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RESEARCH ARTICLE | *Working Memory: Neural Mechanisms*

Object maintenance beyond their visible parts in working memory

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Chen S, Töllner T, Müller HJ, Conci M. Object maintenance beyond their visible parts in working memory. *J Neurophysiol* 119: 347–355, 2018. First published October 25, 2017; doi:10.1152/jn.00469.2017.—Completion of a partially occluded object requires that a representation of the whole is constructed based on the information provided by the physically specified parts of the stimulus. Such processes of amodal completion rely on the generation and maintenance of a mental image that renders the completed object in visual working memory (VWM). The present study examined this relationship between VWM storage and processes of object completion. We recorded event-related potentials to track VWM maintenance by means of the contralateral delay activity (CDA) during a change detection task in which composite objects (notched shapes abutting an occluding shape) to be memorized were primed to induce either a globally completed object or a noncompleted, mosaic representation. The results revealed an effect of completion in VWM despite physically identical visual input: change detection was more accurate for completed compared with mosaic representations when observers were required to memorize two objects, and these differences were reduced with four memorized items. At the electrophysiological level, globally completed (vs. mosaic) objects gave rise to a corresponding increase in CDA amplitudes. These results indicate that although incorporating the occluded portions of the presented shapes requires mnemonic resources, the complete object representations thus formed in VWM improve change detection performance by providing a more simple, regular shape. Overall, these findings demonstrate that mechanisms of object completion modulate VWM, with the memory load being determined by the structured representations of the memorized stimuli.

NEW & NOTEWORTHY This study shows that completion of partially occluded objects requires visual working memory (VWM) resources. In the experiment reported, we induced observers to memorize a given visual input either as completed or as noncompleted objects. The results revealed both a behavioral performance advantage for completed vs. noncompleted objects despite physically identical input, and an associated modulation of an electrophysiological component that reflects VWM object retention, thus indicating that constructing an integrated object consumes mnemonic resources.

amodal completion; contralateral delay activity; visual working memory

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INTRODUCTION

Amodal completion refers to the phenomenon that occluded parts of an object are perceptually “filled in” (Michotte et al. 1991), that is, missing information is (re)constructed based on the partial physical stimulation available (see Fig. 1, composite, for example stimuli). Representing amodally completed objects has been suggested to rely on mental imagery (Nanay 2010). Although completion is largely dependent on the structural properties of a given stimulus (van Lier et al. 1994), it may additionally be influenced by background information, such as semantic knowledge about a given object or the context within which it is presented, providing further information about what the occluded parts of an object (may) look like (Hazenberg and van Lier 2016; Rauschenberger et al. 2004). Construction of a mental image typically engages visual working memory (VWM) resources (Baddeley and Andrade 2000). On this view, rather than just subserving passive maintenance of visual information for short periods of time, VWM does also involve active processes of generating (hidden) parts of objects in memory. The current study was designed to investigate such active object completion processes in VWM, that is, to elucidate how physically specified parts of a stimulus are combined with completed fragments to generate a coherent, whole object representation.

A common and widely used paradigm for studying VWM is change detection (Luck and Vogel 1997). In this paradigm, participants are asked to remember a set of objects in an initial memory display. After a retention interval, a test display is presented and participants have to indicate whether a change has occurred in one of the objects in the test compared with the memory array. The typical finding is that some three to four objects can be maintained concurrently in VWM (Cowan 2001; Luck and Vogel 1997). However, the number of items that can be stored has also been shown to be influenced by the information load associated with the individual objects to be memorized. For instance, Alvarez and Cavanagh (2004) demonstrated that change detection performance varies as a function of stimulus complexity, with a reduced number of only about one memorized item for more complex objects (e.g., Chinese characters, shaded cubes) compared with four items for more simple objects (e.g., colored squares). Thus VWM is limited in capacity: it can represent only relatively few items, where the overall number of items that can be retained varies for different types of objects.

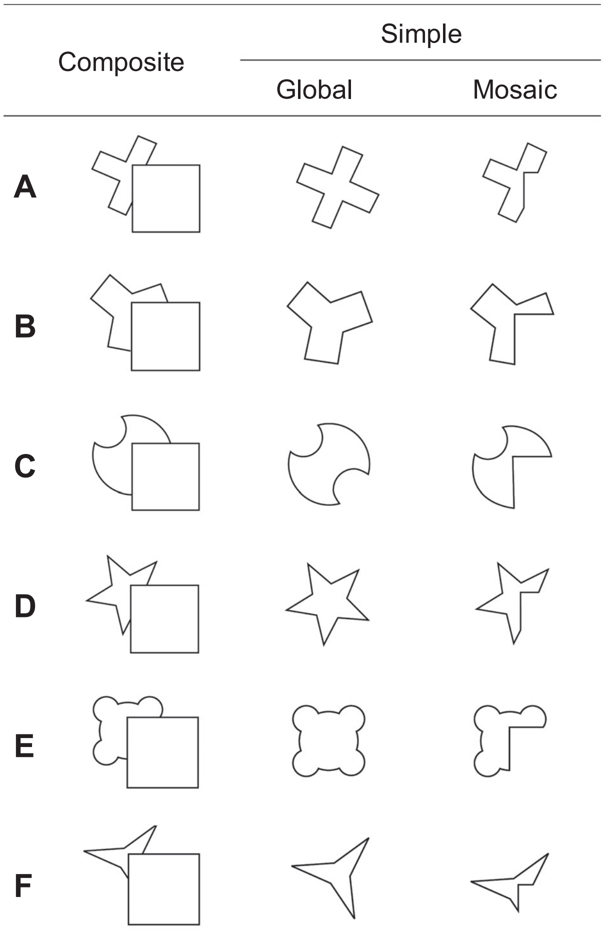

Fig. 1. *A–F*: illustrations of the experimental stimuli with their respective composite and simple versions (global and mosaic interpretations).

