Research Report

A relational account of visual short-term memory (VSTM)

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A B S T R A C T

Visual short-term memory (VSTM) is an important resource that allows temporarily storing visual information. Current theories posit that elementary features (e.g., red, green) are encoded and stored independently of each other in VSTM. However, they have difficulty explaining the *similarity effect*, that similar items can be remembered better than dissimilar items. In Experiment 1, we tested (N = 20) whether the similarity effect may be due to storing items in a context-dependent manner in VSTM (e.g., as the reddest/yellowest item). In line with a relational account of VSTM, we found that the similarity effect is not due to feature similarity, but to an enhanced sensitivity for detecting changes when the relative colour of a to-be-memorised item changes (e.g., from reddest to not-reddest item; than when an item underwent the same change but retained its relative colour; e.g., still reddest). Experiment 2 (N = 20) showed that VSTM load, as indexed by the CDA amplitude in the EEG, was smaller when the colours were ordered so that they all had the same relationship than when the same colours were out-of-order, requiring encoding different relative colours. With this, we report two new effects in VSTM — a *relational detection advantage* that describes an enhanced sensitivity to relative changes in change detection, and a *relational CDA effect*, which reflects that VSTM load, as indexed by the CDA, scales with the number of (different) relative features between the memory items. These findings support a relational account of VSTM and question the view that VSTM stores features such as colours independently of each other.

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1. Introduction

Visual short-term memory (VSTM) allows us to encode and recall relevant information of visual stimuli over brief periods of time. One prominent theory of VSTM is the *slot model*, which postulates that VSTM is a discrete resource with a fixed capacity of three to four items (slots) (Adam, Vogel, & Awh, 2017; Cowan, 2001; Luck & Vogel, 1997; Rouder, et al., 2008). On the other hand, *resource-based models* propose that VSTM resources can be divided up among items, resulting in a trade-off between the numbers of items encoded and the precision

with which they are remembered. Thus, as the number of memorised items increases, the precision (or quality) of the memory representation decreases (Bays, 2018; Bays & Husain, 2008; Keshvari, van den Berg, & Ma, 2013).

Despite the important differences between the VSTM models, both assume that elementary features (e.g., different colours) are encoded and maintained independently of each other (Bays, 2018; Cowan, 2001). Previous research has already reported significant deviations of this assumption, demonstrating that memory items can interact in VSTM. For example, VSTM is sensitive to the ensemble or summary statistics of multiple items (e.g., Brady & Alvarez, 2015), their spatial configuration (e.g., Jiang, Olson, & Chun, 2000) and their similarity (e.g., perceptual grouping; Woodman, Vecera, & Luck, 2003). Similarity between memory items can thereby have either detrimental or beneficial effects on VSTM, depending on the degree of similarity: Memory performance is enhanced when items belong to different categories (e.g., faces and landscapes) than when trying to memorise stimuli from the same category (e.g., all faces; e.g., Cohen, Konkle, Rhee, Nakayama, & Alvarez, 2014; Yang & Mo, 2017). This *cross-categorical advantage* is thought to reflect reduced interference between neurons that encode and maintain visual information over time (e.g., *cortical resource theory*; Cohen et al., 2014; see also multiple resource theory; Wheeler & Treisman, 2002). However, when the stimuli all belong to the same category (e.g., all faces), highly similar items are remembered better than dissimilar items (e.g., Jiang, Lee, Asaad, & Remington, 2016; Yang & Mo, 2017; see also; Bae & Luck, 2017; Kiyonaga & Egner, 2016). For instance, Jiang et al. (2016) found that very similar faces created by morphing faces together were remembered better than faces of different individuals (see also Yang & Mo, 2017). Moreover, Lin and Luck (2009) reported better memory performance for highly similar colours (e.g., different shades of red) than for dissimilar colours (e.g., red, green, blue; see also Sims, Jacobs, & Knill, 2012, for similar results with line orientation and length).

This *similarity effect* is difficult to explain in current VSTM models, because detecting a change among similar items would seem to require a *higher precision*, which should lead to *worse performance* − not better performance. *Information-theoretic accounts* have proposed that the higher variability of dissimilar stimuli could act as noise that interferes with encoding and thus, limits the ability to maintain memory representations with high precision (e.g. Sims et al., 2012). Related, Lin and Luck (2009) speculated that memorising similar stimuli could lead to a sharpening of the representation via local inhibitory connections between neurons that respond to similar colours (see also Kiyonaga & Egner, 2016; Yang & Mo, 2016). Other explanations are also conceivable (e.g., Lin & Luck, 2009; Ma, Shen, Dziugaite, & van den Berg, 2015; Yang & Mo, 2017).

Of note, these explanations of the similarity effect assume that the difference between similar and dissimilar colours resides at the encoding stage, with similar colours being encoded with higher precision. Moreover, the explanations are quite narrowly focussed on the similarity effect and do not provide a more comprehensive account that would allow deriving further, readily testable predictions.

A more mechanistic explanation for the similarity effect could be derived from the *Relational Account* (Becker, 2010) that was originally developed to explain early visual attention and eye movements. Previous studies have shown that early visual selection operates on the relative features of items (e.g., reddest, darkest, largest item) rather than exact feature values (e.g., orange, dark, medium), which can explain similarity effects in spatial cueing and visual search (e.g., Becker, Folk, & Remington, 2010, 2013; Becker, 2010; Martin & Becker, 2018; Schönhammer, Grubert, Kerzel, & Becker, 2016), feature priming (aka priming of pop-out) effects (e.g., Becker, 2013; Becker, Harris, Venini, & Retell, 2014; Meeter & Olivers, 2014), and linear separability/search efficiency in visual search (Bauer, Jolicoeur, & Cowan, 1996). Moreover, VSTM has been shown to be tightly linked to attention (e.g., Emrich, Lockhart, & Al-Aidroos, 2017; Hamblin-Frohman & Becker, 2019; Olivers & Eimer, 2011; Schmidt, Vogel, Woodman, & Luck, 2002), rendering it feasible that the relational account could explain the similarity effect.

According to the Relational Account, memory representations would not only contain information about the specific features of memory items, but also information about their relative features (e.g., reddest, yellowest, greenest, bluest item). In the commonly used change detection task, the similarity effect could thus be due to the fact that changes in the relative features of an item (e.g., from reddest to non-reddest item in the display) are more noticeable. With similar colours, changing a colour will often (in ~50% of trials) lead to a change in the relative colour; for instance, if the initial display contains a red item and a red-orange item, changing the red item to orange will change its relative colour from reddest to non-reddest (as the red-orange item is then the reddest item). In dissimilar displays, the colours in the memory display are from different colour categories (red, green, blue), so that the same change (red to orange) does not change the relative colours of any items (i.e., the reddest item remains the reddest item). Thus, a higher sensitivity to detecting relative changes can explain the similarity effect. However, the effect would not be due to a better memory for similar colours than dissimilar colours, or to differences in encoding similar vs. dissimilar colours. Rather, the similarity effect would be due to memorising the relative colours of the memory items (e.g., reddest/bluest/greenest), and the fact that the relative colours only change with similar colours, not with dissimilar colours (with the kind of change implemented in previous studies; e.g., Jiang et al., 2016; Lin & Luck, 2009; Yang & Mo, 2017).

Experiment 1 tested this prediction of the Relational Account, and found that changes in the relative colour were indeed detected with higher accuracy. In turn, when the memory colour changed without a change in the relative colour, similar items did not differ from dissimilar items, indicating that the similarity effect is due to changes in the relative colours, not similarity per se.

In Experiment 2, we sought to provide more direct, neurophysiological evidence for the claim that features relationships are stored in VSTM, along with information about the exact feature values. To that aim, we assessed the CDA in the EEG of participants. The CDA is a contra-lateral negativity at posterior electrode sites during the delay (maintenance) period and is commonly interpreted as reflecting VSTM load

(Vogel & Machizawa, 2004). Previous studies have found that the CDA reliably increases in amplitude with the number of items held in memory, and saturates when individual memory capacity limitations are reached (e.g., Balaban & Luria, 2015; Feldmann-Wüstefeld, Vogel, & Awh, 2018; Gao, Yin, Xu, Shui, & Shen, 2011; Kuo, Stokes, & Nobre, 2012). In Experiment 2, we tested whether increases in CDA amplitude with set size are solely due to increases in the number of to-be-stored feature values (e.g., red, orange) or to increases in the number of feature relationships (e.g., redder, yellower) that usually accompany increases in set size. To that aim, we manipulated the number of feature relationships between the items in the memory display while holding the number of features constant, and measured the CDA during the delay period. In line with the Relational Account, we found a significantly larger CDA when the items in the memory display had diverse relationships than when the items could be encoded via a single relationship. This provides the first direct demonstration that relative features take up memory resources, which varies with the number of different relative features in the display.

2. Experiment 1

The aim of Experiment 1 was to provide a first test whether the Relational Account of attention and eye movements can be extended to VSTM; specifically, if the Relational Account can explain the similarity effect (e.g., Jiang et al., 2016; Lin & Luck, 2009; Yang & Mo, 2017). According to the Relational Account, the similarity effect is not due to differences in how stimuli are encoded, but to an enhanced sensitivity to detecting changes on a subset of change trials — those that resulted in a change of the relative colour of the memory items (e.g., from reddest to not-reddest).

