because parameter estimates are noisy and unreliable when the number of trials is low.

Coupling of colour and size precision across trials. We tested whether colour and size responses to an object showed systematic trial-to-trial coupling, or whether responses were independent from each other. To this end, we computed a non-parametric correlation coefficient (Spearman's *rho*) for each participant based on absolute colour errors and absolute normalised size errors. To control for the possibility of inflated or biased correlations between colour and size responses, we excluded extreme high errors (absolute colour/size errors of an absolute deviation greater than 2 *SDs* from the median). We also report results for coupling analysis based on uncorrected errors; we observed no significant difference to the results for corrected errors (cf. Supplementary Material, 1B). We computed strength of coupling specifically for C1S1 trials, on which the feature load was equivalent for colour and size. To test whether coupling patterns were different from zero, we evaluated bootstrapped 95% confidence intervals (CIs) of the distribution of sampled means of *rho* (sampling with replacement, $N = 1,000$ iterations) and conducted a one-sample Wilcoxon signed-rank test.

Load effects on response precision. To assess effects of feature load across a set of three objects, we conducted a repeated measures ANOVA with Feature Load as factor, separately for colour and size precision. We report Greenhouse-Geisser-corrected *p*-statistics when assumptions of sphericity were violated, as indicated by a significant Mauchly test statistic. To measure the effect of increased within- versus cross-dimensional feature load on mnemonic precision, we computed two types of difference scores: (a) *Delta-s*, which reflects the change in response precision as load in the same feature dimension increases across objects, and (b) *Delta-o*, which reflects the change in precision as load in the other feature dimension increases across objects. More specifically, "*Delta-s size load 1*" of colour precision reflects the change in colour precision with increased colour load, but stationary size load (i.e., C3S1 – C1S1); "*Delta-o colour load 1*" of colour precision reflects the

change in *colour precision* with increased size load, but stationary colour load (i.e., C1S3 – C1S1). Likewise, “*Delta-s colour load 1*” of *size precision* signifies the change in *size precision* with increased size load, but

(a) Colour precision (P_c)

$$\text{Delta-s size load 1} = P_{c_{C3S1}} - P_{c_{C1S1}}$$

$$\text{Delta-o size load 1} = P_{c_{C1S3}} - P_{c_{C1S1}}$$

In Equation 1a, *Delta-s* and *Delta-o* are for colour precision (P_c), and in Equation 1b, *Delta-s* and *Delta-o* are for size precision (P_s).

We assessed whether Delta scores were significantly different from zero by evaluating non-parametric CIs of the distribution of sampled means of Delta-s and Delta-o. Specifically, we sampled with replacement ($N=1,000$) from the observed distributions of Delta-o and Delta-s and computed the mean of sampled data in each iteration. We then computed the bootstrapped 95% CIs based on the sampled mean data. The CI provides information about the precision of the Delta estimate and the potential generalisability of the estimate. It reflects an indicator of practical significance (cf. Banjanovic & Osborne, 2016). If upper and lower boundaries of CIs of the sampled mean *Delta scores* did not overlap with zero, we interpreted interference effects as being significantly different from zero.

Furthermore, we tested whether Delta-s and Delta-o were significantly different from each other, using pairwise permutation analysis. We repeatedly shuffled Delta scores between two interference conditions (same vs. other) and computed the difference between the group means based on the randomly shuffled data in each iteration ($N=1,000$). To assess whether the observed difference between group means was due to chance, we counted the number of absolute permutation difference scores that were higher than the absolute true difference score, and divided this number by 1,000 to compute the two-tailed p -statistic.

Standardised metrics of colour and size responses. Precision had to be calculated differently for colour and size judgements, given that the stimulus spaces were circular and linear, respectively (see above). To be able to use the same metric for the two types of judgements, we computed z -scores of colour and size errors separately for each participant—that is, we subtracted the mean of all error responses from each individual error response and divided those responses by the SD of all responses. Distributions of z -standardised errors between the two features across participants were similar in range and variability for C1S1 (colour z -error range=9.42, $M=0.01$, $SD=0.65$;

stationary colour load (i.e., C1S3 – C1S1); and “*Delta-o size load 1*” of *size precision* signifies the change in size precision with increased colour load, but stationary size load (i.e., C3S1 – C1S1) (see Equations 1a and b):

(b) Size precision (P_s)

$$\text{Delta-s color load 1} = P_{s_{C1S3}} - P_{s_{C1S1}} \quad (1)$$

$$\text{Delta-o color load 1} = P_{s_{C3S1}} - P_{s_{C1S1}}$$

size z -error range=10.39, $M=-0.05$, $SD=0.78$) and when the same feature was high in load (C3S1: colour z -error range=12.61, $M=0.01$, $SD=1.26$; C1S3: size z -error range=10.13, $M=0.09$, $SD=1.17$), suggesting a comparable level of difficulty in remembering the colour versus size of an object.

Effect of the position of colour versus size sliders. To assess whether performance was affected by whether colour or size slider was presented on top of each other, we conducted a mixed ANOVA with Slider Position as a between-subject factor and Feature Load as a within-subject factor, separately for colour and size error magnitude. For both colour and size responses, results showed no significant effect of Slider Position on precision, colour: $F(df=1, 28)=1.85$, $p=.18$; size: $F(df=1, 28)=0.5$, $p=.48$, and no significant interaction between Slider Position and Feature Load, colour: $F(df=2, 56)=0.04$, $p=.96$; size: $F(df=2, 56)=1.97$, $p=.15$, suggesting that differences in slider position did not greatly affect mnemonic performance.

Results

Trial-to-trial coupling of size and colour precision. To test whether distinct features belonging to the same object were segregated or integrated in visual WM, we evaluated the strength of coupling of individual colour and size responses for a given object across trials in which the load was identical for colour and size. Colour-size coupling across C1S1 trials was on average $\rho=.007$ ($SD=0.15$, $Mdn=0.007$, $Min.=-0.27$, $Max.=0.30$). Across participants, the strength of coupling was not significantly different from zero, as indicated by non-parametric bootstrapped 95% CIs (CI[bs] lower, upper=[-0.04, 0.06]) and Wilcoxon signed-rank test ($p=.89$).