Studies that examined participants' electroencephalogram (EEG) in change detection tasks showed that an event-related difference wave manifesting during the delay period (between the memory and test displays) over lateral posterior parietal and occipital electrode sites, referred to as "contralateral delay activity" (CDA), can serve as an online marker of current VWM load: the CDA amplitude increases with the number of items (to be) held in memory, until it reaches an asymptotic limit indicative of an individual's memory capacity (Vogel and Machizawa 2004). Given that the CDA (which is obtained in the delay period) reflects processes of maintenance (independent of later processes involved in the comparison of the memorized items with the test probe; see Awh et al. 2007), it can be used to directly examine how stimuli are represented in VWM. For instance, with relatively few items to be memorized, CDA amplitudes were found to be larger for more complex (random polygons) than for simple objects (colored squares), in line with the view that VWM is modulated by stimulus attributes and the load they place on processes of maintenance (Gao et al. 2009; Luria et al. 2010; Töllner et al. 2013). Moreover, larger CDA amplitudes were observed for identical stimuli when the task required the encoding of objects with high precision (Machizawa et al. 2012). This demonstrates that identical visual input may change the memory load depending on top-down demands (see also Balaban and Luria 2016). Nevertheless, it remains an open issue whether the CDA varies with the extent to which processes of completion modify a given object in VWM.

The question at issue here, namely, the role of object completion in VWM, was recently examined in a behavioral study employing the change detection paradigm (Chen et al. 2016). In that study, we presented memory displays that were physically identical but varied the structural information of the objects' representations in memory by introducing additional, contextual information. The memory displays participants were presented with were essentially comparable to the example displays depicted in Fig. 2 (except that, in Chen et al. 2016, participants were not precued to the task-relevant side of the display by an arrow symbol). A given memory display consisted of either composite objects (i.e., presenting a notched figure adjacent to a square) or simple objects (i.e., comparable shapes but without the adjacent square). Importantly, the simple object could be one of several possible interpretations of the notched figure, with a global, symmetrical shape that provides a completed interpretation of the composite object (Fig. 1, global) or a so-called "mosaic" figure (Fig. 1, mosaic), where mosaic simply refers to a two-dimensional (2-D) cutout outline shape identical to the visible part of the figure (Sekuler and Palmer 1992). Presentation of the memory display was followed by a brief delay, after which a (simple object) test probe appeared. The task was to decide whether this probe was the same as or different from the corresponding item in the memory display. Each block of trials presented only one type of (simple) objects (either global or mosaic figures) to enforce, or "prime," a consistent interpretation of the composite objects within the given block. The results revealed global objects to yield higher change detection accuracy, indicative of an advantage in retaining completed wholes over partial shapes (*Experiment 1* in Chen et al. 2016). This advantage for completed, relative to mosaic, composite objects disappeared when global and mosaic simple object displays were presented randomly intermixed within trial blocks (*Experiment 2* in Chen et al. 2016), indicating that the effect of completion is determined by some top-down set provided by a consistent context of the available simple object interpretations.

Importantly, Chen et al. (2016) compared change detection accuracy for physically identical composite objects that participants were made to interpret as either completed wholes or noncompleted mosaic objects. Consequently, rather than being attributable to an influence of perceptual shape discriminability, the performance advantage for global (relative to mosaic) composite objects obtained by Chen et al. (2016) in *Experiment 1* can only be attributed to the additional completion process, which renders binding of the physical parts of the object with the occluding parts of the surface. If VWM load is indeed modulated by the completion of the memorized objects, this would predict that the alternative representations of the composite object would manifest in a modulation of the CDA amplitude. On this view, the CDA amplitude reflects not only the passive retention of items but also the resource demands associated with processes required for integrating fragments into a coherent, whole object representation. This viewpoint contrasts with a more passive conception of VWM, where the CDA would only be related to the basic storage of individuated items without any concurrent processing of the retained stimulus material.