In previous studies change trials always included a change to another similar colour within the same colour category (e.g., red item changed to another shade of red; Lin & Luck, 2009; see also Jiang et al., 2016; Yang & Mo, 2017). With this, a change in the relative colour would have occurred on about half of all change trials in the similar condition, and none of the trials in the dissimilar condition (because the reddest item remained the reddest item with all changes; Lin & Luck, 2009).

To test this explanation of the Relational Account, we conducted a change detection task in which participants had to remember 3 differently coloured stimuli that could be either similar (i.e., same colour category) or dissimilar to each other (i.e., different colour categories). On change trials, one of the colours changed, always within the same category (as in Lin & Luck, 2009). Critically, in the similar condition, half of all changes involved a change in the relative colour of the memory items (*Relation Different Change*; e.g., the reddest item changing to orange, and another item becoming the reddest item, or *vice versa*), whereas the other half did not (*Relation Same Change*; e.g., the reddest item changing to orange, but still being the reddest).

If relative features are encoded into VSTM and this explains the similarity effect, detection performance should be better on Relation Different Trials than Relation Same Trials, which in turn should not differ from dissimilar trials (where

the relative features of all items always remained the same). Conversely, if the similarity effect is due to similar colours being encoded or remembered with higher precision, change detection performance should be better on similar than dissimilar trials, with no difference between Relation Same and Relation Different trials.

2.1. Methods

2.1.1. Participants

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. To determine the required sample size, we computed the effect size of the similarity effect of Lin and Luck (2009), Experiment 1 from the F value and degrees of freedom (partial eta squared [η_p^2] of .44; Richardson, 2011). A power analysis (G*Power; Faul, Erdfelder, Lang, & Buchner, 2007) revealed that a sample size of 20 participants was needed to detect a significant effect at $p < .05$ with a power of .80, which corresponds to the sample size of Lin and Luck (2009) in their Experiment 1.

Hence, we recruited 20 participants (11 females, 9 males, with a mean age of 21.40 ($SD = 2.84$), range: 18–32 years) from the University of Queensland to participate in Experiment 1 for compensation of AU$10. All participants gave informed consent. All methods and procedures used in the present studies were in line with the Declaration of Helsinki and approved by the Ethics Committee of The University of Queensland, Australia.

2.1.2. Apparatus

Stimuli were presented using PsychoPy2 (Peirce et al., 2019) on a personal computer (PC) equipped with an Intel Core i5-4790 CPU and an Intel(R) HD Graphics 4600 card, attached to a 19" colour LCD monitor with a resolution of 1280 × 1024 pixels and a refresh rate of 60 Hz. Manual responses were collected using a standard keyboard and participants were tested individually in a normally lit room with a viewing distance of approximately 70 cm.

2.1.3. Stimuli

All stimuli were presented against a white background (sRGB: 255, 255, 255). The Memory Display consisted of 3 coloured squares (measuring 1.48° × 1.48°) that were presented randomly at three out of eight possible locations on an imaginary circle with a radius of 3.68°. There were three colour categories (red, blue, and green) that each contained eight different colours (see Fig. 1A for colours and sRGB values).

In the Similar condition, Memory Displays were composed of 3 different colours within one colour category (e.g., different hues of red); in the Dissimilar condition, Memory Displays contained one colour of each of the 3 different categories (i.e., one hue from the red, blue or green category). The Test Display could be identical to the Memory Display (*No-Change Trial*) or contain a change in one of the colours (*Change Trial*).

On Change Trials, the colour of one of the memory items could change by either 2 shades (2-shade change: e.g., 2nd colour changing to 4th colour; see Fig. 1) or 3 shades (3-shade change: e.g., 3rd colour changing to 6th colour). Furthermore,
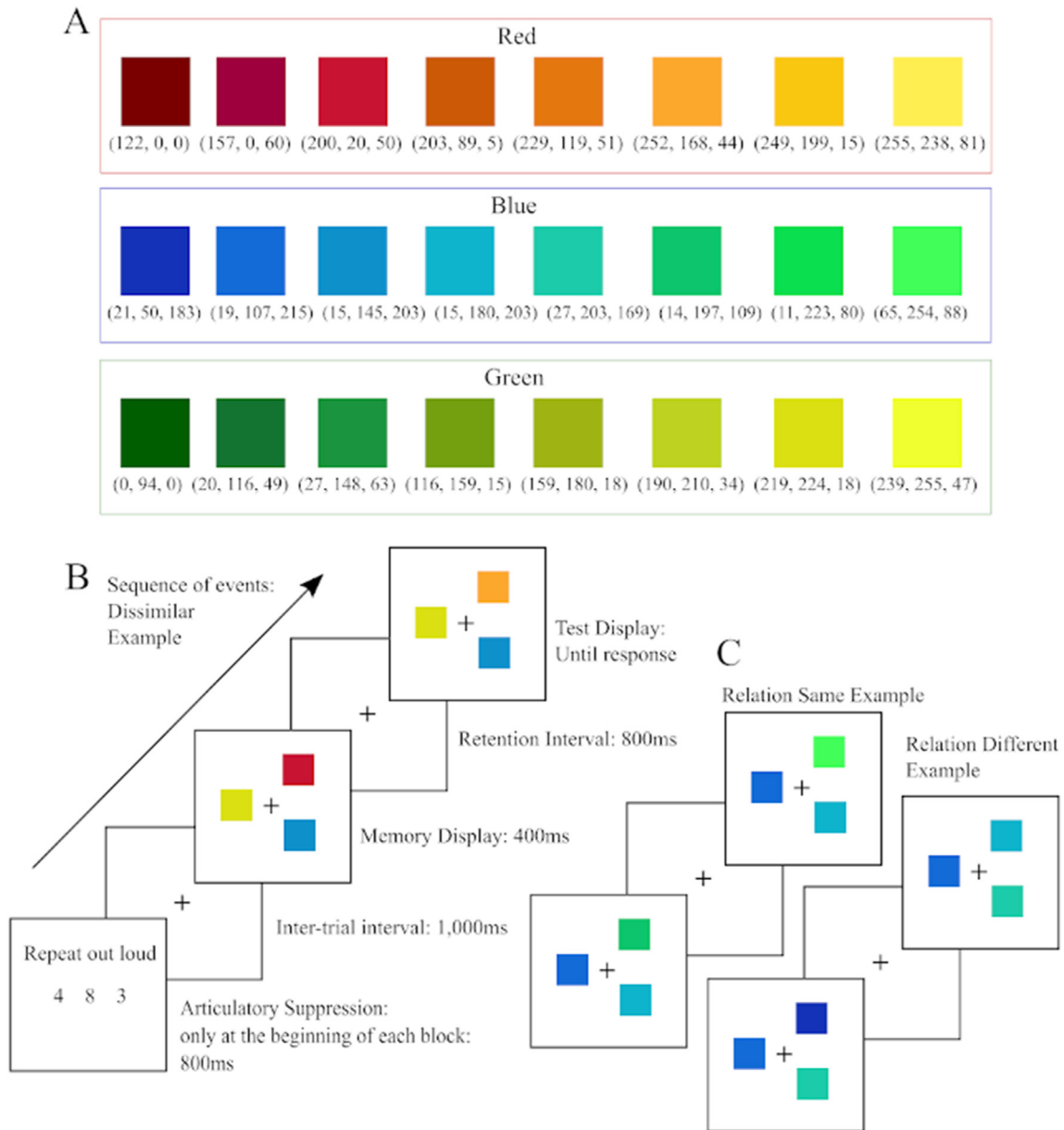
Fig. 1 − Stimuli and sequence of events for Experiment 1. A) The top showcases the three colour categories red, blue, and green, with sRGB values listed below each colour. B) The bottom left shows the sequence of events in the experiment. While continuously reciting the numbers of the articulatory suppression task, participants had to remember the stimuli in the Memory Display, and report whether one of the stimuli had changed or not in the Test Display. The example shows colours of the Dissimilar condition, in which the top square undergoes a two shade-change. C) The left panel shows an example for a Relation Same, 2-shade change, in which the greenest stimulus at the top of the display changes to a different green, but remains the greenest stimulus. The right panel depicts an example of a 2-shade Relation Different trial, in which the bluest stimulus at the top of the Memory Display changes to an intermediate blue in the Test Display, and the left stimulus becomes the bluest stimulus.

within each condition (i.e., 2- or 3-shade change) we distinguished Relation Same vs Relation Different trials.