Colour response precision: effects of feature load. Colour precision was significantly affected by the different feature load combinations, $F(df=2, 58)=68.73$, $p<.0001$ (see Figure 2a). We observed higher colour precision for C1S1 than C3S1, $t(df=58)=10.24$, $p<.0001$, but no difference between C1S1 and C1S3, $t(df=58)=0.17$, $p=.98$. Delta-s

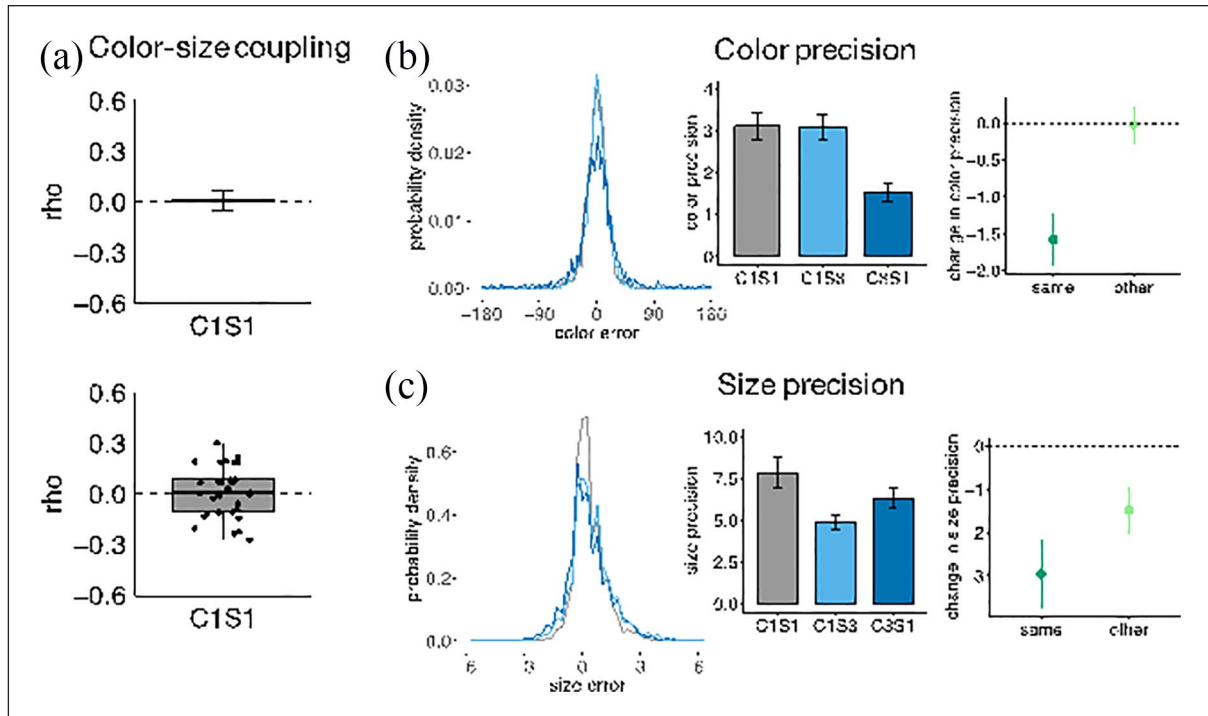


Figure 2. Results of Experiment 1. (a) Colour-size response coupling (ρ) or trials for C1S1 trials, on which the load was identical for colour and size. We observed no significant coupling across participants ($N=30$) (see upper plot; error bars correspond to the 95% confidence intervals). Notably, there were substantial individual differences in coupling strength, ranging from positive to negative ρ values (see box and whisker plot; dots correspond to each participant's ρ s). Distribution of colour errors (b) and size errors (c) for each feature load condition (i.e., C1S1, C1S3, C3S1) across participants and the corresponding mean response precision. Effects of increased load in the same (Delta-s) versus other (Delta-o) feature dimension across three objects on colour response precision (b) and size response precision (c). Error bars correspond to 95% confidence intervals.

Table 1. Summary and bootstrap statistics of changes in (a) colour precision and (b) size precision with increased load in the same versus other feature across objects in Experiment 1.

(a) Delta colour precision								
Load (3 – 1)	Delta	<i>M</i>	<i>SD</i>	<i>Mdn</i>	Min.	Max.	95% CI[bs] lower	95% CI[bs] upper
C3S1 – C1S1	same SI	-1.58	0.97	-1.33	-3.19	0.00	-1.91	-1.23
C1S3 – C1S1	other CI	-0.03	0.69	-0.15	-1.61	1.52	-0.27	0.23
(b) Delta size precision								
Load (3 – 1)	Delta	<i>M</i>	<i>SD</i>	<i>Mdn</i>	Min.	Max.	95% CI[bs] lower	95% CI[bs] upper
C1S3 – C1S1	same CI	-2.96	2.11	-2.69	-8.41	0.90	-3.69	-2.24
C3S1 – C1S1	other SI	-1.49	1.48	-1.41	-4.23	1.44	-2.01	-0.99

CI[bs] = bootstrapped confidence interval. Italic font for lower/upper CIs indicates comparisons for which the CI included zero and were therefore deemed non-significant.

was significantly different from zero (cf. CIs[bs] for Delta-same; see “(a) Delta colour precision” in Table 1). Thus, colour response precision was higher for a colour load of 1 than 3 (Figure 2a). By contrast, colour response precision showed no significant difference for a size load of 3 than 1 (Figure 2a, Delta-other; see “(a) Delta colour precision” in Table 1). Permutation testing revealed significant greater

Delta-s than Delta-o ($p=.0009$). Thus, colour load but not size load affected colour precision.

Size response precision: effects of feature load. Size precision was significantly affected by the different feature load combinations, $F(df=(2, 58)=43.66, GG_{\epsilonpsilon}=0.81, p<.0001$, with higher size precision for C1S1 than C1S3,

$t(df=58)=9.34, p<.0001$, and also for C1S1 than C3S1, $t(df=58)=4.71, p<.0001$. Thus, size precision declined with an increased load in the same feature as well as the other feature. Delta-s and Delta-o were both significantly different from zero (cf. CIs[bs]; see “(b) Delta size precision” in Table 1), although Delta-o was significantly smaller than Delta-s ($p=.005$). In sum, size precision was negatively affected by size load—and also by colour load, albeit to a lesser degree (Figure 2b).

In summary, the results of precision coupling analysis revealed independent fluctuations for colour and size features, suggesting that features from different dimensions belonging to one object can be stored independently from each other. Across a set of objects, a load increase for one feature interfered with response precision for that feature, such that increased colour load reduced colour precision, and increased size load reduced size precision. In addition, increased colour load reduced size precision. However, there was less cross-feature interference with size precision than within-dimensional interference, suggesting that different features are not represented in exactly the same way.

Experiment 2

In Experiment 1, we found that colour and size precision for a given object were uncorrelated at the feature-level, suggesting that features can be stored separately in WM—at least under low attentional and WM demands (C1S1). At the object-level, we observed that colour response precision was affected by increased colour load, and that size response precision was affected by both increased size and colour load. That is, there was interference at the object-level. Next, we sought to test whether these conclusions would change as a function of hemisphere of encoding.

Here, we examined hemispheric effects on representational precision with a modified version of the task involving lateralized stimulus presentation. We combined the visual WM task with a divided visual half-field paradigm, a method that has been used to test for hemispheric asymmetries for a number of cognitive processes (Bourne, 2006). With specific parameters for stimulus duration and placement in the visual field, specified below, this type of paradigm allows to test how each hemisphere is engaged in cognitive processes (Bourne, 2006; Young & Bion, 1980). We verified with eyetracking that the participant’s eyes were centrally fixated and removed trials on which they did not fixate centrally, such that only the hemisphere opposite to the side of visual stimulus presentation could have encoded the information (Beaumont, 1983; Bourne, 2006).