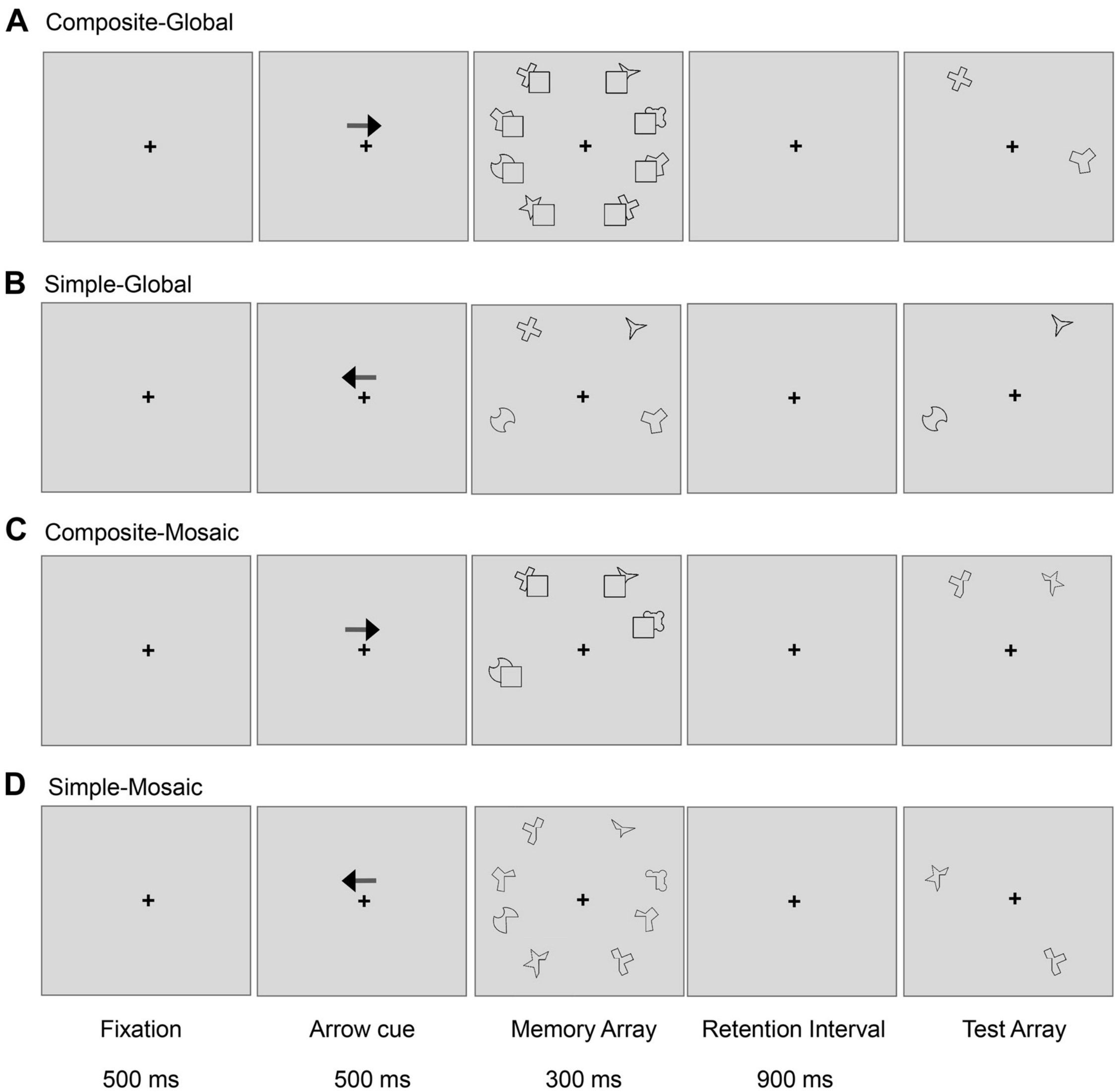

Fig. 2. Trial sequence. Example trial in *A* shows a set size 4, composite-object memory display followed by a test display supporting a global interpretation. Participants were instructed to memorize only the stimuli presented on the side indicated by the arrow before the memory display. The correct response would be "same." Example trial in *B* presents a set size 2, simple-object memory display, with global (i.e., symmetric) shapes (correct response: "same"). Note that the example trials in *A* and *B* were presented in the same block (in randomized order) to coherently support a "global" interpretation of the occluded objects. Example trials in *C* and *D* show a composite- and a simple-object memory display with 2 and 4 objects, respectively. Displays as depicted in *C* and *D* engender a "mosaic" interpretation and were also presented within the same block (correct responses: "different").

The present study was designed to decide between these two alternative views and to extend our previous, purely behavioral findings regarding the relationship between VWM storage and the completion of objects (Chen et al. 2016). To this end, we combined behavioral measures with analysis of the CDA as an electrophysiological marker of VWM load. Event-related potentials (ERPs) were recorded from young adults while they performed a change detection task. On each trial (Fig. 2), observers were first presented with an arrow cue indicating the relevant, to-be-memorized half of the display. Next, a brief bilateral array presented composite or simple objects (either global or mosaic shape interpretations; see Fig. 1) for 300 ms. The (300 ms) presentation time of the memory display was set in accordance with previous studies (Chen et al. 2016; Gerbino and Salmaso 1987; Rauschenberger et al. 2004; Sekuler and Palmer 1992), which showed that completion only occurs when a given partially occluded stimulus is presented for at least 100–200 ms. Moreover, we provided a consistent context of simple object trials within a given block so as to effectively enforce a given interpretation of the partially occluded objects (Chen et al. 2016; Rauschenberger et al. 2004). The participants' task was to remember the items in the cued hemifield and indicate, after a brief delay, whether a subsequently presented test display did or did not contain a changed object. If completion modulates VWM load, the identical composite objects should yield a difference in performance for globally completed vs. mosaic interpretations.

METHOD

Participants

Seventeen right-handed volunteers (8 men), with normal or corrected-to-normal vision (mean 24.22 yr, SD 2.90 yr), took part in this study for payment of €8.00 per hour. All participants provided written informed consent. The experimental procedures were approved by the local ethics committee (Department of Psychology, Ludwig-Maximilians-Universität München). Sample size was determined on the basis of previous, comparable studies (e.g., Luria et al. 2010), aiming for 85% power to detect an effect size of 0.8 with an alpha level of 0.05.

Apparatus and Stimuli

Stimuli were black line drawings (0.2 cd/m^2) presented against a light gray background (178 cd/m^2) on a 19-in. computer monitor (1,024 × 768 pixel screen resolution, 85-Hz refresh rate). The stimulus set was based on six different shapes (adapted from Plomp and van Leeuwen 2006; Sekuler et al. 1994; van Lier et al. 1995; see Fig. 1). The composite figure included a square with a second shape positioned partly occluded next to the square (Fig. 1, composite). The simple figure was presented in two possible alternative interpretations of the composite object: global and mosaic (Fig. 1, simple global, simple mosaic). Global figures presented a globally completed, symmetrical shape, whereas a mosaic figure simply presented a 2-D cutout outline shape identical to the visible part of the partly occluded figure. At a viewing distance of 60 cm, each simple figure touched a circular region with a radius of 0.6° of visual angle. The square of the occluded objects subtended 1.1° × 1.1°. For each memory display, 4 or 8 distinct objects of the same completion type were presented randomly at 10 positions within a circular region with a radius of 5.0°, with 2 or 4 objects in each hemifield. A given shape could appear only twice at most in the same display. The test probe was identical to the item in the same position of the memory display in half the trials and different in the other half. It should be noted that "same" or "different" in this experiment refers to object identity, rather than to the completion type. For example, the occluded cross in Fig. 1*A* (composite) would be considered the same object as the other two variants of simple objects presenting a cross-shaped item (Fig. 1*A*, simple).