On Relation Same trials, the memory item changed such that the item in the Test Display had the same relative colour as in the Memory Display (e.g., if an item was reddest in the Memory Display, then after changing 2 or 3 shades it would still be the reddest in the Test Display). On Relation Different trials, the change led to a change in the relative colour of the item (e.g., if an item was reddest in the memory display, then after the colour changed 2 or 3 shades, it would be an intermediate item among redder and yellower other items in the Test Display; see Fig. 1C for examples of Relation Same vs Different displays, and Fig. 2 for an illustration how Relation Same vs Different trials were created).
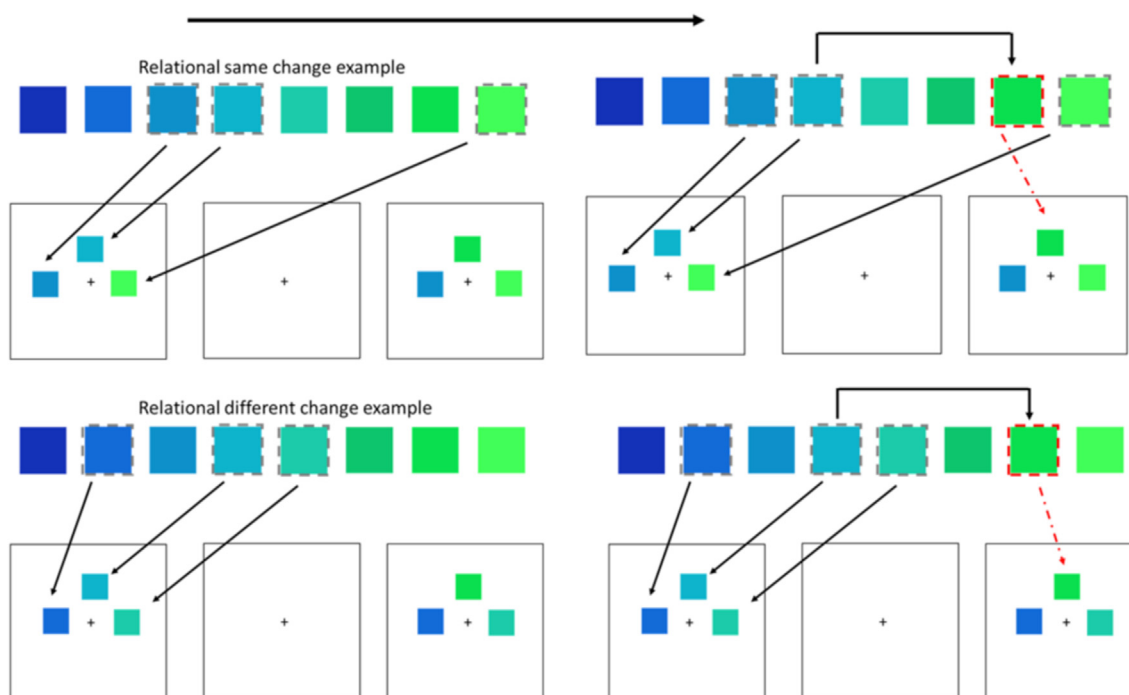
Fig. 2 – Examples showing a Relation Same *vs* Relation Different change using the blue to green colours with a three-shade change. The top row illustrates a Relation Same change, whereby an intermediate colour at the top of the display changes 3 shades to a different color that is relatively still an intermediate colour in comparison to the bluest and greenest items in the display. The bottom row illustrates a Relation Different example, in which the bluest item in the top of the display changes three shades to become an intermediate colour in the test display (i.e., neither the bluest nor the greenest item). Note that this example depicts only one possible combination, whereby the changes were counterbalanced such that an intermediate colour could change to a more extreme colour to the left or right border colours, or an extreme left or right colour could become a more intermediate colour.

2.1.4. Design

Similar and dissimilar colours were blocked, and the order of blocks was counterbalanced across participants. Change and No-Change trials varied within each block, and in the similar condition, Relation Same and Different trials also varied within each block.

In the Similar condition, there were multiple possible combinations to create Relation Same or Relation Different changes with a 2 or 3-shade change. Of the possible combinations, we selected 8 combinations within each of the 3 colour categories (24 combinations) for each Relation Same and Relation Different trials so that (1) half of the combinations realised a 2-shade change, and half a 3-shade change, (2) half of these changes occurred on a relatively extreme item (e.g., the reddest or yellowest item), and half on an intermediate item (not the reddest or yellowest item), (3) half of each of these combinations contained an outward change towards a more extreme colour (e.g., orange changed to a redder or yellower shade), and the other half contained an inward change (e.g., a red or yellow colour changed to an orange-ish colour), and (4) half of each of these changes resulted in a change to a colour on the left of the original colour (e.g., redder) and half of the changes resulted in a change to the right of the original colour (e.g., yellower, in the red-yellow colours; see Fig. 1A). All of these combinations were realised

equally across the 3 different colour categories, resulting in 96 trials for the Relation Same and Different conditions, each.

Relation Same and Relation Different trials (33% each) were randomly interleaved with No Change trials (33%), for a total of 288 trials in the Similar condition. The Dissimilar condition contained 192 trials, half of which were Change Trials, in which all 3 colour categories and 2- and 3-shade changes were equally represented. The trials of the Similar and Dissimilar conditions were sub-divided into two blocks each, with the order of blocks being counterbalanced across participants (in the fashion ABAB or BABA).

2.1.5. Procedure

Prior to each block, participants were provided with written and verbal instructions about the stimuli and the tasks. To encourage encoding of the colours by their visual properties and discourage participants from using semantic labels in the memory task, we used an articulatory suppression task (Shapiro & Miller, 2011; for a similar procedure, see; Lin & Luck, 2009). At the beginning of each block, we presented 3 random numbers (in black, Arial, 20 pixels in height 4.0° apart) that participants had to repeat aloud during the memory task. All participants were supervised by an experimenter, who verified that participants completed the articulatory suppression task accurately and continuously (with occasional

prompts from the experimenter). No trials had to be excluded because of non-compliance with the task.

For the VSTM task, participants were instructed to memorise the 3 colours in the Memory Display and to press the right arrow key if they thought one of the colours in the Test Display had changed, and the left arrow key if the display had not changed. Moreover, participants were instructed to keep their gaze fixated on the small black fixation cross (.57° × .57°) that was continuously visible during the VSTM task.

Prior to the experiment, participants completed 40 practice trials in the task (not recorded). After the practice phase, the experiment started with the articulatory suppression task. In the VSTM task, the memory display was presented for 400 msec, followed by a delay period (800 msec), in which only a fixation cross was presented. The test display was presented until the participant's response. After an intertrial interval of 1000 msec, the next trial started with a new memory display (see Fig. 1B for an overview of the sequence of events). Participants were provided with a break after each block to avoid fatigue.

2.2. Results

2.2.1. Data
Sensitivity rates (d') were analysed for Experiments 1 and 2 using the statistical program JASP (JASP Team, 2017). Bayesian statistics are reported using BF_{10}. Effect sizes were reported as partial eta-squared (η_p^2) and Cohen's d. Plots were created using the 'ggplot2' (Wickham, 2009) package in R (R Core Team, 2016). No part of the study procedures or analyses was preregistered prior to the research being conducted. Materials, data and analysis scripts for Experiment 1 and 2 can be accessed on the Open Science Framework via https://osf.io/dx7hf/.

2.2.2. Sensitivity (d')
A 3 (Condition: Relation Same, Relation Different, Dissimilar) x 2 (colour change: 2-shade change, 3-shade change) repeated measures ANOVA was computed over d' (z-transformed hit rate (i.e., correctly identified changes) minus z-transformed false alarm rate (i.e., reported change on no-change trials)). The results showed a significant main effect of condition, F (2, 38) = 11.64, $p < .001$, $\eta_p^2 = .38$, and of colour change, F (1, 19) = 176.51, $p < .001$, $\eta_p^2 = .90$, with a higher d' for 3-shade changes ($M = 2.07$, $SEM = .11$) than 2-shade changes ($M = 1.41$, $SEM = .10$). The interaction between the two variables was not significant, $F < 1$, $p > .745$.

Paired two tailed t-tests showed that for a 2-shade change among the similar colours, sensitivity for detecting Relation Different changes was higher than for Relation Same changes, $BF_{10} = 3,886.04$, t (19) = 6.25, $p < .001$, 95% CI [.23, .46], $d = 1.40$, and for changes among the Dissimilar colours, $BF_{10} = 31.47$, t (19) = 3.81, $p = .001$, 95% CI [.14, .50], $d = .85$ (see Fig. 3A). However, there was no significant difference between Relation Same changes in the Similar condition and changes in the Dissimilar colours, $BF_{10} = .24$, $t < 1$, $p = .768$.

Similar results were found for a 3-shade change: Relation Different changes were more readily detected than Relation Same changes among similar colours, $BF_{10} = 5.67$, t (19) = 2.92, $p = .009$, 95% CI [.08, .47], $d = .65$, and changes among the Dissimilar colours, $BF_{10} = 7.53$, t (19) = 3.07, $p = .006$, 95% CI [.10, .55], $d = .69$ (see Fig. 3B), whereas Relational Same changes did not differ from Dissimilar colour changes, $BF_{10} = .25$, $t < 1$, $p = .421$.

2.3. Discussion

The results of Experiment 1 clearly show that the similarity effect first reported by Lin and Luck (2009) is due to the subset of trials in the Similar condition, in which the relative colour of the memory items changed (i.e., in which the reddest item in the memory display changed to an intermediate colour or *vice versa*). When the relative colour of all items remained the same, there was no differences in sensitivity between Similar and Dissimilar colours − despite the fact that the amount of colour change was exactly the same (i.e., 2-shade or 3-shade change).