We probed precision for colour and size judgements as in Experiment 1, albeit with four feature load conditions across a set of objects (i.e., C1S1, C2S1, C1S2, and C2S2). Participants viewed a sequence of two rather than three items per trial, both to ensure an equal amount of

stimulation of each hemisphere under mixed encoding conditions and to keep WM demands below potential capacity limits.

We tested coupling strength for both lower and higher WM demands (i.e., C1S1 and C2S2) and leveraged the hemispheric encoding manipulation to probe coupling of colour and size features of a given object. Specifically, we tested whether the features of a single object are more segregated in one hemisphere and more integrated in the other hemisphere; based on the literature on hemispheric asymmetries reviewed above, one might expect that the features would be more integrated in the RH. In addition, we tested whether the level of interference across the two objects was affected by whether the second object was presented to the opposite hemisphere from the first (mixed encoding) or whether both were presented to the LH or the RH. If it is true that the two hemispheres have fully independent WM stores (Buschman et al., 2011), there should be no interference when the objects are encoded by different hemispheres. At the very least, the encoding of one object in each hemisphere should reduce object–object interference relative to pure LH or RH encoding, by enhancing parallel processing. Another plausible outcome is that objects interfere with each other less within the RH, as this hemisphere has been proposed to play a privileged role in visual WM (Sheremata et al., 2010; Sheremata & Shomstein, 2014).

Methods

Participants. An independent sample of 29 right-handed volunteers completed Experiment 2 for course credit. Inclusion and exclusion criteria and the institutional review board protocol were the same as in Experiment 1. Three participants were excluded from all analyses because no reliable eyetracking data could be collected due to technical problems during the session or because saccades during encoding were observed on more than 25% of the trials. The final sample consisted of 26 participants, mean age 19.85 (± 2.6) years, range 18–30 years, 73% females.

Task procedure and eyetracker apparatus. Participants were tested individually in a quiet room in a single session lasting approximately 1.5 hr. They completed the same neuropsychological assessment as in Experiment 1. In the lateralized WM task (Figure 3), participants briefly viewed, and were instructed to memorise, a sequence of two laterally presented items that could vary in colour and/or size. After a brief delay, they reported both the colour and size of one randomly chosen item using a continuous response format (see also Experiment 1).

Participants were instructed to memorise the colour and size of each object as precisely as possible while maintaining central fixation. The presentation of a trial was initiated when fixation was maintained at least for 700 ms.

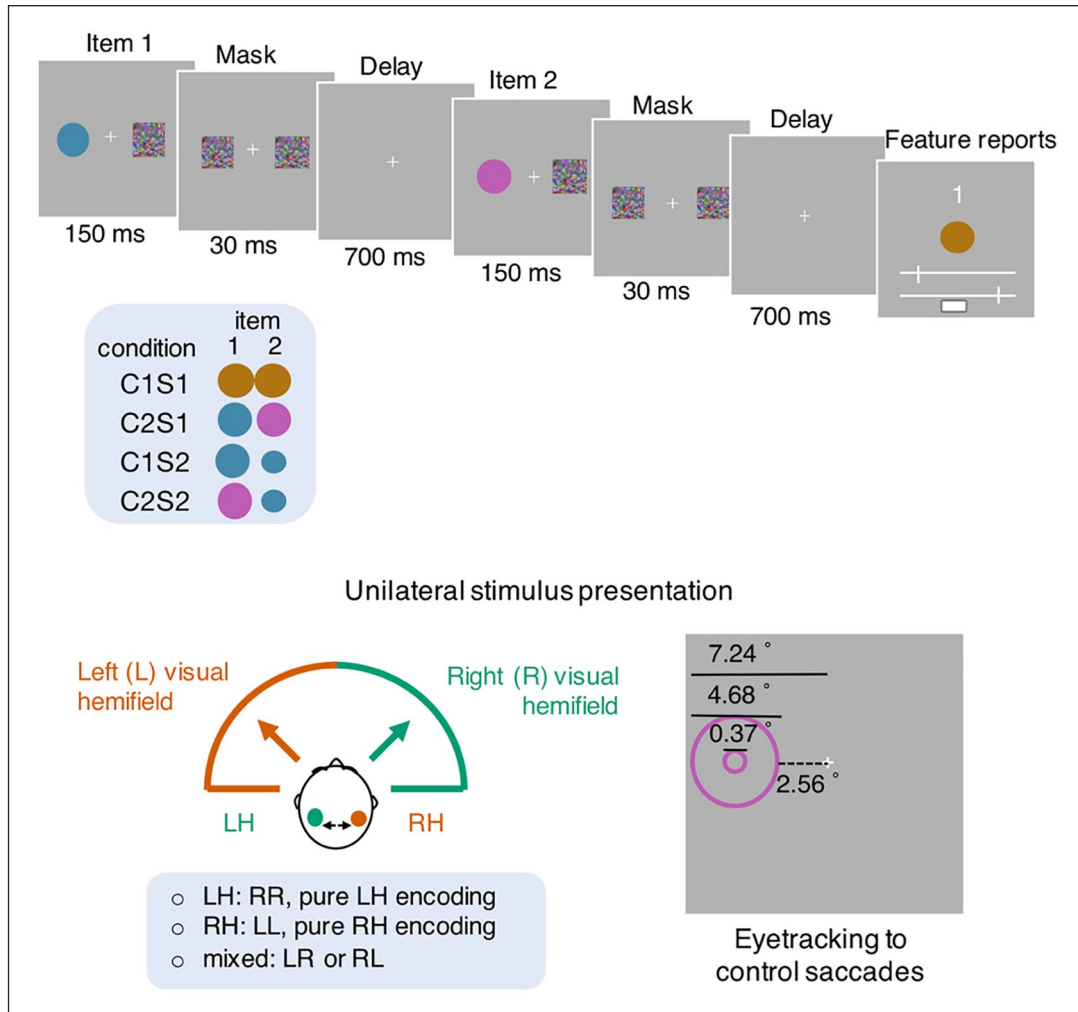


Figure 3. Visual half-field method and lateralized visual WM paradigm (example showing “C2S1, pure RH” trial). Participants were asked to maintain fixation while encoding both the colour and size of two sequentially presented objects. Eyetracking was used to monitor and control for eye movements. Participants reproduced the colour and size of the indicated probe item using sliders. Distributions of colour and size errors were obtained for each participant (see upper panel). Stimuli were presented unilaterally by controlling the stimulus duration and the placement in the visual hemifield: objects presented in the left visual hemifield are initially encoded by the right hemisphere, and objects presented in the right visual hemifield are initially encoded by the left hemisphere. The distance between the central fixation cross hair and the inner edge of the item was at least 2.56 visual angle and the maximum item size was 4.68 visual angle (diameter of circle) to ensure peripheral visual encoding and equivalent visual acuity between differentially sized items (Bourne, 2006) (see lower panel).