Procedure and Design

Each trial started with the presentation of a central fixation cross for 500 ms, followed by an arrow cue pointing to either the left or the right for 500 ms. Next, participants were presented with a memory display of either simple or composite objects for 300 ms. Following a blank screen of 900 ms, the test display was presented until a response was issued. Participants were instructed to memorize the stimuli presented in the hemifield indicated by the arrow cue and respond with left and right mouse keys to indicate whether the test probe in the cued hemifield was the same as or different from the corresponding item in the memory display. Left/right responses were counterbalanced across observers to control for stimulus-response compatibility effects. Observers were asked to respond as accurately as possible, without stress on response speed. Trials were separated from each other by a random interval between 300 and 400 ms. Figure 2 illustrates typical examples of a trial sequence.

There were eight experimental blocks, with 160 trials each. Each block presented only one type of possible interpretation (global or mosaic) to consistently enforce the respective interpretation of the composite objects within a given experimental block (Chen et al. 2016). The eight blocks were presented in random order. Within each block, the different configurations (simple, composite) and change/no-change trials were presented in randomized order across trials. All participants performed 8 practice blocks of 40 trials each on the day before the experiment, to become familiar with the task.

EEG Recording and Data Analysis

The EEG was continuously recorded using 64 Ag-AgCl active electrodes (Brain Products, Munich, Germany) according to the international 10-10 system with a sampling rate of 1,000 Hz. Vertical and horizontal eye movements were monitored with electrodes placed at the outer canthi of the eyes and, respectively, the superior and inferior orbits. The electrode signals were amplified using BrainAmp amplifiers (Brain Products) with a 0.1- to 250-Hz bandpass filter. All electrode impedances were kept below 5 kΩ. During data acquisition, all electrodes were referenced to FCz, and re-referenced offline to averaged mastoids. Before the EEG was segmented, the raw data were visually inspected to manually remove nonstereotypical noise. Next, an infomax-independent component analysis was run to identify components representing blinks and horizontal eye movements, and to remove these artifacts before backprojection of the residual components. Subsequently, the data were bandpass filtered using a 0.1- to 40-Hz Butterworth infinite impulse response filter (24 dB/octave). Signals were then averaged offline over a 1,200-ms epoch relative to a 200-ms prestimulus (memory display) baseline. Trials with artifacts, defined as any signal exceeding ±60 μV, bursts of electromyographic activity (as defined by voltage steps/sampling point larger than 50 μV), and activity lower than 0.5 μV within intervals of 500 ms (indicating bad channels), were excluded from averaging. The contralateral delay activity (CDA) was measured at parieto-occipital electrodes (PO7/8) as the difference in mean amplitude between the ipsilateral and contralateral waveforms relative to the memorized display, with a measurement window of 500–1,200 ms after the onset of the memory display. Trials with incorrect behavioral responses were discarded from the ERP analyses.

Differences in behavioral accuracy and neural measures (CDA amplitudes) were examined for composite objects by performing two-way repeated-measures analyses of variance (ANOVAs) with the factors set size (2, 4) and interpretation (global, mosaic). Note that the focus of the analysis on the maintenance of identical composite objects with varying interpretations (global vs. mosaic) controls for the influence of differential (perceptual) feature discriminability between the memory displays. Thus any difference in the CDA components between global and mosaic representations can only be due to their differential maintenance demands, rather than to perceptual dissimilarity or memory-test comparisons. In addition to this main analysis of composite objects, we performed analogous analyses for simple objects.

RESULTS

Composite Objects

Behavioral data. Figure 3*A* depicts the mean percentage of correct responses for composite objects, as a function of set size, separately for the different interpretations. A repeated-measures ANOVA on the accuracy data was performed with the factors set size and interpretation, yielding main effects of set size [$F(1, 16) = 767.07$, $P < 0.0001$, $\eta_p^2 = 0.980$] and interpretation [$F(1, 16) = 39.06$, $P < 0.0001$, $\eta_p^2 = 0.709$]. Accuracy was higher for set size 2 (84%) than for set size 4 (67%), and higher for global (77%) than for mosaic interpretations (74%). The interaction between set size and interpretation was also significant [$F(1, 16) = 11.62$, $P = 0.004$, $\eta_p^2 = 0.421$]: a significant difference between global (86%) and mosaic interpretations (81%) manifested with set size 2 [$t(16) = 6.66$, $P < 0.0001$], whereas this difference was reduced for set size 4 [global: 68%; mosaic: 67%, $t(16) = 1.88$, $P = 0.078$]. Replicating our previous findings (Chen et al. 2016), this reduction in performance can be attributed to the reduced scanning time available per object with an increased set size. As a result, not all objects are effectively completed for the larger, four-item display. With larger memory arrays, there would then also be a higher chance of guessing, because attention is less likely focused on the object that is tested later on, so that this item might not have been