These results show, for the first time, that colour changes are more noticeable when the relative colour of an item changes, demonstrating that feature relationships are encoded and stored in VSTM. As change detection performance also depended on the magnitude of the change (2-shade *vs* 3-shade change), specific feature values are apparently also encoded and stored in VSTM. However, the similarity effect (Lin & Luck, 2009) was shown to depend on feature relationships, not on similarity, as the differences between Similar and Dissimilar colours were abolished when the relative features remained the same. The absence of a similarity effect in this condition (BF: .24 - .25; null hypothesis is 4 times more likely than a similarity effect) is difficult to explain on current accounts of the similarity effect, which assume that similar stimuli are encoded differently in virtue of their stimulus characteristics, and indicates that the effect should perhaps be re-labelled.

3. Experiment 2

Experiment 1 showed that information about feature relationships is stored in VSTM and can aid change detection, by rendering us more sensitive to changes in the relative features. Information about relative features may be stored like a 'meta-object' or a 'meta-representation' that contains information about the locations of the reddest, 2nd reddest, 3rd reddest item, etc. (e.g., akin to a priority map; Wolfe, 1994). Underlying this representation are algorithms or a number of visual processes that tag relative features and locations, with the resulting representation being stored in visual working memory. This relational meta-representation should also add VSTM load, or take up significant working memory resources.[1] The aim of Experiment 2 was to explore how much VSTM resources are taken up by storing relative information, as well

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[1] According to the laws of algorithmic efficiency in computer science, an algorithm can either be fast and use a lot of working memory resources, or it can be slow and use minimal working memory resources. As relational information is available at a very early stage of visual search (e.g., Hamblin-Frohman & Becker, 2021), it appears that a relational representation would probably take up a rather large amount of memory resources.
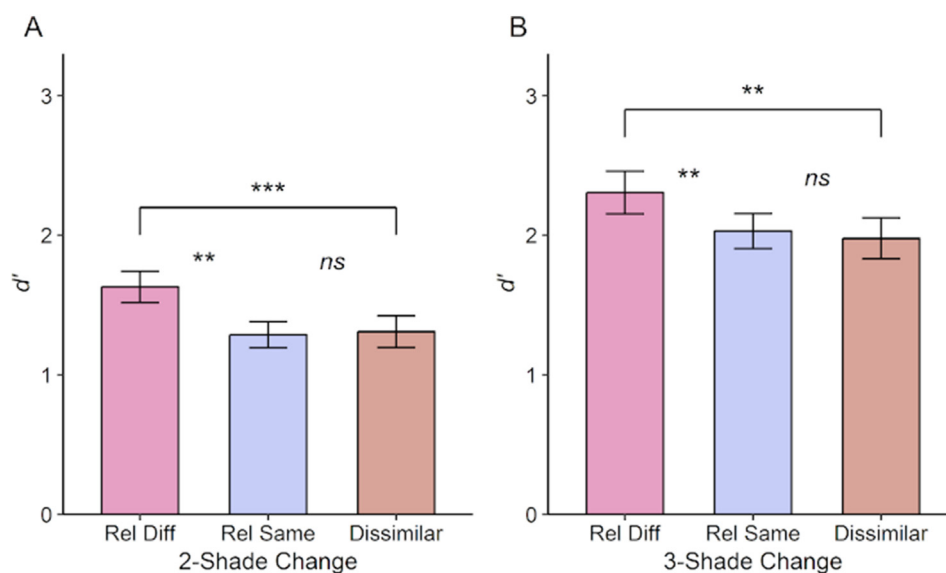
Fig. 3 – Mean sensitivity (*d'*) for Experiment 1, depicted separately for 2-shade *vs* 3-shade colour changes, and Relation Same *vs* Different changes (Similar condition), as well as changes to the Dissimilar colours. Across both 2-shade and 3-shade changes, sensitivity was significantly higher for a Relation Different change compared to a Relation Same change or a changes to the Dissimilar colours. Meanwhile, there was no difference between a Relation Same change and the Dissimilar condition. **p* < .05; ***p* < .01, ****p* < .001, as per two-tailed *t*-test. *ns*: not significant. Error bars represent 1 ± SEM.

as to provide additional evidence for the claim that VSTM stores relational information – ideally from the encoding/maintenance stage, without recourse to response-related effects that may be influenced by other processes (e.g., decisional or response-related processes; Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010).

One way to track working memory load is by measuring the CDA, a lateralised potential in the EEG of participants during the delay period. Previous research has shown that the CDA amplitude increases with the number of items that need to be stored, and saturates when individual working memory capacity is exceeded (e.g., Vogel & Machizawa, 2004; for an overview see; Luria et al., 2010). Previous studies have estimated working memory capacity to be 3–4 items. However, the results of Experiment 1 suggest that VSTM also stores the relative features of 3–4 items, in addition to their specific feature values. As the number of relationships between the stimuli increases with increases in the number of stimuli, part of the CDA amplitude increase with set size could be due to the requirement to store a larger number of relative features.

In Experiment 2, we assessed whether and to what extent the CDA amplitude increase with the number of items is due to storing relative features, by manipulating the number of relative features between the memory items. To that aim, we presented 3 or 4 memory items in a horizontally aligned fashion (see Fig. 3), and in one condition (*In Order*), ordered similar colours so that the colours all had the same relative colour to the neighbouring colours (e.g., redder, from left to right; see Fig. 3). In the other condition (*Out of Order*), the same colours were randomly distributed across the locations, so that the relative colours differed, and increased with the number of items. Assessing the CDA in the In Order *vs* Out of

Order condition across the two memory set sizes (3, 4) allows assessing the contribution of storing relative features to the CDA amplitude increase, as the number of feature relationships in the In Order condition was always constant (i.e., one), whereas it was allowed to naturally increase with the number of items in the Out of Order condition.

The manipulation is similar to one used by Gao et al. (2011), where the authors presented memory displays with 1 item, 4 items of the same colour, or 4 items of different colours. The results of that study showed that the CDA for the 4 items with the same colour resembled the CDA for the 1-item display, and was significantly smaller than when the displays contained 4 differently coloured items. The main difference to this study is that in Experiment 2, we always presented different colours, but kept the relative colours constant (and at a minimum of one) in the In Order condition, while the relative colours were allowed to vary with the set size in the Out of Order condition.

If storing relative colours adds to the overall VSTM load, the CDA amplitudes should be significantly smaller in the In Order conditions, in which the memory items all had the same relative feature, than in the Out of Order conditions, in which the memory items had different relative features, across both set size conditions.

Despite the lower VSTM load in the In Order conditions, we did not expect to find generally higher accuracies in the In Order condition: As shown by the results of Experiment 1, relative colours are evidently encoded and stored automatically, including when there are multiple different relative colours involved. Moreover, the task required responding to absolute (not relative) colours, and a lower VSTM load in the In Order conditions (due to encoding only a single relative

feature) may not translate into a higher precision or probability of encoding absolute colours.[2]

Encoding of relative colours was assessed as in Experiment 1, by comparing Relation Same vs Different changes. We hypothesised that the requirement to store (too) many relative features may eliminate the advantage for detecting Relation Different changes. This would be most likely to occur in Out of Order, Set Size 4 condition, as this was the most resource-demanding condition. However, as it is currently unknown what kind of capacity limitations apply for encoding and storing relative colours, this outcome could not be confidently predicted. Hence, our key measure to assess VSTM load across the different conditions remained the CDA, which was measured during the delay period.

3.1. Methods

3.1.1. Participants
Twenty self-reported neurologically normal, right-handed participants (10 female, with a mean age of 19.25 years ($SD = 2.45$), range: 17–24) participated in Experiment 2. All participants gave informed consent and were either awarded partial course credits or reimbursed with AU$30.

3.1.2. Apparatus
Stimuli were presented on a 28" colour LCD monitor with a resolution of 1920 × 1080 pixels and a refresh rate of 60 Hz, and were viewed from a distance of 76 cm. The experiment was controlled by PsychoPy2 (Peirce et al., 2019) run on a PC with an Intel(R) Core(TM) i7-4790 CPU, and equipped with an NVIDIA GeForce GTX 745 graphics card. Manual responses were collected using a standard keyboard and participants were tested individually in a normally lit room.

3.1.3. Stimuli
The same colours and colour categories were used as in Experiment 1. A black fixation cross '+' measuring .38° × 38° was presented at the centre for the entire trial, to aid participants to maintain fixation (and avoid oculomotor artefacts in the EEG). An arrow cue ('<' signaling left, and '>' signaling right) was shown at the start of the trial directly underneath the fixation point to indicate which stimulus set should be memorized (see Fig. 4A for sequence of events.). The to-be-remembered stimuli were coloured squares (size: 1.21° × 1.21°) that were aligned horizontally on both sides of the fixation point, starting at 1.28° from fixation to the centre of the first square. Memory displays contained either 3 items on each side of the screen (Set Size 3), or 4 items on either side (Set Size 4).

Across two conditions, colours could either appear In Order or Out of Order. In Order colours varied along a gradient or continuum either from bluest to greenest, reddest to yellowest or yellowest to greenest, from left to right (or vice versa). Out of Order colours did not gradually vary from left to right, but were positioned without any underlying order (see Fig. 4B for an example of the conditions).

3.1.4. Design
The conditions were the same as in Experiment 1, with the following changes: Only 3-shade changes and Similar colours were used. Moreover, the stimuli in the Memory Display were presented In Order or Out of Order, and participants had to memorise either three or four coloured items (Set Size 3, 4) that were presented on the right and left of the display (with cued and uncued side always containing the same number of stimuli). Order was blocked, whereas the side of presentation (e.g., Laterality) and the Set Size varied within blocks. Change trials (66.66%) were intermixed with no change (33.33%) trials within blocks, and as in Experiment 1, we distinguished between Relation Same and Relation Different change trials (50% each; to see whether we could replicate the results of Experiment 1).