This method ensured that participants’ gaze was redirected to the centre of the screen at the beginning of each trial. Participants then briefly viewed a sequence of two items (each 150 ms), each of which was presented on the left or right side of the fixation cross. For each item, a visual pattern mask (squared shape with random colour pattern) was presented on the opposite side of the screen. The second pattern mask (30 ms) was presented, overlaid on the location of the previous item and the contralateral mask, to reduce any after-image perceptual influences followed by a delay period of 700 ms, which consisted of a blank display. After the delay period following the second item, participants were asked to report the features of one randomly

chosen target item that was cued by the respective number in the sequential sample array (i.e., “1” or “2”). The method of responding during recall was the same as in Experiment 1.

To ensure that the lateralized stimulus presentation resulted in unilateral stimulus encoding, participants performed the task while seated in front of a Tobii T120 eyetracker (17-inch monitor, 1280 × 1024 pixel resolution) to ensure that they kept their eyes at the centre of the screen during stimulus encoding. Participants were seated comfortably with their heads stabilised by a chin and head rest in front of the eyetracker. Distance to the eyetracker was 60 cm. Eye gaze data were recorded with a temporal

resolution of 120 Hz, and the camera simultaneously recorded data of the left and right eyes.

All stimuli were presented at the eyetracker and generated in Python (v2.7) using the PsychoPy software package (Peirce, 2009). PyGaze, an open-source eyetracking software (Dalmaijer et al., 2014), was used to combine experimental task with eyetracking recordings. Under unilateral encoding conditions, objects were presented to a single visual hemifield by controlling the stimulus duration and placement in the visual hemifield (Bourne, 2006; Young & Bion, 1980). Objects were circles presented at least 2.56° from central fixation (i.e., the distance to the inner point of the biggest circle). Stimuli were presented within 7.24° from central fixation to ensure that differentially sized circles were processed within equivalent perceptual acuity (Figure 3). Stimulus exposure was limited to 150 ms to control eye movements and to increase the probability that the stimulus remained in the periphery (Bourne, 2006).

Objects were displayed on the left or right side of a white fixation cross (0.37°). The centres of the circles, the fixation cross, and the masks were fixed to the same vertical height. Each circle consisted of two distinguishing features (i.e., colour and size) that varied along a continuous quantitative dimension, enabling a direct measure of mnemonic quality (Wilken & Ma, 2004) (see Experiment 1). Each circle was pseudorandomly allotted one of 360 isoluminant, equally spaced colours that were drawn from the CIE 1976 (L^* , a^* , b^*) circular colour space, centred at $L=54$, $a=18$, $b=-8$ (Fougnie et al., 2012). We controlled for potential influences of similarity between memory items in the same way as in Experiment 1. Colour errors could range from -180 to 180 arc degrees. The size dimension encompassed 58 different sizes (i.e., diameters) that were drawn from a Cartesian size space ranging from 0.37° to 4.68° (15 – 189 pixels) in visual angle, with increments in size of 0.07 visual degrees (3 pixels). Thus, size errors could range from -4.31 to 4.31 visual degrees. Size errors were normalised and transformed prior to the computation of size precision in the same way as in Experiment 1.

Design. Hemispheric encoding was manipulated by presenting objects either on the right or the left visual hemifield, resulting in three types of hemispheric presentation: “LH,” “RH,” and “mixed.” “LH” corresponds to exclusive visual stimulus presentation to the LH (i.e., both circles were presented on the right visual hemifield within a trial); likewise, “RH” corresponds to pure stimulus presentation to the RH. On “mixed” trials, the first item was either presented to the left or right visual hemifield, while the second item was presented to the opposite hemifield (Figure 3). Mixed trials differed from pure LH or RH ones not only in terms of the encoding hemisphere but also in terms of spatial distance between items: that is, in the pure encoding conditions, stimuli were always presented at the same

location, whereas in the mixed condition they were not. Thus, the mixed condition could reduce interference between items in two ways: first, by placing demands on different hemispheres and second by separating them in visual space.

Similar to Experiment 1, WM demands were manipulated by simultaneously varying feature load across two objects for colour and size features. The conditions were C1S1, C2S1, C1S2, and C2S2. These were fully crossed with the hemispheric manipulation: pure LH, pure RH, and “mixed.” The hemispheric encoding condition was chosen randomly from trial to trial. Participants performed four practice trials followed by six blocks of 36 trials per block. The total number of trials per participant was 216 trials (~ 54 per feature load combination). Participants received feedback in the same manner as in Experiment 1.

Data analysis. Behavioural and eyetracking data were analysed in R-statistics (<http://www.r-project.org>; R Core Team, 2016). We measured the colour and size error for a given object to assess trial-to-trial coupling between colour and size responses for a given object, depending on feature load as well as whether that object was encoded by the LH or RH. We also measured colour and size response precision as a function of within- and cross-dimensional feature load across two objects and hemispheric encoding conditions (LH, mixed, and RH). Colour and size precision were formalised as in Experiment 1 (see the “Methods” and “Data analysis” sections; Supplementary Material, 2A).

Exclusion of trials involving saccades. We excluded trials from all behavioural analyses if left and right eye gaze positions were biased towards the attended hemifield rather than maintained at central fixation. Trials were excluded if the distance of horizontal gaze position from the centre was greater than or equal to 2.6 visual degrees towards the stimulus presentation side during encoding phase. After removal of trials based on this exclusion criterion, 94.92% of all data points were available on average across participants (% excluded trials: $M=5.08\%$, $Mdn=3.01\%$, $SD=5.87\%$, $Min.=0\%$, $Max.=20.83\%$). The average number of trials left per participant and feature load condition (C1S1, C2S1, C1S2, C2S2) was 50.91 ($SD=0.61$), and 67.89 ($SD=1.18$) per hemispheric encoding condition (LH, mixed, RH).

Standardised metrics of colour and size responses. For C1S1, the range of z -transformed colour errors was 8.26 ($M=-0.01$, $SD=0.60$) and the range of size errors was 6.47 ($M=-0.08$, $SD=0.83$). For C2S1, the colour error range was 10.95 ($M=0.01$, $SD=1.15$); for C1S2, the size error range was 9.36 ($M=0.00$, $SD=1.06$). For C2S2, the colour error range was 10.86 ($M=-0.03$, $SD=1.20$) and the size error range was 8.42 ($M=-0.05$, $SD=1.07$). Thus, distributions of z -standardised errors between the

two features across participants were similar in range and variability, suggesting a comparable level of difficulty between features.