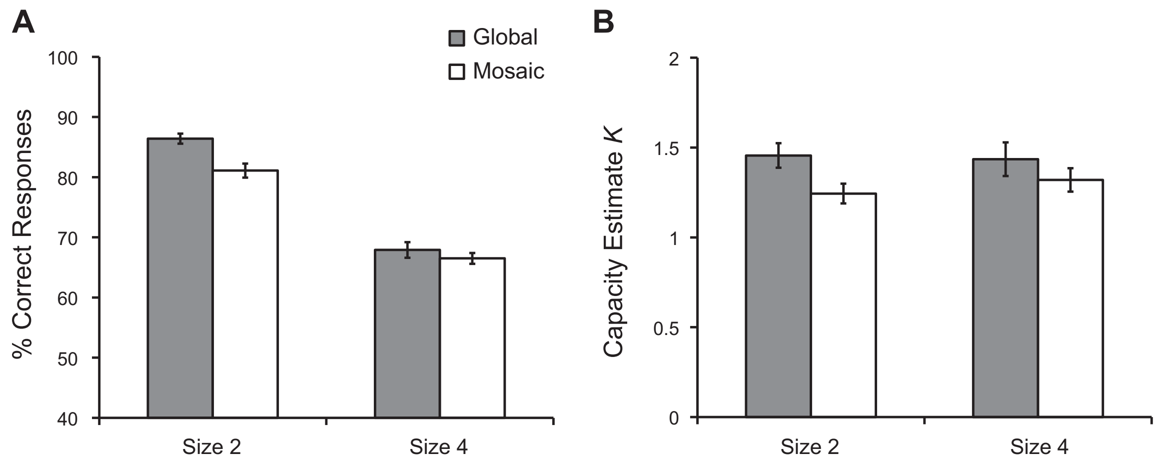

Fig. 3. Mean percentage of correct responses (*A*) and capacity estimate *K* (*B*) as a function of memory set size are shown for the different interpretations (global, mosaic) of the composite objects. Error bars indicate 95% (within-participant) confidence intervals.

encoded with sufficient detail. Moreover, accuracy might also be compromised by errors arising from the comparison of an item held in memory with the test probe presented (Awh et al. 2007), and these comparison errors might also increase with set size.

In a next step, we computed Cowan's *K* (Cowan 2001), an estimate of visual memory capacity, which allows correcting for errors that result from memory storage failures. Note, however, that *K* does not take care of errors arising from the comparison process, which is why *K* might somewhat underestimate the number of items stored (although this underestimation should be comparable for global and mosaic interpretations). Essentially, this correction assumes that if an observer can hold *K* items in memory from an array of *S* items, the item that changed should be one of the items being held in memory on *K*/*S* trials, resulting in correct performance on *K*/*S* of the trials on which an item changed. *K* is computed according to the formula:(proportion hits $-$ proportion false alarms) $\times$ set size, where the perceptual sensitivity (the difference between hits and false alarms) is multiplied by set size to take into account the number of items to be memorized. The capacity *K* estimated in this way revealed that effectively only one to two composite objects could be remembered (see Fig. 3*B*). A repeated-measures ANOVA of the *K* estimates yielded a main effect of interpretation [$F(1, 16) = 23.36$, $P < 0.0001$, $\eta_p^2 = 0.593$]: significantly more items were maintained with global ($K = 1.45$) compared with mosaic ($K = 1.28$) representations. No other significant effects were obtained (all $P > 0.25$).

ERP data. The corresponding ERP waves for composite objects are plotted in Fig. 4*A*. An ANOVA on the mean CDA amplitudes with the factors set size and interpretation revealed a main effect of interpretation [$F(1, 16) = 6.12$, $P = 0.025$, $\eta_p^2 = 0.277$]. As depicted in Fig. 4*B*, the mean CDA amplitude was larger for the global (-1.22 μV) compared with the mosaic interpretation (-0.88 μV). No other significant effects were obtained (all $P > 0.25$). This finding mirrors the pattern of the capacity estimate *K* (Fig. 3*B*), demonstrating an effect of interpretation on the amplitude of the CDA.

The individual differences in the CDA amplitude between global and mosaic interpretations also correlated with the corresponding differences in accuracy [with values averaged across set sizes: $r = -0.66$, 95% CI (-0.84, -0.42), $P = 0.004$; Fig. 4*C*]. The statistical significance of the correlation coefficient was determined by comparing the observed correlations with results derived from 10,000 permutations of the two variables (i.e., the difference in accuracy and the difference in the CDA amplitude between global and mosaic interpretations). This ensures that the significant correlation is not attributable to any outliers in the data.

Simple Objects

Behavioral data. Figure 5 displays the mean percentage of correct responses (Fig. 5*A*) and the corresponding capacity estimates *K* (Fig. 5*B*) for simple objects as a function of set size, separately for the different interpretations. A repeated-measures ANOVA on the accuracy data with the factor set size and interpretation yielded main effects of set size [$F(1, 16) = 479.30$, $P < 0.0001$, $\eta_p^2 = 0.968$] and interpretation [$F(1, 16) = 42.34$, $P < 0.0001$, $\eta_p^2 = 0.726$]. Accuracy was higher for set size 2 (88%) than for set size 4 (70%) and higher for global (82%) than for mosaic interpretations (77%). The interaction was nonsignificant ($P > 0.25$). Moreover, calculation of the capacity estimates *K* (as in the analysis above) again revealed that only one to two simple objects could be remembered (see Fig. 5*B*). A repeated-measures ANOVA on the *K* estimates revealed a main effect of interpretation [$F(1, 16) = 26.71$, $P < 0.0001$, $\eta_p^2 = 0.625$] with higher capacity for global ($K = 1.73$) than for mosaic interpretations ($K = 1.43$). No other significant effects were obtained (all $P > 0.25$).

ERP data. The corresponding ERP waves for the simple objects in the global and mosaic conditions are plotted in Fig. 6. An ANOVA on the mean amplitudes of the CDA with the factors set size and interpretation revealed a main effect of interpretation [$F(1, 16) = 4.77$, $P = 0.044$, $\eta_p^2 = 0.230$]: of note, the mean CDA amplitude was larger for the mosaic shapes (-1.24 μV) than for the global shapes (-1.00 μV); recall that the reverse pattern was found with composite objects. No other significant effects were obtained [set size: $F(1, 16) = 1.67$, $P = 0.21$, $\eta_p^2 = 0.095$; interaction: $F(1, 16) = 1.25$, $P = 0.28$, $\eta_p^2 = 0.073$].