Crossing the In Order vs Out of Order, Set Size (3, 4), Side of stimuli (right, left) and Relation Same vs Different change trials resulted in 16 conditions per colour category, to which we added 8 No Change trials (which included all combinations of Order, Set Size and Side), which yielded 24 trial combinations. As in Experiment 1, the number of changes on outward (extreme) vs inward items was equal across Relation Same and Different trials and across the Set Size conditions. Relation Different trials contained an equal number of trials where inward items changed to outward items and vice versa (50%). On no change trials, none of the items changed on either side of fixation. When the cued side was In Order, the uncued side was In Order, and when the cued side was Out of Order the uncued side was Out of Order. To ensure that we had enough trials for the analysis of the CDA, we collected 1008 trials in total from each participant, 512 in each block, with the order of blocks being counterbalanced across participants and one break in between the two blocks.

3.1.5. Procedure
Similar to Experiment 1, each block started with a display of 3 randomly generated numbers (presented for 800 ms) yoked to a silent articulatory suppression task, in which participants were instructed to mentally recite the numbers for the duration of the block (without saying them aloud, to avoid muscular artefacts in the EEG). At the end of each block, the participants had to report the three numbers to the experimenter. Each trial started with the presentation of the fixation and cue display (presented for a random period of 300–500 ms), followed by the memory display (200 ms), a retention period (800 ms), and the test display, which was presented until the participant's response had been recorded ('a' key for change trials, and the 'l' key for no change trials).

Prior to the experiment, participants completed 12 practice trials (not recorded), which contained a mixture of the trials from either the In Order or Out of Order conditions (not analyzed). On average it took 50 min to complete the experiment.

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[2] Predicting higher accuracies for the In Order condition (which requires storing only one relative features) would imply that it is possible to trade memory resources between absolute colours and relative colours – such that storing only one relative feature would allow more left-over capacity resources for remembering absolute colours. As this possibility has not been established and would be highly speculative, we are refraining from predicting differences in accuracy for the In Order vs. Out of Order conditions.
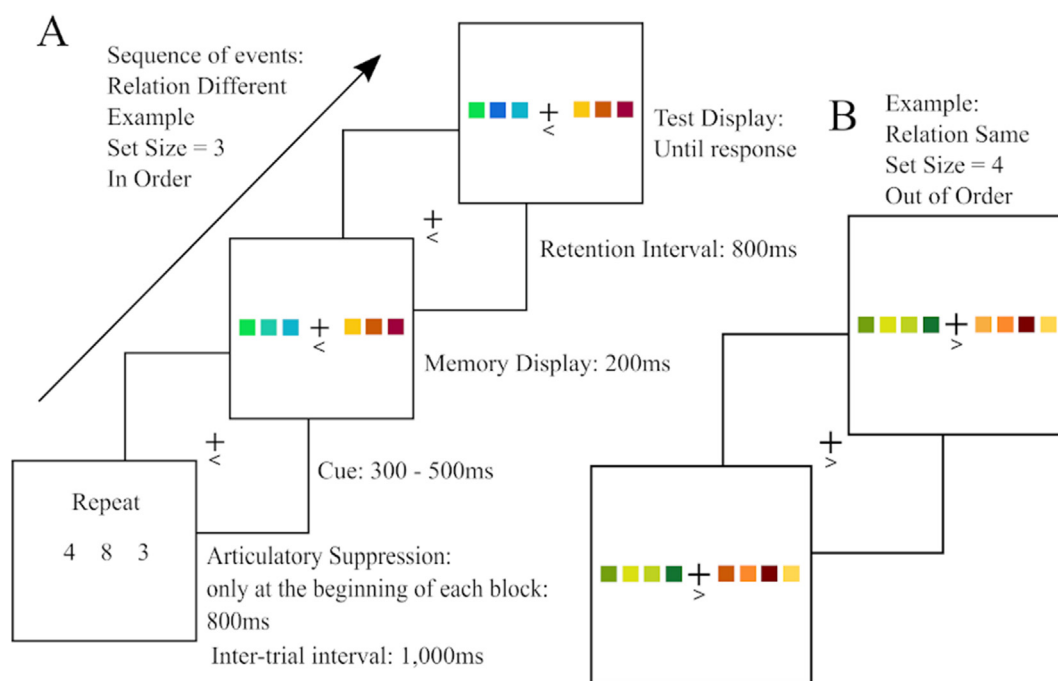
Fig. 4 – Stimuli and procedure for Experiment 2. A) An example of the sequence of events: Each block started with an articulatory suppression task, in which participants had to continuously mentally recite three random numbers. Each trial started with a cue (<or >) indicating the relevant colours (left or right) that had to be remembered during the retention interval, during which we measured the CDA. In the Test Display, participants had to report with a button press whether one of the relevant colours had changed or not. The example shows a Memory Display in which the relevant colours are In Order, Set Size 3, and the Test Display contains a Relation Different change (as the central square changed from an intermediate blue item to the bluest one). B) The bottom right panel shows an example of the Out of Order condition, Set Size 4. The Test Display contains a Relation Same change, as the square closest to fixation retains an intermediate red hue despite undergoing a 3-shade change.

3.1.6. EEG recording and analysis

EEG was recorded from a 64-scalp electrode setup in an elastic cap and measured continuously at 1024 Hz using the Biosemi ActiveTwo EEG system (Biosemi, B. V., Amsterdam, The Netherlands). External electrodes were placed on the outer canthi of both eyes (e.g., HEOG) and underneath the right eye to monitor eye movements. Two reference electrodes were placed on the earlobes. Impedances were kept below 30 kΩ and EEG data were analysed with Brain Vision Analyzer 2.0 software (Brain Products, Gilching, Germany).

EEG data were pre-processed by resampling the data to 500 Hz, applying a low cut-off filter of .1 Hz, and a high cut-off filter of 40 Hz. All electrodes were re-referenced offline to the average of the linked earlobes.

Trials that contained blinks exceeding ±80 μV in the VEOG channel (i.e., AF8 minus electrode under right eye), or horizontal eye movements that exceeded ± 80 μV in the HEOG channel,[3] or muscular artefacts exceeding ± 100 μV in all other

channels were excluded from EEG analysis (for similar exclusion criteria, see Allon, Balaban, & Luria, 2014; Balaban, Drew, & Luria, 2018; Balaban & Luria, 2015; 2016). The remaining trials were segmented into epochs from 200 msec prior to the onset of the Memory Display to 1200 msec post stimulus onset, with the −200 msec to 0 time window serving as a baseline.

Event related potential (ERP) waveforms were computed separately for each type of stimulus condition (i.e., Set Size 3 In Order, Set Size 3 Out of Order, Set Size 4 In Order and Set Size 4 Out of Order) and coded separately for contralateral and ipsilateral electrodes (i.e., contralateral to the side of the Memory Display containing the relevant colours). The mean CDA amplitudes were computed using the average of P5/P6 and P7/P8 electrodes in the epoch of 400–1000 msec from the onset of the memory display (for a similar procedure see, e.g., Balaban & Luria, 2015, Gunseli, Meeter, & Olivers, 2014; McCollough, Machizawa, & Vogel, 2007).

3.2. Results

3.2.1. Data

Incorrect trials were excluded from the analysis of the EEG data, leading to a loss of 28.70% trials. Furthermore, 13.57% of trials were lost due to excessive vertical eye movements and 7.13% of trials were lost due to excessive horizontal eye movements. Overall, these exclusions led to a similar loss of trials across

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[3] To check whether there was any influence from horizontal eye movements, the mean activity from the HEOG channel was compared between the CDA epoch of 400–1,000 ms compared to −200 to 0 baseline, to see if horizontal eye movements were significantly different from baseline activity. A 2 (Epoch: Baseline, CDA) x 2 (Order: In Order, Out of Order) x 2 (Set Size: 3, 4) ANOVA was conducted for the HEOG channel. There were no significant main effects or interactions, all $Fs < 2.42$, *all ps* > .136, indicating that the differences cannot be attributed to eye movements.

conditions (e.g., a loss of 10.95% of data from the Set Size 3 In Order condition, 12.16% from Set Size 3 Out of Order condition, 12.51% from the Set Size 4 In Order condition, and 13.77% from the Set Size 4 Out of Order condition). Data were analysed using a repeated-measures ANOVA and pairwise t-tests. ERP plots were created in R (R Core Team, 2016) using the 'ggplot2' (Wickham, 2009) and 'reshape2' (Wickham, 2007) packages.

3.2.2.   Sensitivity (d')

The sensitivity (d') for the In Order vs Out of Order colours are displayed in Fig. 5, separately for each Set Size condition and Relation Same vs Different changes. A 2 (Set Size: Set Size 3, Set Size 4) x 2 (Order: In Order, Out of Order) x 2 (Relation: Same, Different) repeated-measures ANOVA computed over d' showed significant main effects of Set Size, $F(1, 19) = 64.30$, $p < .001$, $\eta_p^2 = .77$, and Relation, $F(1, 19) = 17.49$, $p < .001$, $\eta_p^2 = .48$, as well as a significant interaction between Set Size and Relation, $F(1, 19) = 4.86$, $p = .040$, $\eta_p^2 = .20$ (all other Fs < 2.73, ps > .114).