Effect of the position of colour versus size sliders. We assessed effects of slider position with a mixed ANOVA, with Slider Position as between-subject factor and Feature Load and Hemispheric Encoding as within-subject factors, separately for colour and size error magnitude. For both colour and size responses, results showed no significant effect of Slider Position, colour: $F(df=1, 24)=2.05$, $p=.16$; size: $F(df=1, 24)=0.66$, $p=.42$, no significant interaction between Slider Position and Feature Load, colour: $F(df=3, 72)=0.47$, $p=.70$; size: $F(df=3, 72)=1.61$, $p=.19$, or Hemispheric Encoding, colour: $F(df=2, 48)=0.01$, $p=.98$; size: $F(df=2, 48)=0.72$, $p=.49$, and no significant interaction between Slider Position, Feature Load, and Hemispheric Encoding, colour: $F(df=6, 144)=0.30$, $p=.93$; size: $F(df=6, 144)=1.17$, $p=.32$. Thus, as in Experiment 1, differences between participants in slider position were unlikely to significantly bias mnemonic performance.

Coupling of colour and size precision across trials. We tested whether colour and size responses to an individual object showed systematic trial-to-trial coupling under LH and/or RH encoding. We conducted these analyses specifically for C1S1 and C2S2 trials, for which feature load was matched for colour and size. Given that we sought to examine precision for individual objects, we combined LH, mixed, and RH conditions—which were defined based on the two objects—thereby substantially increasing the number of trials from which we could derive a coupling measure. For each hemispheric encoding condition, and separately for C1S1 and C2S2 trials, we computed

(a) Colour precision (P_c)

$$\begin{aligned} \text{Delta-s size load 1} &= P_{c_{C2S1}} - P_{c_{C1S1}} \\ \text{Delta-s size load 2} &= P_{c_{C2S2}} - P_{c_{C1S2}} \end{aligned}$$

$$\begin{aligned} \text{Delta-o colour load 1} &= P_{c_{C1S2}} - P_{c_{C1S1}} \\ \text{Delta-o colour load 2} &= P_{c_{C2S2}} - P_{c_{C2S1}} \end{aligned}$$

Interactions between hemispheric encoding and feature load. To determine whether effects of object-to-object load of the same versus other feature on mnemonic precision were modulated by hemisphere, we evaluated Delta scores based on combined feature load conditions for pure LH, pure RH, and mixed encoding. To obtain a sufficient number of trials for the estimation of colour precision and size precision for each hemispheric encoding condition crossed by feature load, feature load conditions were combined in terms of “same” versus “other” feature load 1 or load 2.

response coupling in the same way as in Experiment 1 (see also Supplementary Material, 2B). We applied bootstrapped statistics (95% CIs of the distribution of sampled means of ρ ; sampling with replacement, $N=1,000$ iterations) and Wilcoxon signed-rank test to assess whether coupling patterns differed from zero. Furthermore, we assessed effects of feature load and hemispheric encoding on coupling strength with a repeated measures ANOVA with Feature Load (C1S1 vs. C2S2) and Hemisphere (LH vs. RH) as factors.

Effects of hemispheric encoding and feature load on response precision. To measure main effects of hemispheric encoding, we estimated colour and size response precision for each participant and hemispheric encoding condition, collapsing across the feature load conditions to maximise the number of trials. Effects were assessed with one-way repeated measures ANOVA with Hemisphere as a factor, separately for colour and size precision. We reported Greenhouse-Geisser-corrected p -statistics when assumptions of sphericity were violated, as indicated by a significant Mauchly test statistic. Correspondingly, we estimated precision for each of the feature load combinations to assess effects of same versus other feature load, collapsing across hemispheric encoding conditions. We measured the effect of increased within- versus cross-dimensional feature load on mnemonic precision with Delta-s and Delta-o by considering whether the respective other feature had a load of 1 or 2 (see Equations 2a and b). We then tested whether Delta scores were significantly different from zero by evaluating non-parametric CIs of the distribution of sampled means of Delta-s and Delta-o. As in Experiment 1, we tested whether Delta-s and Delta-o were significantly different from each other, based on pairwise permutation analysis:

(b) Size precision (P_s)

$$\begin{aligned} \text{Delta-s color load 1} &= P_{s_{C1S2}} - P_{s_{C1S1}} \\ \text{Delta-s color load 2} &= P_{s_{C2S2}} - P_{s_{C2S1}} \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Delta-o size load 1} &= P_{s_{C2S1}} - P_{s_{C1S1}} \\ \text{Delta-o size load 2} &= P_{s_{C2S2}} - P_{s_{C1S2}} \end{aligned}$$

For colour precision, for example, “C2S1 and C2S2” correspond to trials of “same” feature load 2, while “C1S2 and C2S2” are trials of “other” feature load 2. We then calculated Delta-s and Delta-o for each hemispheric condition based on feature load 2–feature load 1 same and other combinations for colour and size precision.

We evaluated, separately for each hemispheric encoding condition, (1) whether Deltas were different from zero, based on bootstrapping statistics (95% non-parametric bootstrapped CIs) (see the “Methods” section, Experiment

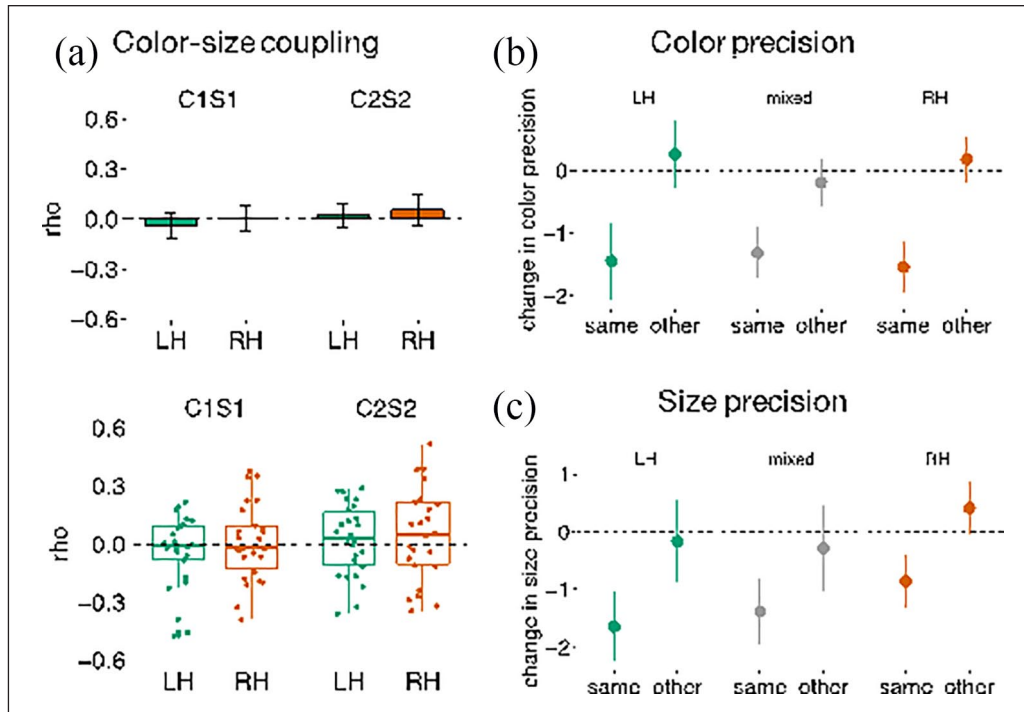


Figure 4. Results of Experiment 2. (a) Colour-size response coupling (ρ) under low (C1S1) and higher (C2S2) WM demands for trials in which the probe was encoded by the LH or RH. There was no significant coupling for LH or RH encoding across participants (see upper plot; error bars correspond to the 95% confidence intervals). However, individuals substantially differed in their coupling strength, ranging from positive to negative ρ values (see box and whisker plot; dots correspond to individual ρ s). (b) For each hemispheric encoding condition (i.e., LH, mixed, RH), colour response precision dropped with increased load in the same feature (Delta-s) but not the other feature (Delta-o). A more negative Delta corresponds to a larger drop in response precision, while Deltas around zero indicate no load-related changes in precision. Delta scores showed no significant difference between the hemispheric encoding conditions. (c) In all hemispheric encoding conditions, size response precision dropped with increased load in the same feature (Delta-s) but not the other feature (Delta-o). Hemispheric encoding differentially modulated these effects, with stronger interference from colour load (i.e., Delta-s) under LH than RH encoding.