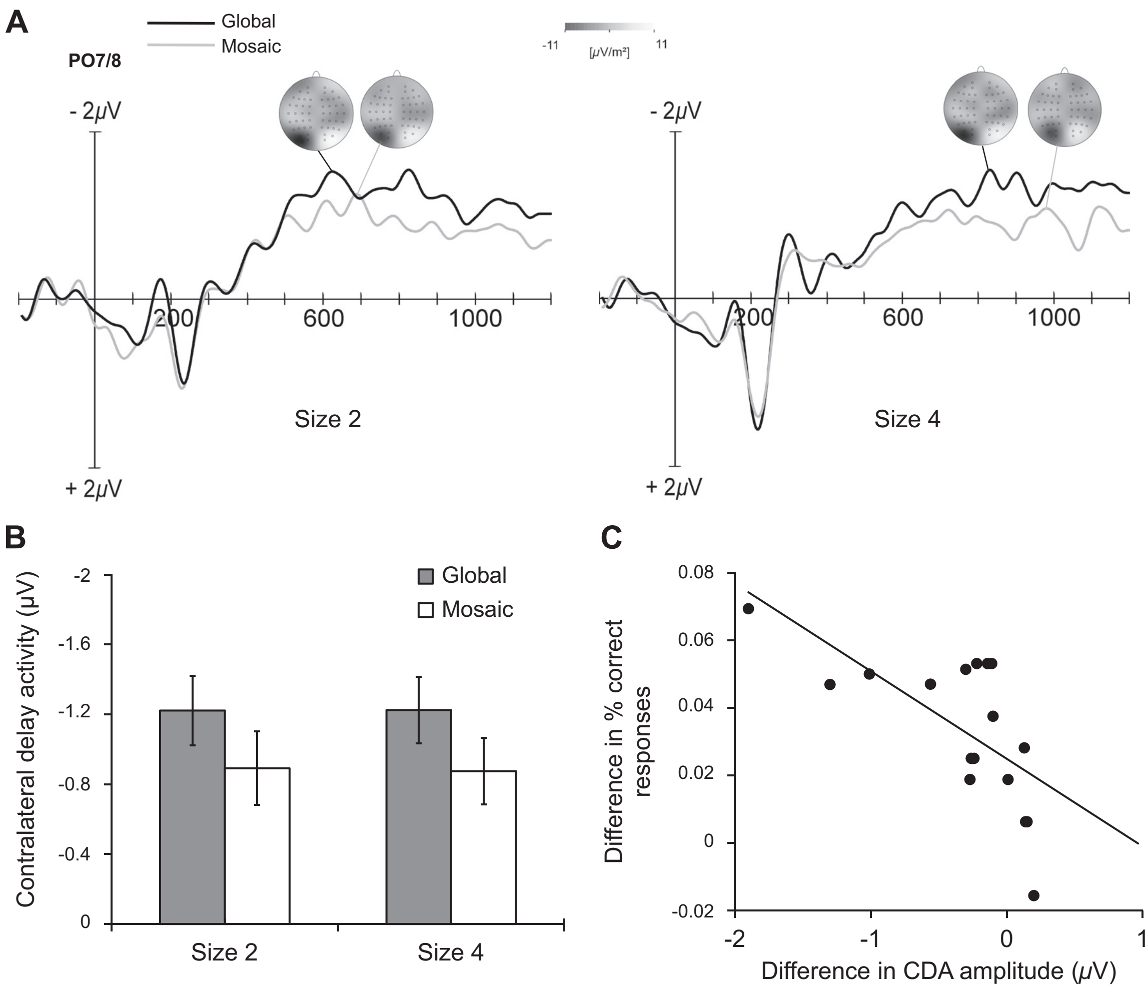

Fig. 4. ERP results for composite objects. *A*: grand-average ERP waveforms (contralateral minus ipsilateral activity relative to the memorized display hemifield) time-locked to the onset of the memory display at electrodes PO7/8 in the composite-object condition for set size 2 (*left*) and set size 4 (*right*). Scalp distribution maps depict the point in time at which the respective difference waves reached their maximum. For illustration purposes, the grand-average waveforms shown were low-pass filtered at 12 Hz (24 dB/octave). *B*: mean CDA amplitudes in the time window of 500–1,200 ms after the onset of the memory display at electrodes PO7/8 as a function of memory set size, shown separately for the different interpretations (global, mosaic). Error bars indicate 95% (within-participant) confidence intervals. *C*: correlation between the difference in CDA amplitudes and the corresponding difference in accuracy between global and mosaic interpretations (averaged across set sizes).

DISCUSSION

The present results show that VWM load is directly influenced by processes of object completion given identical physical input. For the composite objects, the behavioral result pattern replicates previous findings (Chen et al. 2016): there was an advantage in representing globally completed over (uncompleted) mosaic interpretations in VWM, where this advantage for completed shapes decreased with an increase in the number of items that were to be memorized. An advantage for global over mosaic interpretations was also evident in the behavioral estimate of memory capacity *K*, which showed that, with the current stimulus material, a maximum of one to two objects could be successfully retained in VWM. The ERP analyses revealed larger CDA amplitudes for completed vs. mosaic representations, for both set sizes, thus mirroring the effect pattern of the *K* estimate. Moreover, the differences in CDA amplitude and behavioral accuracy between completed and mosaic representations were significantly correlated. To our knowledge, these findings provide the first demonstration that VWM load, as measured by the CDA wave, is determined by processes of object completion.

The pattern for simple objects also closely replicated our previous findings (Chen et al. 2016): more regular, symmetric, global shapes led to higher performance than more irregular and complex mosaic objects. The corresponding CDA analysis for simple objects revealed a larger amplitude for more complex mosaic shapes than for simpler global shapes, thus contrasting with the pattern observed for composite objects (for which the CDA was larger for global than for mosaic objects).