Paired two tailed t-tests showed that for Set Size 3, d' was significantly higher on Relation Different trials, compared to Relation Same trials, both when colours were In Order, $BF_{10} = 19.01$, $t(19) = -3.55$, $p = .002$, 95% CI [−.39, −.10], $d = .79$, and Out of Order, $BF_{10} = 3.93$, $t(19) = -2.71$, $p = .014$, 95% CI [-.039, −.05], $d = .61$. For Set Size 4, detection rates were significantly higher on Relation Different trials compared to a Relation Same trials when colours were In Order, $BF_{10} = 2.05$, $t(19) = -2.34$, $p = .031$, 95% CI [−.29, −.02], $d = .52$. However, there were no significant differences between Relation Different and Same trials when colours were Out of Order in the Set Size 4 condition, $BF_{10} = .30$, $t(19) = .76$, $p = .459$, 95% CI [−.09, .18], $d = .17$, which points to the possibility that the requirement to store the relative colours of 4 items may exceed VSTM capacity for relative features.

Overall, these results replicate and extend the results from Experiment 1, by demonstrating better change detection performance for Relation Different than Relation Same changes in 3 out of the 4 tested conditions.

3.2.3.   CDA amplitude

To test whether VSTM load was reduced when the colours were presented In Order rather than Out of Order, a 2 (Set Size: Three, Four) x 2 (Order: In Order, Out of Order) x 2 (Laterality: Ipsilateral, Contralateral) repeated measures ANOVA was computed over the mean CDA amplitudes in the 400−1,000 ms post-stimulus interval (see Fig. 6). There was a significant main effect of Laterality, $F(1, 19) = 40.93$, $p < .001$, $\eta_p^2 = .68$, and a significant interaction between Order and Laterality, $F(1, 19) = 13.40$, $p = .002$, $\eta_p^2 = .41$. No other main effects or interactions were significant, all Fs < 2.41, ps > .137.

Paired t-tests revealed a significant CDA (larger negativity for contralateral compared to ipsilateral condition) across all conditions of the experiment; In Order Set Size 3, $BF_{10} = 2.86$, $t(19) = 2.53$, $p = .020$, 95% CI [.07, .74], $d = .57$, In Order Set Size 4, $BF_{10} = 38.13$, $t(19) = 3.90$, $p < .001$, 95% CI [.37, 1.24], $d = .87$, Out of Order Set Size 3, $BF_{10} = 1,081.03$, $t(19) = 5.58$, $p < .001$, 95% CI [.63, 1.38], $d = 1.25$, and Out of Order Set Size 4, $BF_{10} = 261.00$, $t(19) = 4.87$, $p < .001$, 95% CI [.76, 1.92], $d = 1.09$.

To compare the CDA amplitudes between the different conditions, paired t-tests were computed over the mean difference waves (contralateral minus ipsilateral waveforms, see Fig. 6C). In the Set Size 3 condition, the results revealed a smaller CDA amplitude for In Order colours ($M = -.41$, $SEM = .16$) than Out of Order colours ($M = -1.00$, $SEM = .18$), $BF_{10} = 9.21$, $t(19) = 3.18$, $p = .005$, 95% CI [.20, .99], $d = .71$. The same pattern was observed for the Set Size 4 condition, with a significantly smaller CDA for In Order colours ($M = -.81$, $SEM = .21$) than Out of Order colours ($M = -1.34$, $SEM = .28$),
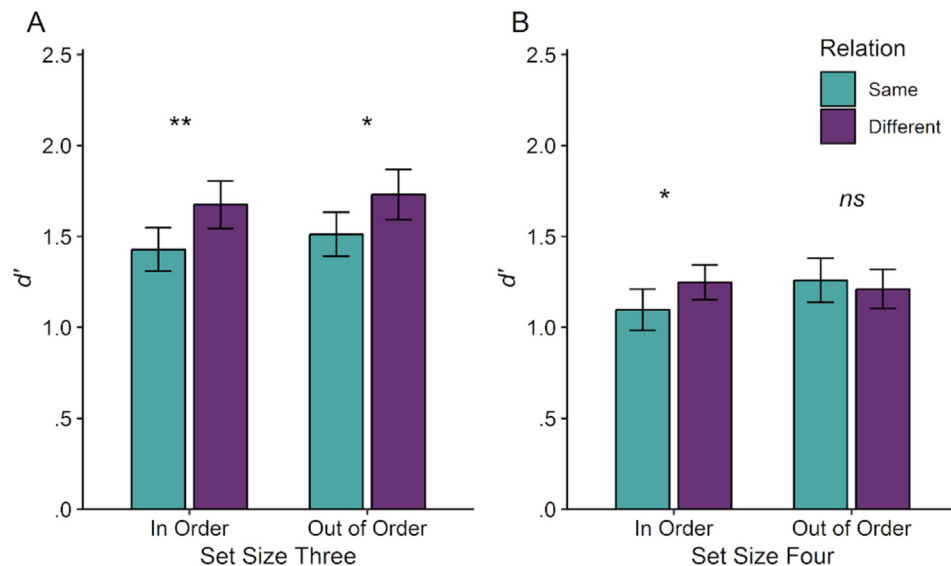

Fig. 5 − Sensitivity (d') for Experiment 2. For Set Size 3 (left panel), sensitivity was significantly higher for Relation Different changes than Relation Same changes, both when colours were In Order and Out of Order. For Set Size 4 (right panel), Relation Different changes were also more noticeable than Relation Same change when colours were In Order; however, there was no difference for Out of Order colours. *p < .05; **p < .01, ***p < .001, as per two-tailed t-test. Error bars represent ± 1 SEM.
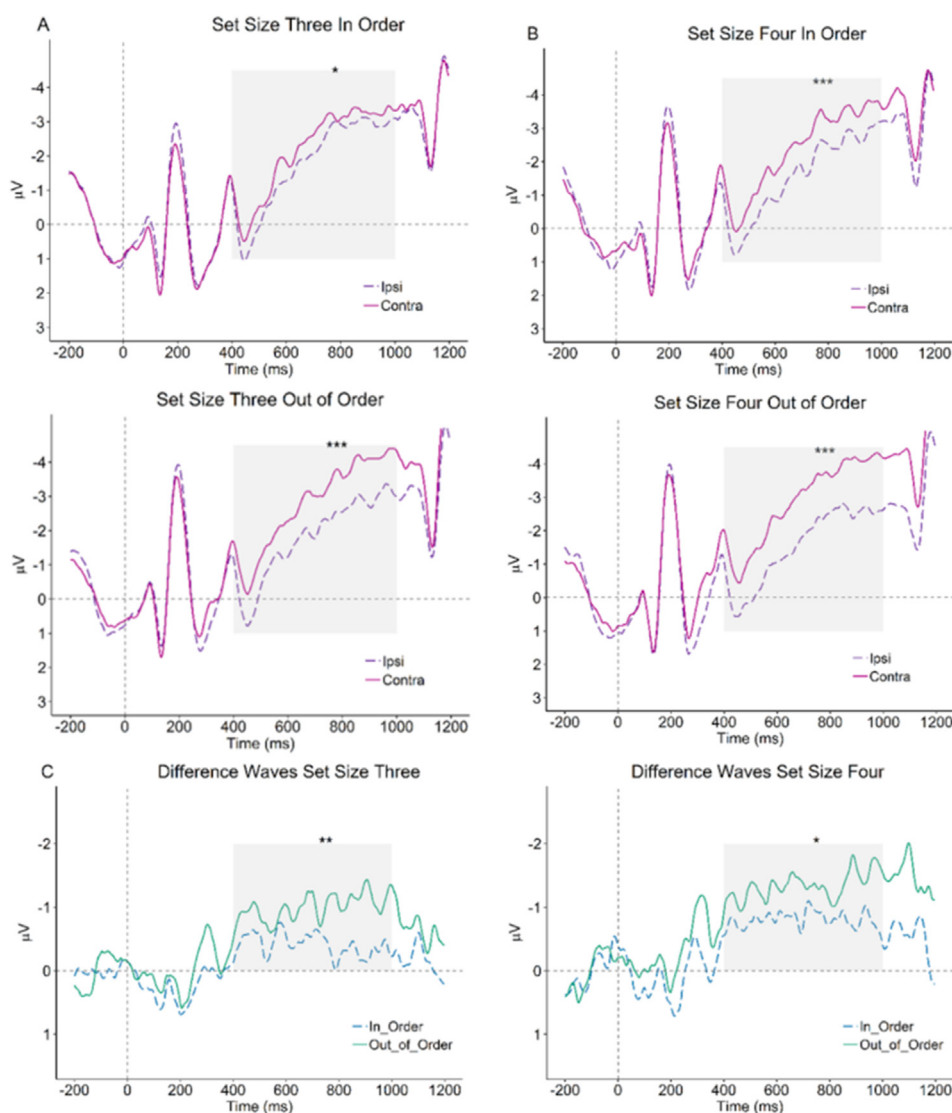
Fig. 6 — The ERPs of Experiment 2, showing the averaged electrodes P5/P6 and P7/P8 in the epoch of −200 pre-stimulus to 1200 msec post-stimulus onset. A significant CDA was observed 400−1000 msec post-stimulus for A) the Set Size 3 condition, both for In Order and Out of Order colours, and B) for the Set Size 4 condition, both for In Order and Out of Order colours. C) Difference waves (contralateral − ipsilateral waveforms) showed the predicted smaller CDA for the In Order colours than the Out of Order colours for both Set Sizes. *$p < .05$; **$p < .01$, ***$p < .001$, as per two-tailed t-test. A high cut off filter of 17 Hz was applied for display purposes.