1) and (2) whether they were significantly different between the hemispheric encoding conditions, using pairwise permutation analysis. Specifically, we repeatedly shuffled Delta-s or Delta-o scores between two hemispheric encoding conditions and computed the difference between the group means based on the randomly shuffled data in each iteration ($N=1,000$). To assess whether the observed difference between group means was due to chance, we counted the number of absolute permutation difference scores that were higher than the absolute true difference score and divided this number by 1000 to compute the two-tailed p -statistic.

Results

Trial-to-trial coupling of size and colour precision. We observed no significant coupling in the precision of colour and size responses under LH or RH encoding across either C1S1 trials (LH: $p=.56$; RH: $p=.9$) or C2S2 trials (LH: $p=.47$; RH: $p=.34$) (Figure 4a and Table 2). Thus, individual colour and size absolute errors were largely uncorrelated, regardless of whether the probe object was encoded

by the LH or RH (see Figure 4a). For both LH and RH encoding conditions, there was a significant range of values of ρ across participants, ranging from negative to positive values (from $-.47$ to $+.52$; see Figure 4a and Table 2). However, even the individuals with the highest absolute values of ρ showed only weak-to-moderate positive or negative coupling. Although there appeared to be a hint of a hemispheric asymmetry, such that participants who exhibited stronger positive coupling did so under RH encoding, a repeated measures ANOVA showed no significant effect of Hemisphere, $F(df=1, 25)=0.71$, $p=.41$, no significant effect of Feature Load, $F(df=1, 25)=1.81$, $p=.19$, and no significant interaction between Hemisphere and Feature Load, $F(df=1, 25)=0.02$, $p=.89$. Thus, the coupling strength of colour and size features of an object was non-significant, on average, under both RH and LH encoding.

Effects of hemispheric encoding and feature load conditions. Collapsing across feature load conditions, colour precision, and size precision showed no significant differences between hemispheric encoding conditions (Table 3;

Table 2. Summary and bootstrapped statistics of response coupling analysis in Experiment 2.

Hemisphere	Load	M	SD	Mdn	Min.	Max.	95% CI[bs]	
							Lower	Upper
LH	C1S1	-0.04	0.18	-0.01	-0.47	0.22	<i>-0.11</i>	<i>0.03</i>
RH		0.00	0.20	-0.02	-0.39	0.37	<i>-0.07</i>	<i>0.08</i>
LH	C2S2	0.02	0.18	0.03	-0.36	0.29	<i>-0.05</i>	<i>0.09</i>
RH		0.05	0.24	0.05	-0.34	0.52	<i>-0.04</i>	<i>0.14</i>

CI[bs] = bootstrapped confidence interval. Italic font for lower/upper CIs indicates comparisons for which the CI included zero and were therefore deemed non-significant.

Table 3. Summary statistics of overall colour and size precision under each hemispheric encoding condition in Experiment 2.

Hemisphere ^a	Colour precision					Size precision				
	M	SD	Mdn	Min.	Max.	M	SD	Mdn	Min.	Max.
LH	1.72	0.54	1.60	0.54	3.06	6.05	1.60	5.57	3.10	9.10
mixed	2.02	0.84	2.08	0.78	4.39	5.97	1.50	5.66	3.70	9.23
RH	1.89	0.67	1.83	0.50	3.17	6.12	1.69	5.58	3.11	8.56

^aANOVA results showed no significant effect of Hemisphere for colour precision, $F(df=2, 50)=3.46$, $GG_{\epsilon} = 0.81$, $p=.05$, and size precision, $F(df=2, 50)=0.16$, $GG_{\epsilon} = 0.82$, $p=.81$)

Table 4. Summary and bootstrap statistics of overall changes in (a) colour precision and (b) size precision with increased load in the same versus other feature in Experiment 2.

Load (2 - 1)	Delta	(a) Delta colour precision							
		M	SD	Mdn	Min.	Max.	95% CI[bs]		
							Lower	Upper	
C2S1 - C1S1	-s size 1	-1.37	0.89	-1.06	-3.65	0.09	<i>-1.70</i>	<i>-1.05</i>	
C2S2 - C1S2	-s size 2	-1.50	0.90	-1.49	-2.80	0.35	<i>-1.84</i>	<i>-1.16</i>	
C1S2 - C1S1	-o colour 1	0.17	0.79	0.27	-1.60	2.06	<i>-0.12</i>	<i>0.46</i>	
C2S2 - C2S1	-o colour 2	0.04	0.72	-0.10	-1.44	2.45	<i>-0.24</i>	<i>0.31</i>	

Load (2 - 1)	Delta	(b) Delta size precision							
		M	SD	Mdn	Min.	Max.	95% CI[bs]		
							Lower	Upper	
C1S2 - C1S1	-s colour 1	-1.69	1.47	-1.69	-6.64	0.98	<i>-2.24</i>	<i>-1.13</i>	
C2S2 - C2S1	-s colour 2	-0.93	1.37	-0.99	-4.69	2.53	<i>-1.44</i>	<i>-0.39</i>	
C2S1 - C1S1	-o size 1	-0.59	1.41	-0.54	-3.80	2.32	<i>-1.15</i>	<i>-0.06</i>	
C2S2 - C1S2	-o size 2	0.17	1.62	-0.09	-2.67	5.68	<i>-0.47</i>	<i>0.77</i>	

CI[bs] = bootstrapped confidence interval. Italic font for lower/upper CIs indicates comparisons for which the CI included zero and were therefore deemed non-significant.

see density plots in Figure S1A, Supplementary Material). Collapsing across hemispheric encoding conditions, colour response precision was affected by colour load (see Delta-s, Table 4) but not size load (i.e., Delta-o, Table 4), regardless of whether the non-changing feature across objects had low or higher WM demands. Size precision also declined with an increased load in size; however, it was also affected by colour load at a size load of 1 (but not a size load of 2) (Table 4).