Our simple object results may be directly compared with previous, related studies that examined how object complexity modulates VWM and the CDA amplitude. For instance, reduced behavioral performance and increased CDA amplitudes were found in a change detection task for rather complex polygon shapes compared with simpler, colored squares (Alvarez and Cavanagh 2004; Gao et al. 2009; Luria et al. 2010), indicative of an increase in perceptual complexity giving rise to increasing VWM demands. That a comparable pattern of results was also found in the present experiment when global

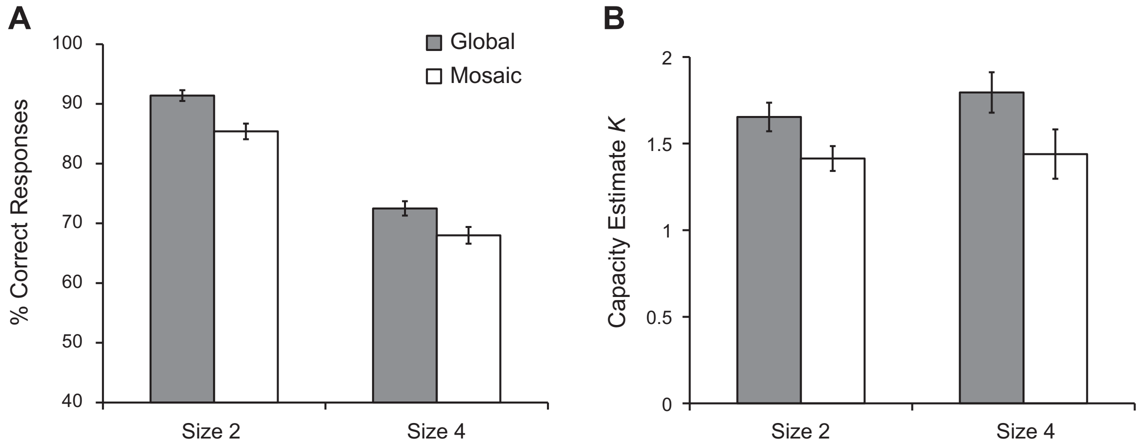

Fig. 5. Mean percentage of correct responses (*A*) and capacity estimate *K* (*B*) as a function of memory set size are shown for the different interpretations (global, mosaic) of the simple objects. Error bars denote 95% (within-participant) confidence intervals.

and mosaic variants of the simple (nonoccluded) objects were compared confirms that VWM maintenance demands depend on stimulus complexity: less complex global, symmetric objects engender a lower VWM load along with a reduced CDA amplitude compared with more irregular, rather complex mosaic shapes.

Over and above these established effects of perceptual complexity in VWM, our results for composite objects demonstrate a novel link between object completion and memory load. In particular, our findings show that identical perceptual input may lead to differences in the way an object is completed, depending on the prevailing simple object context. This suggests that observers effectively use past perceptual experience, including long-term familiarity as well as short-term priming, to construct a perceptual representation that, in the global interpretation, incorporates the occluded portions of a given object (Chen et al. 2016).

Evidence for such context-dependent object completions was found in both behavioral performance and the CDA amplitude. Completion of the occluded part of an object to represent a whole renders a more elaborate but at the same time less complex memory representation. Specifically, for global objects, completion resulted in a more regular and symmetric representation, with these simpler shapes in turn yielding an improved performance accuracy compared with uncompleted but more complex shapes in mosaic-type representations (see also van der Helm 2014). At the neural level, we observed a sustained increase of the CDA amplitude for globally completed objects. Although this is in line with the proposal that more elaborate processing, involving mnemonic resources, is required to create complete-object representations from physically specified fragments (Biederman 1987), it also suggests that persistent mnemonic activity is required to maintain the resulting representations in a readily accessible form (see also Ewerdwalbesloh et al. 2016; Pun et al. 2012). Convergent evidence for this proposal is provided by studies that used a shape-from-motion paradigm (Emrich et al. 2008; Pun et al. 2012). Here, too, the CDA exhibited a sustained increase in amplitude in a task that required an (integrated) object to be extracted and maintained from fragmentary perceptual information. Thus, on this view, the occluded objects engage some additional, completion-related process while being actively maintained in VWM, which is reflected in its increased CDA compared with that for the noncompleted mosaic representations. Completion, in turn, renders a rather simple object representation, supporting an improvement in performance relative to the more complex mosaic representation. [Of course, completion might, in principle, also generate a relatively complex, nonsymmetrical shape (e.g., some form of local shape completion; see Chen et al. 2016), which does not translate into a comparable performance advantage as for the globally completed, symmetric shape.]

In sum, we interpret the observed increase in CDA amplitudes for the global interpretation to reflect the increased demand associated with the imagery process for completing the occluded object parts to represent the whole object, whereas the observed increase in accuracy for the completed objects derives from the simple and symmetric object representation rendered by this process. This is also reflected in the significant correlation between the completion effect in the CDA amplitude and behavioral accuracy, that is, the advantage for representing completed interpretations in VWM comes at a cost in terms of the mnemonic resources required.

Previous studies have shown that the CDA amplitude increases systematically with the number of objects stored in VWM, up to the maximum load (see for review Luria et al. 2016; Vogel and Machizawa 2004). Our results show that the capacity limit in the current experiment is at ~1.5 items, as indicated by the estimates of *K*. Comparable capacity estimates were reported previously for other geometric objects (e.g., Alvarez and Cavanagh 2004). Owing to this relatively low capacity, at set size 4, the number of items to be remembered exceeds the maximum load by more than half, as a result of which only a subset of up to two items is encoded. This is reflected in the CDA being comparable between the two set sizes, that is, the available resources were already maximally invested with two-item memory displays so that no further resources could be mustered when the number of objects to be remembered was increased to four (see also Gao et al. 2009; Luria et al. 2010).