$BF_{10} = 2.24$, $t (19) = 2.39$, $p = .027$, 95% CI [.07, 1.00], $d = .53$. These results show that the number of relative features encoded substantially contribute to the CDA amplitude increase.

In this experiment, the CDA amplitude differences between In Order and Out of Order conditions were fairly large (.6 and .5 in the Set Size 3 and 4 conditions, respectively) and seemingly larger than the difference caused by an increase in Set Size (.4 and .3 for In Order and Out of Order conditions), but it should be kept in mind that the In Order vs Out of Order conditions comprise the difference between a single relative feature vs 3 or 4 relative features, whereas the set size manipulation only captures the − much smaller − difference between 3 vs 4 items. The difference in the magnitude of the two manipulations prevents a direct comparison between

CDA amplitude increases that are due to the number of absolute features vs relative features. Still, the results of Experiment 2 show clear evidence that relative features are encoded into VSTM and contribute to the CDA amplitude increase with increases in the set size.

3.3. Discussion

Experiment 2 provided the first evidence that encoding and maintenance of relative features can modulate VSTM load, as indexed by the CDA. As predicted, the CDA amplitude increased substantially with the number of different relative features between the memory items, compared to a condition in which the relative features between the memory items were kept the same. These results indicate that the well-

known effect of an increased CDA amplitude with an increase in set size is in part due to an increase in (different) relative features between the memory items. That is, the increase in CDA amplitude with an increase in set size is in part due to a *relational CDA effect*.

The relational CDA effect observed in the present study was also fairly large, as reflected in the large differences between the In Order *vs* Out of Order conditions. However, the relative contributions of the number of absolute colours *vs* relative colours to the CDA amplitude increase cannot be straightforwardly estimated, as the number of to-be-encoded relative colours varied substantially, between a single feature relationship that covered all items (In Order) versus various feature relationships between 3 or 4 colours (Out of Order), whereas the number of absolute colours varied only between 3 and 4 items.

As a further caveat, it should be noted that it is still unknown how relative features are exactly encoded and hence, what the exact source of the observed relational CDA effect is. Presenting the colours in an order ensured that the relative colour between the memory items was continuously repeated across the positions. When the relative feature is the same across all positions, it can *theoretically* be condensed into a single relative feature (over multiple positions), but it is not certain if the visual system operates on this principle, or whether encoding In Order colours takes up less VSTM resources because the relative features are all repeated across positions. That is, it is possible that the same *number* of relative features was encoded and stored in the In Order and Out of Order conditions, and that the reduction in VSTM load reflects that it takes up less resources to store the same relative feature 3 or 4 times than to store different relative features. What is clear from the present study is that the visual system efficiently exploited the reduced information content in the In Order condition, to encode relative features in a less resource-demanding manner in VSTM.

Of note, In Order colours also systematically varied in their similarity, in the sense that the first colour was always more similar to the second colour than to the third colour. However, the reduced CDA is unlikely to be due to a hidden similarity effect: Of note, the colours were chosen from a set of eight colours, so that each colour could either be quite similar or dissimilar from the adjacent colour. Thus, attending to similarity itself could not aid with the task. Another possibility is that the order of the similarity relations was encoded (e.g., first colour more similar to second colour than to third), rather than the relative colour itself (e.g., first colour redder than second or third colour). However, this information would still be relational (i.e., 'more similar than' is a relation that characterises different degrees of similarity). Similarity is also unlikely to account for the present results because similarity and/or colour contrast failed to modulate CDA amplitude in previous studies (Ikkai, McCollough, & Vogel, 2010 (Exp. 1); Luria et al., 2010 (Exp. 4)), whereas the present results clearly showed an effect of In Order *vs* Out of Order colours on the CDA.

A second important finding was that Experiment 2 replicated the main finding of Experiment 1: Change detection performance was significantly better when the relative colours changed than when the colours underwent the same physical change while retaining their feature relationships. In the Set Size 4 condition, this result was only obtained for In Order colours, but not when the colours were Out of Order. This could be due to the task exceeding the capacity limit for relative features, or to incomplete encoding of relative features in the Set Size 4 Out of Order condition. If the capacity limit for relative features was exceeded in the Set Size 4 Out of Order condition, relative features may not have been encoded at a sufficiently high quality or with sufficient precision to aid in the change detection task, explaining why we did not find significant differences between the Relation Same and Relation Different conditions. Alternatively or additionally, it is possible that encoding all the relative colours in the Set Size 4 Out of Order condition would have required more time than was available, so that encoding remained incomplete, again explaining why Relation Different changes were not detected with higher accuracy than Relation Same changes in this condition. While this explanation is still speculative, an increased sensitivity to changes in the relative colour was observed across 3 out of 4 conditions of Experiment 2, and only failed to obtain in the condition that was predicted to require encoding the largest number of relative features, which was also reflected in the large CDA amplitude in this condition. With this, the results of Experiment 2 confirm the findings of Experiment 1, and indicate a hypothetical capacity limit for storing different relative features of 4 items.

A third interesting finding of Experiment 2 was that the In Order and Out of Order conditions did not show significant differences in change detection accuracy. Despite the fact that the CDA amplitude was much smaller in the In Order condition, accuracies in this condition were not higher than in the Out of Order conditions; even when comparing only Relation Different trials. This suggests that both absolute and relative features were encoded approximately equally well in the In Order and Out of Order condition (up to the potential capacity limit of 4 different relations), and that it may not be possible to trade resources. That is, the requirement to store only a single relative feature apparently does not lead to a higher probability or a more precise memory representation of either absolute or relative features, which would translate into higher change detection performance. It is currently unclear if this finding reflects an important difference between remembering relative *vs* absolute features, or if it is due to the fact that relative features were task-irrelevant. Of note, the relative colours were never mentioned to the observers and storing relative features was not necessary to complete the task. Thus, our paradigm tapped into purely automatic processes that were not subject to any top-down modulation. It is possible that better performance with a reduced VSTM load depends on explicit instructions to encode and retain relative features and/or the motivation to use resources maximally efficiently. As shown by studies on *Irrelevance-Induced Blindness*, available VSTM resources are not always used to encode or retain irrelevant features with higher fidelity – even when the irrelevant feature is in close proximity of other task-relevant items, or if it is part of a task-relevant item (e.g., Eitam, Yeshurun, & Hassan, 2013). Future experiments should render either absolute features or relative features irrelevant in otherwise identical tasks, and collect electrophysiological and behavioural data to assess whether optimal use of

available resources depends on task-relevance, or on the type of feature to be remembered (absolute *vs* relative).

4. General discussion

The present study yielded several important results. First, the results of Experiment 1 clearly show that the similarity effect first reported by Lin and Luck (2009) is due to the subset of trials in the Similar condition, in which the relative colour of the memory items changed (i.e., in which the reddest item in the memory display changed to an intermediate/non-reddest item or *vice versa*). When the relative colour of all items remained the same, there were no differences in sensitivity between Similar and Dissimilar colours – despite the fact that the amount of colour change was exactly the same (i.e., 2-shade or 3-shade change).

These results demonstrate, for the first time, that colour changes are more noticeable when the relative colour of an item changes. This shows that feature relationships are encoded and stored in VSTM. As change detection performance also depended on the magnitude of the change (2-shade *vs* 3-shade change), the specific feature values (e.g., orange) are apparently also encoded and stored in VSTM. However, the similarity effect (Lin & Luck, 2009) was shown to depend on feature relationships, not on a difference between Similar *vs* Dissimilar colours, as the differences between Similar and Dissimilar colours were abolished when the relative features remained the same. The finding that memory for Similar and Dissimilar colours is indistinguishable once changes in the relative colours are controlled for suggests that there may not be a genuine similarity effect. Similar results were also obtained in the domain of attention research, where it was shown that the similarity effect (e.g., Duncan & Humphreys, 1989; Folk & Remington, 1998) was in fact due to top-down tuning to relative features (e.g., Becker, 2010; Becker, Folk, & Remington, 2013; York & Becker, 2020). However, further research is required to establish whether the Relational Account can explain all the occurrences of similarity effects reported in previous VSTM studies (e.g., Jiang et al., 2016; Yang & Mo, 2017).

The Relational Account differs from the other accounts of the similarity effect in several notable respects; most notably, in that it assumes that similar and dissimilar features are encoded in the same way (i.e., both with their absolute and relative features), with the similarity effect being due to the type of change introduced on change trials. This account is in line with the reported failure to find differences in the CDA with similar *vs* dissimilar stimuli (Ikkai et al., 2010; Luria et al., 2010), but differs largely from other accounts, which typically assume that similar stimuli require additional processes that are absent in encoding of dissimilar stimuli (e.g., Jiang et al., 2016; Lin & Luck, 2009; Yang & Mo, 2017).