Interactions between feature load and hemispheric encoding. To directly test whether interference effects of the same versus other feature on precision were modulated by hemispheric encoding, we evaluated changes in precision with increased within- or cross-feature load for pure LH, pure RH, and mixed encoding, separately for colour and size precision. Bootstrap analysis on Delta-s revealed significant interference from colour load on colour precision under each hemispheric encoding condition (Figure

4b; Delta-s, Table S3a). By contrast, size load did not significantly interfere with colour precision for any hemisphere condition (Figure 4b, Delta-o; Table S3a). Permutation analysis revealed no significant differences in Delta-scores for LH versus RH encoding (Delta-s: $p = .78$, Delta-o: $p = .83$), LH versus mixed encoding (Delta-s: $p = .73$, Delta-o: $p = .17$), or RH versus mixed encoding (Delta-s: $p = .42$, Delta-o: $p = .16$). For all hemispheric encoding conditions, then, colour load but not size load affected colour WM precision; within-dimensional interference was equally strong for each hemispheric encoding condition (Figure 4b).

Size precision was also affected by size load under each hemispheric encoding condition (Figure 4c, Delta-s; Table S3b). Permutation analysis revealed a hemispheric effect on Delta-s scores, such that size load interfered with size response precision more strongly under LH than RH encoding ($p = .03$). The mixed encoding condition had intermediate values that did not differ from either LH ($p = .54$) or RH encoding ($p = .16$). However, colour load did not significantly interfere with size precision for any hemispheric encoding condition (Figure 4c, Delta-o; Table S3b). We found no significant differences in Delta-o for any hemispheric comparison (LH–RH: $p = .17$, LH–mixed: $p = .82$, RH–mixed: $p = .12$). To summarise, size load affected size precision the most when the two objects were both presented to the LH, and the least when the objects were both encoded by the RH. By contrast, colour load did not affect size precision under any hemispheric encoding condition: Delta-o was not reliably different from zero, and Delta-s was larger than Delta-o (Figure 4c). Thus, when each object was presented to a single hemisphere, there was within-feature interference but not cross-feature interference. Furthermore, the RH showed an advantage for size WM, as it exhibited lower within-feature interference than the LH.

Discussion

How do we maintain precise visual information in WM? What are the factors that influence fidelity of WM? Can distinct features of an individual object, or even across a set of objects, be represented in parallel in different “channels” of WM, or do they rely on a common WM resource? Here, we approached these broad questions and assessed WM capacity at both the feature- and object-level, within- and across hemispheres. To this end, we designed a novel visual WM paradigm in which two objects were presented in a sequence, and measured WM precision for both the colour and size of one of the objects. We first ran this paradigm under natural viewing conditions (Experiment 1). This experiment set the stage for an exploration of the effects of a hemispheric encoding manipulation (Experiment 2). Here, we presented objects sequentially at the centre of the screen, such that

they were encoded by both hemispheres simultaneously. With our design, we could ask several questions about feature binding at the feature- and object-level: Does the extent to which features of an object are bound together differ between hemispheres? Do two objects or object features interfere with each other less if they are encoded by different hemispheres? Or, is one hemisphere consistently better at encoding visual features, such that participants would show worse performance when one or both stimuli are encoded by the non-optimal hemisphere?

Are the colour and size of an object represented separately in WM?

We tested whether the absolute magnitude in recall fidelity for one feature fluctuated from trial to trial in tandem with fidelity for the other feature of an individual object. If the precision of colour and size responses for an individual object were strongly negatively coupled across trials, indicating a tradeoff, we would conclude that greater fidelity for one feature means that fewer resources are available for representing the other one, possibly due to attentional competition at encoding. Alternatively, no evidence of coupling would suggest that the two features are represented separately. Finally, positive coupling would indicate that they rise and fall together as a result of attentional fluctuations, consistent with the hypothesis that the features are encoded together.

We observed no significant coupling at the group level between size and colour fidelity under either centralised or lateralized stimulus presentation, consistent with independent representation of these two features. There was wide variability at the individual subject level, with coupling ranging from weak or moderate negative values to weak or moderate positive values. The positive coupling patterns observed for some participants may arise from attentional fluctuations during WM encoding, which could be a source underlying variable precision from trial to trial (e.g., Palmer, 1990; van den Berg et al., 2012). The negative coupling observed for other participants might be explained by prioritisation of one feature over the other during encoding. Overall, the pattern of results across the two experiments suggests that the colour and size of an object are not systematically bound into a single mnemonic representation in WM, consistent with previous studies showing independent feature stores for colour and orientation WM (Bays et al., 2011; Fougny & Alvarez, 2011; Fougny et al., 2013; Shin & Ma, 2017; Wang et al., 2017; Wheeler & Treisman, 2002).

Does increased feature load across objects negatively affect precision for the same feature?

In Experiment 1, we found that an increase in load for a given feature across a set of objects was associated with decreased precision for that same feature. Colour response precision

was strongly affected by colour load across all hemispheric conditions. Likewise, size precision was affected by size load in both experiments across all hemispheric conditions. Thus, consistent with a large body of prior work (e.g., Bays et al., 2011; Fougny & Alvarez, 2011; Palmer, 1990; Wilken & Ma, 2004; van den Berg et al., 2014; for reviews see Ma et al., 2014; Schneegans & Bays, 2019), these results show that WM precision degrades with increased load, rather than being all-or-none. Most of these previous studies manipulated load by varying the number of to-be-encoded objects, and probed precision only for one feature (e.g., colour). Here, we examined how precision for a spatial feature and a non-spatial one varied as a function of load.

In Experiment 2, we again found within-feature interference. Critically, this was true even when the two objects were encoded in different hemispheres, as shown by equal effects under mixed versus pure (LH or RH) hemispheric encoding. Thus, interference was not reduced when demands were placed on different hemispheres and separated in visual space as compared with when items were presented to a single hemisphere at the same location. This finding suggests that within-feature interference was due to a limitation at the level of WM storage capacity—that is, after information was transferred between hemispheres rather than during lateralized encoding of two sequentially presented stimuli. These results are at odds with the hypothesis that there are independent limited-capacity visual WM stores in the two hemispheres (Buschman et al., 2011)—at least, in humans. Rather, these results indicate that colours are represented in a distributed manner across the two hemispheres (Gegenfurtner & Kiper, 2003; Witzel & Gegenfurtner, 2011).

Is there a hemispheric asymmetry in load effects on precision for the same feature?

The within-dimensional load effect on colour precision was also similar whether both stimuli were presented to the LH or to the RH. By contrast, the within-dimensional load effect on size precision was greater in the LH than RH: Size load affected size precision the most when the two objects were both presented to the LH, and the least when the items were both encoded by the RH. Thus, size might be represented in a different way than colour at the object-level, such that size WM is less susceptible to interference when objects are encoded by the RH, while colour might be represented with sufficient capacity within both hemispheres. This result suggests a slight RH advantage for one aspect of visual WM (Sheremata et al., 2010; Sheremata & Shomstein, 2014), as discussed further below.

Does increased feature load across objects negatively affect precision for the other feature?