As concerns the limits on the storage capacity of working memory, one view proposes that VWM consists of a pool of resources that can be allocated flexibly to provide either a small number of high-quality representations or a larger number of low-quality representations (Bays and Husain 2008); by contrast, others have suggested that the number of items that can

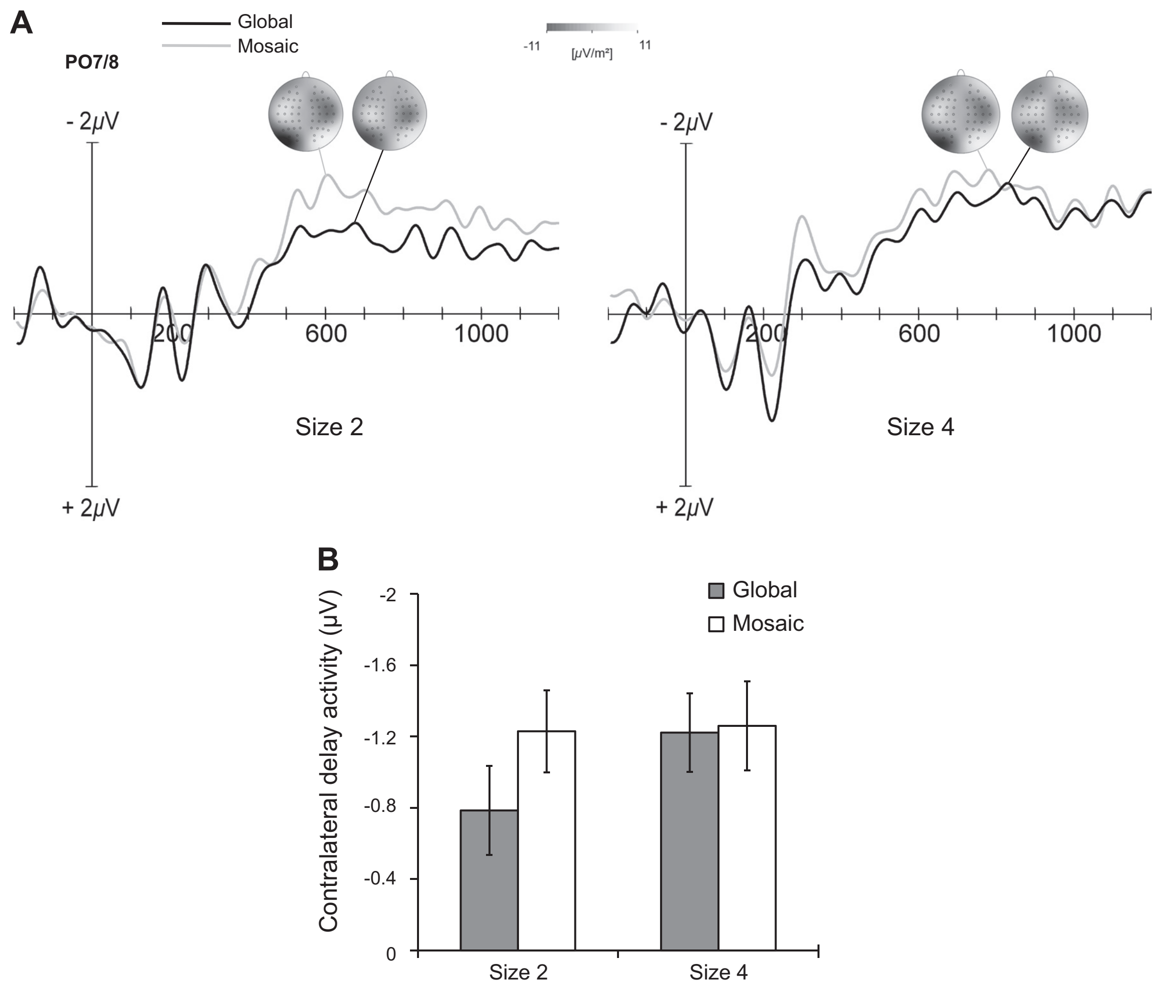

Fig. 6. ERP results for simple objects. *A*: grand-average ERP waveforms (contralateral minus ipsilateral activity relative to the memorized display hemifield) time-locked to the onset of the memory display at electrodes PO7/8 in the simple object condition for set size 2 (*left*) and set size 4 (*right*). Scalp distribution maps depict the point in time at which the respective difference waves reached their maximum. For illustration purposes, the grand-average waveforms shown were low-pass filtered at 12 Hz (24 dB/octave). *B*: mean CDA amplitudes in the time window of 500–1,200 ms after the onset of the memory display at electrodes PO7/8 as a function of memory set size, shown separately for the different interpretations (global, mosaic). Error bars indicate 95% (within-participant) confidence intervals.

be stored in VWM is limited and cannot change (Luck and Vogel 1997; Zhang and Luck 2008). In the present study, we found no evidence that observers could increase the number of representations by decreasing the quality of the representations in VWM. Instead, we show that, when presented with more objects than the maximum capacity, observers can still store high-quality representations of a subset of the objects without retaining any information about the others. However, within the limited number of items that can be retained, a variable resource is available to represent the objects to be memorized (Nie et al. 2017; Zhang and Luck 2008).

In summary, the present study shows that the construction of an integrated object requires VWM resources that depend on structural information of the (to be) represented objects: constructing a completed representation from the physically specified parts of the stimulus involves additional mnemonic demands relative to (in terms of information content) uncompleted, mosaic representations. This argues that object representations in VWM are modulated by completion processes, in turn suggesting that the CDA does not only, or simply, reflect the passive retention of items in memory, but also some additional, active processes, or the resource demands associated with these processes, that support the integration of fragmentary parts into wholes. Thus representing integrated wholes requires mnemonic resources, but with the constructed representations rendering simple and regular shapes, thus enhancing change detection performance.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.C., T.T., H.J.M., and M.C. conceived and designed research; S.C. performed experiments; S.C., T.T., and M.C. analyzed data; S.C., T.T., H.J.M., and M.C. interpreted results of experiments; S.C. prepared figures; S.C. drafted manuscript; S.C., T.T., H.J.M., and M.C. edited and revised manuscript; S.C., T.T., H.J.M., and M.C. approved final version of manuscript.

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