Another important finding of the present study was that relative features contribute to the VSTM load. In particular, Experiment 2 provided the first evidence that VSTM load is reduced when the memory items are ordered in a fashion that allows encoding and storing only a single relative feature for all items. This was reflected in the significantly reduced CDA for In Order colours compared to Out of Order colours. This is the first

demonstration that the order of otherwise identical stimuli can modulate the CDA, and shows that VSTM load (as indexed by the CDA) is to some extent determined by the number of (different) feature relationships between the memory items.

Our behavioural results moreover indicated that the capacity for encoding and maintaining different relative features may be limited to ~4 items, similar to previous results estimating capacity limitations for absolute feature values (e.g., Vogel & Machizawa, 2004), as reflected in the lack of an advantage for detecting Relation Different changes in the Set Size 4 condition with Out of Order colours. However, this conclusion is currently still speculative and cannot be ascertained with certainty, as relative colours were not task-relevant in the present study, which may account for some of the observed effects in the behavioural measure.

Overall, our results show that features are not encoded and stored completely separately and independently of each other, but in relation to surrounding colours. According to the Relational Account, relative features can be represented by vectors in a feature space (e.g., colour space). The two end points of each vector in feature space would indicate the specific feature values of the items (e.g., red, orange). The direction of the vectors specifies how an item differs from the other items (e.g., redder *vs* yellower), and the length of the vector would specify how much the items differ from each other (feature contrast or similarity measure; Becker, 2010). It is possible that multiple features are indeed encoded and stored in the visual system as vectors, which together form a meta-representation of the involved feature values and relative features. However, it is equally possible that the three kinds of information (feature value, relative feature, feature contrast) are encoded and stored separately. In fact, it is not clear whether feature contrast would be encoded and stored at all, as previous studies failed to find a modulation of the CDA by feature contrast (e.g., Gao et al., 2011; Ikkai et al., 2010; Luria et al., 2010; Ye, Zhang, Liu, Li, & Liu, 2014).

The present study provided evidence that both the absolute colours and the relative colours of the memory items were encoded and stored. Thereby, we were able to identify two different effects: First, in a standard change detection task, changes to a memory item that involved a change in the relative features of memorised items were more readily detected than changes that left the relative features intact. Hence, a *relational detection advantage* was observed, whereby there is enhanced detection sensitivity for relative features. Second, VSTM load, as indexed by the CDA, was reduced when the items were presented in an ordered fashion that reduced the number of (different) relationships between the items. Thus, a *relational CDA effect* was discovered, suggesting that relative colours add to the VSTM load, which is reduced for ordered stimuli.

Importantly, these results were obtained even though participants had no incentive to encode or store colours in a context-dependent manner in VSTM: In both experiments, participants received the standard instructions for change detection tasks, and change trials equiprobably contained a change of the relative colour or no change of the relative colour. These results suggest that encoding and maintenance of relative features occurs automatically, and influences both VSTM capacity and change detection performance.

These results are at odds with some previous work that suggested stimuli are primarily encoded and stored completely independently in VSTM, which is an assumption inferred by both slot models and resource models (Barton, Ester, & Awh, 2009; Bays, 2018; Fougnie & Alvarez, 2011; Wilken & Ma, 2004). The finding that VSTM contains a context-dependent representation of memory items seems especially difficult to reconcile with slot models. However, context-dependent representations are also not considered in current resource models. Hence, the current findings indicate the need to modify existing accounts of VSTM to accurately predict memory performance and VSTM load.

Previous studies already highlighted the possibility that the visual system performs clustering/chunking or grouping operations over memory items (e.g., Brady & Alvarez, 2015), and showed that statistical regularities can play a role in determining encoding or maintenance of VSTM contents (e.g., Brady, Konkle, & Alvarez, 2009). The current study expands on this work by showing that feature relationships can also modulate VSTM. In particular, our Study 2 indicates that VSTM load is composed of both (1) information about exact feature values (colours and positions); and (2) information about relative colours and (relative) positions (e.g., Jiang et al., 2016). The CDA also reflects this combined memory load, as shown by the modulation of CDA amplitude with ordered relative colours vs. out-of-order relative colours.

It is currently unknown how relative colours are encoded or stored in VSTM. However, the finding that Out of Order colours take up more VSTM resources than In Order colours suggests the existence of structured feature spaces across colour and position that are linked by a set of simple transition rules (or similar computations). In the absence of any computations, it would be difficult to explain the higher VSTM load for Out of Order colours. This suggests an account where VSTM is not a merely passive storage system that 'mindlessly' retains visual information about individual visual features (e.g., in individual slots). Instead, it may be more accurate to conceive of VSTM as a mini-processor that is capable of making simple computations over memory items and/or storing the results of these computations over short time periods (whereby the computations are probably mostly parallel rather than purely serial). Another important insight is that the complexity of these computations can modulate the VSTM load, as indexed by the CDA.

Previous studies have already shown that the CDA does not only reflect changes in storage related activity, but also scales with changes in attentional demands and/or demands in control-related processes (e.g., Berggren & Eimer, 2016; Feldmann-Wüstefeld et al., 2018; see also; Emrich, Ruggall, LaRocque, & Postle, 2013). Hence, it is an interesting question whether VSTM indeed performs the computations associated with maintaining information about relative colours, or if these computations are performed at an earlier (e.g., attentional) stage, for instance, when selecting the items. A similar question arises for other, related processes such as ensemble encoding and chunking and feature integration (or binding) and grouping, which can reduce the information load (Brady & Alvarez, 2011; Luria et al., 2010; Miller, 1956; Nie, Müller, & Conci, 2017). As highlighted above, the Relational Account can explain a range of effects that reside in early

visual selection or eye movements (e.g., Becker, 2010; Becker et al., 2014; Martin & Becker, 2018; Meeter & Olivers, 2014), rendering it likely that computations over relative features are performed at the level of selection and simply 'passed on' to VSTM, which actively maintains this information. In line with this explanation, Salahub, Lockhart, Dube, Al-Aidroos, and Emrich (2019) found that VSTM load, as reflected in the CDA amplitude, comprises not only the memory contents but also the amount of resources devoted to the task of remembering the stimuli ('flexible resource allocation'), and other studies found similar CDAs in memory tasks when the stimuli were continuously visible vs invisible during the delay period (e.g., Tsubomi, Fukuda, Watanabe, & Vogel, 2013), indicating that the CDA may index processes performed over representations rather than memory-specific processes. In a similar vein, it is possible that the increase in CDA amplitude with Out of Order stimuli reflects higher resource demands in encoding multiple relations at an early stage of selecting the items and/or performing computations over these representations rather than storing them in the classical sense.[4]

Even if subsequent studies show that the differences in VSTM load or the CDA amplitude are ultimately due to processes that were instigated at an early, attentional stage, the present results still provide important insights into VSTM and the interplay of attention and VSTM. To further elucidate the interplay between attention and VSTM and the time point at which multiple relative features take effect would require further experiments that directly investigate the effects of relative features on the N2pc and CDA.

Previous studies have revealed that relative features play an important role in visual selection and in directing attention to task-relevant items. However, so far the evidence was confined to tasks that require participants to respond to a single, pre-defined target that can be surrounded by multiple irrelevant items (e.g., visual search; spatial cueing; RSVP). As shown in previous eye movement studies and in EEG studies assessing the N2pc (a marker for visual attention; Eimer, 1996; Eimer & Grubert, 2014), attention is not top-down biased to the particular feature of a pre-specified target (e.g., orange), but to the relative colour of the target (e.g., yellower, when the context contains mainly red items; Becker, 2010; Becker et al., 2013; Schoenhammer et al., 2016). The present results extend on these previous findings, by showing that the relative colours of multiple items are also encoded when feature relationships are irrelevant to the task and there is no clearly defined, single target (as in visual selection tasks), and by showing that information about relative features is maintained in memory tasks. These findings confirm previous

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[4] In line with the possibility that the larger CDA amplitude may reflect a higher resource demands at an early stage of encoding the stimuli, the N2pc (an electrophysiological marker of attention; e.g., Eimer, 1996) also already seems larger in the Out of Order conditions than in the In Order conditions. However, assessing the N2pc in the time-window 200–300 ms post stimulus onset revealed no significant N2pc in any of the conditions, and no differences between In Order and Out of Order N2pc difference waves. Significant differences in the predicted direction could only be found in an extended time window (200–340 ms post stimulus onset), which however may already encompass the CDA rather than the N2pc. (Data available upon request.)

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reports that attention and VSTM are closely linked with each other (e.g., Hamblin-Frohman & Becker, 2019; Olivers & Eimer, 2011; Schmidt, et al., 2002), by demonstrating that they both operate on similar principles, despite the large differences in the affordances between these tasks.

Further studies are necessary to clarify how selective attention is involved in VSTM tasks, or whether both are based on the same processes. What seems to be clear from the current study is that previous findings about the role of feature relationships in early visual attention can be extended to VSTM, as they influence both VSTM load/maintenance processes, and sensitivity to detecting changes in standard change detection tasks.

Credit author statement

Aimee Martin: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization.

Stefanie I Becker: Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision.

Open practices

The study in this article earned Open Data and Open Materials badges for transparent practices. Data and materials for this study can be found at: https://osf.io/dx7hf/?view_only=ac20127786214d8d86cc0652ded5ba35.

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