We tested whether precision for one feature was reduced if the other feature varied across a set of objects. We considered three possible outcomes. The first is that precision for

each feature would be reduced by increased load in the other feature, supporting the idea that distinct features rely on a common WM store. The second possibility was that precision for each feature would be unaffected by increased load in the other feature, consistent with independent stores for colour and size. Finally, the third possibility was feature asymmetry, whereby the precision for one feature dimension would depend on the precision for the other dimension, but not the other way around. This third prediction was based on findings from previous research (Fougny & Alvarez, 2011; Markov et al., 2019) and was borne out by the present data when objects were encoded simultaneously by each hemisphere: In Experiment 1, under natural viewing conditions, size precision was affected by colour load, but colour precision was not affected by size load. This asymmetric pattern for colour and size is consistent with a prior study showing that orientation was affected by colour, but not the other way around (Markov et al., 2019).

What could explain this observed asymmetry? In our study, participants encoded one object at a time, which could have increased encoding precision of the two features as a result of undivided attention on each object. Attentional capacity could be prioritised for colour, possibly because it is more salient than size, resulting in reduced capacity for size when colour load was high. Prioritisation of colour information could also explain why colour was processed more efficiently than orientation in a visual-search paradigm (Huang, 2015). At the feature-level, we found that colour and size can be represented separately under naturalistic viewing conditions; by contrast, at the object-level, size was no longer fully independent from colour under naturalistic viewing conditions. This finding supports the idea of hierarchically organised mnemonic representations of features and objects (Brady et al., 2011; Fougny & Alvarez, 2011).

In Experiment 2, neither visual feature was systematically affected by the load of the other feature, suggesting largely independent feature stores under lateralized viewing conditions. We observed a colour-size asymmetry only when collapsing across hemispheric conditions, and with a size load of 1 (C2S1 vs. C1S1), but not with a size load of 2 (C2S2 vs. C1S2). Thus, size WM was susceptible to interference from the encoding of colours when distinct colours were assigned to two identical shapes (cf. Allen et al., 2006). This interference could stem from confusion between representations that were bound to overlapping features, or blurring as a result of the superposition of multiple overlapping representations (Oberauer & Lin, 2017).

Examining effects of feature load separately for each hemispheric encoding condition, we found that when each object was presented to a single hemisphere, size precision was unaffected by colour precision. This was true across hemispheric encoding conditions. It is possible that the colour load in Experiment 2 (a load of 2, as opposed to 3 in Experiment 1) was insufficiently high to interfere with size

precision. However, this seems unlikely because we had found, when collapsing across hemispheric encoding conditions, that colour load affected size precision at a *lower* overall WM load (C2S1, but not C2S2). Rather, we propose that this discrepancy is related to hemispheric encoding. That is, when an object's size is forced to be encoded by a single hemisphere, it can be stored in a focal manner, independently of colour; by contrast, when viewing conditions encourage broadly distributed storage across both hemispheres, as in Experiment 1, there is greater overlap in the storage of these two features. Further research would be required to determine the conditions under which this asymmetry exists. To summarise, we observed feature asymmetry in favour of colour under naturalistic viewing conditions, when each individual object was encoded by both hemispheres, suggesting that colour information is either prioritised in WM and/or is represented in a more distributed, and therefore more robust, manner. By contrast, when each object was presented to a single hemisphere, the colour-size asymmetry was largely absent, possibly because of reduced overlap between features in distributed WM stores.

Does one hemisphere encode visual stimuli more precisely than the other?

It has long been held that the RH is preferentially tuned to visuospatial information, and the LH for verbal information (Gazzaniga, 2000; Kosslyn, 1987; Mesulam, 1981; Smith & Jonides, 1998; Sperry et al., 1969). However, we observed no difference in overall colour and size precision as a function of whether the two objects were presented in the LH or in the RH, inconsistent with a strong asymmetry. We did, however, find a slight RH advantage in terms of a reduced within-dimensional load effect on size precision.

A load-related RH advantage for size precision suggests that RH might encode multiple features across objects in a different way than the LH. Interference effects between features may be quantitatively but not qualitatively different between hemispheres, with lower interference in the RH than the LH. Thus, visual WM capacity for objects could be greater in the RH, which could be exaggerated in paradigms involving higher loads than the present one, and/or in paradigms presenting objects simultaneously rather than sequentially. Another hemispheric specialisation hypothesis claims that RH is better at coordinate/continuous representations, and LH at categorical/discrete representations (Jager & Postma, 2003; Kosslyn, 1987). One might wonder whether this account could explain why an RH advantage was seen for size, which is represented along a continuous dimension, as compared with colour, which is perceived as categorical. However, our WM precision task required representation along a continuum not only of size but also of colour, and yet we did not find a RH advantage for the within-dimensional load effect on colour precision.

Conclusion

In summary, the lack of trial-to-trial fluctuations in precision for colour and size under either naturalistic or lateralized encoding conditions is consistent with the claim of parallel feature channels during stimulus perception (Treisman & Gelade, 1980). By contrast, the asymmetric feature interference across a set of sequentially presented objects points to partial featural overlap in WM stores. Finally, the finding that neither feature interfered with the other when stimuli were encoded unilaterally suggests that interference observed under naturalistic viewing conditions results from overlap in the storage of the two features across broadly distributed WM stores.

These results highlight the importance of evaluating mnemonic precision for specific features, and how these are encoded and maintained at different levels of information processing during WM (Brady et al., 2011; Schneegans & Bays, 2019). With this study we gained further insights into mechanisms of visual WM by examining how within- and between-hemisphere interactions affect the precision for distinct features of an object. We focused here on temporal rather than spatial feature conjunctions, and showed that visual features are independent within a single object but can interact across objects. These findings suggest that distinct features are registered separately and—as a result of distributed representations across hemispheres—partially integrated in WM stores. Asymmetric feature interference suggests that more salient features are prioritised over less ones by occupying more space in distributed WM stores. Based on the present results, we propose that the extent to which objects are temporally and spatially segregated at encoding affects the units over which WM can operate.

A large body of research has focused on whether separate features are maintained in parallel stores, each with their independent capacities, or whether units can be described in terms of integrated object representations (e.g., Luck & Vogel, 1997; Wheeler & Treisman, 2002). This study goes beyond existing research by investigating how interactions between colour and size features in visual WM affect mnemonic quality of each feature, both within and across hemispheres. Various open research questions emerge from this study, including how interference affects precision if more than two features vary across stimuli or if the number of to-be-encoded items clearly exceeds individual capacity limits. Furthermore, it remains unclear how spatial, rather than hemispheric, separation may affect feature interference in visual WM. Moreover, by using methods that allow for a time-resolved analysis, future work could test when interference is the most critical factor determining representational precision. In addition, the present findings could serve as a foundation for clinical research probing cognitive functioning in patients with unilateral brain injuries or with disrupted communication

between the hemispheres. In turn, this may contribute to our understanding how brain networks within ipsilesional and/or contralesional hemispheres reorganise after injury.

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Supplementary material

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