



Cognitive Neuroscience

Current Debates, Research & Reports

ISSN: 1758-8928 (Print) 1758-8936 (Online) Journal homepage: <https://www.tandfonline.com/loi/pcns20>

Task goals modulate the activation of part-based versus object-based representations in visual working memory

Cody W. McCants, Tobias Katus & Martin Eimer

To cite this article: Cody W. McCants, Tobias Katus & Martin Eimer (2020) Task goals modulate the activation of part-based versus object-based representations in visual working memory, Cognitive Neuroscience, 11:1-2, 92-100, DOI: [10.1080/17588928.2019.1642864](https://doi.org/10.1080/17588928.2019.1642864)

To link to this article: <https://doi.org/10.1080/17588928.2019.1642864>



Published online: 17 Jul 2019.



Submit your article to this journal [↗](#)



Article views: 62



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)



Task goals modulate the activation of part-based versus object-based representations in visual working memory

Cody W. McCants, Tobias Katus and Martin Eimer

Department of Psychological Sciences, Birkbeck, University of London, London, UK

ABSTRACT

Representations of visual objects in working memory (WM) can be part-based or object-based, and we investigated whether this is determined by top-down control processes. Lateralised change detection tasks were employed where sample objects on one task-relevant side had to be memorized. Contralateral delay activity (CDA) components were measured during the retention period as electrophysiological markers of WM maintenance processes. In two critical task conditions, sample displays contained objects composed of two vertically aligned shapes. In the Parts task, test displays contained a single shape that had to be matched with either of the two sample shapes, encouraging the storage of part-based WM representations. In the Whole task, compound-shape objects shown at test had to be matched with memorized compound objects, which should facilitate the formation of object-based integrated WM representations. CDA amplitudes were significantly larger in the Parts task than in the Whole task, indicative of differences in effective WM load. This suggests that the two individual shapes were represented separately in the Parts task, whereas a single compound object was maintained in the Whole task. These results provide new evidence that changes in task goals can result in qualitative differences in the way that identical visual stimuli are represented in WM.

ARTICLE HISTORY

Received 24 January 2019
Revised 26 June 2019
Published online 16 July 2019

KEYWORDS

Working memory; top-down control; event-related brain potentials; part-based representations; object-based representations

Introduction

Working memory (WM) is responsible for the active short-term maintenance of information about sensory objects and events that are no longer perceptually available, but need to be kept accessible to other ongoing cognitive activities (e.g., Baddeley, 2012). One central question for WM research concerns the nature of the representations that are held in WM. It is often assumed that visual WM contains images of memorized visual objects that are very similar to on-line perceptual representations generated during the sensory processing of these objects. Such a view is consistent with recent sensory recruitment accounts of WM (e.g., Postle, 2006), which postulate that WM storage is primarily implemented by the modality-specific sensory brain areas that are also involved in the on-line perceptual analysis of incoming information (see also Emrich, Riggall, LaRocque, & Postle, 2013; Ranganath, Cohen, Dam, & D'Esposito, 2004). Real-world visual objects typically have different features (e.g., a specific form, shape, size, orientation, and colour) and are also frequently composed of multiple component parts. If such objects are stored in WM in a strictly pictorial (analog) format as visual images, all features and parts of these objects will be encoded into WM, regardless of whether they are currently task-relevant or not. Furthermore, these attributes will be

represented in an integrated fashion, and not as separate features. Alternatively, WM may store only those aspects of visual objects that are required for the adaptive control of behaviour, by excluding other attributes that are currently irrelevant. Such task-relevant features could then either be stored as separate part-based or as integrated representations.

The question whether memorized visual objects are represented in WM in an integrated fashion or whether WM storage can be feature-selective remains controversial (see Luck & Vogel, 1997; Wheeler & Treisman, 2002; Olson & Jiang, 2002; Delvenne & Bruyer, 2004; Woodman & Vogel, 2008, for a range of different opinions). As behavioural evidence is inconclusive, additional insights may be obtained with on-line electrophysiological markers of visual WM storage. During the delay period of lateralized WM tasks where visual sample objects on one side have to be memorized in order to be compared to subsequent test stimuli, an enhanced negativity is elicited at posterior electrodes contralateral to the to-be-remembered display side (e.g., McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). This contralateral delay activity (CDA) starts around 300 ms after the onset of the memory sample display, persists throughout the

retention interval, increases in amplitude when memory load was increased, and is sensitive to individual differences in WM capacity. These findings suggest that the CDA reflects the maintenance of task-relevant objects in visual WM, and tracks the number of objects that are currently stored.

Initial CDA evidence suggesting that the storage of visual objects in WM is sensitive to the task-relevance of specific features of these objects was reported by Woodman and Vogel (2008), who measured CDA components to memory sample displays containing oriented coloured rectangles. Observers had to memorize either the colour, the orientation, or colour/orientation conjunctions for two or four objects. As expected, larger CDAs were elicited when four rather than two objects had to be memorized. Critically, and independently of WM load, CDAs were reliably smaller in the colour-only task relative to the orientation-only and conjunction tasks, in spite of the fact that the sample displays were identical in all three tasks (see also Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010, for similar observations). These observations indicate that not all features of memorized visual objects are always encoded in an obligatory fashion into WM. They suggest instead that specific object features can be selectively prioritized, and that other currently irrelevant features of the same object may not be stored at all.

This apparent feature-selectivity of WM representations may not be the only aspect in which the storage of visual information in WM can be modulated by top-down control processes that implement current task intentions. Visual objects often contain multiple dissociable parts, and object recognition is assumed to be based on the rapid analysis of these parts and their spatial arrangements (e.g., Biederman, 1987). At different levels of processing, these objects can be represented either in terms of their component parts, or in an integrated holistic fashion. Neuropsychological cases of integrative agnosia where patients retain their ability to identify object parts but fail to recognize the spatial arrangement of such parts (e.g., Behrmann, Peterson, Moscovitch, & Suzuki, 2006; Riddoch et al., 2008) demonstrate the existence of independent part-based and configural/object-based recognition mechanisms that can be selectively impaired (see also Poljac, de-Wit, & Wagemans, 2012).

The part-based versus holistic nature of visual object representations has been widely discussed in the object perception and recognition literature (most prominently in the context of face processing; e.g., Maurer, Le Grand, & Mondloch, 2002), and also more recently for visual WM (e.g., Vergauwe & Cowan, 2015). Part-based and object-based WM representations may also be dissociated on the basis of CDA components measured during WM maintenance. This was first shown by Balaban and Luria (2016),

who measured CDAs while observers memorized colour-colour conjunction objects. Systematic CDA amplitude differences to physically identical objects were found in different task contexts that facilitated object integration of feature individuation, respectively. This suggests that visual objects can be represented flexibly either in a part-based or in an integrated object-based fashion, depending on current task demands. The goal of the current study was to provide further electrophysiological evidence for the impact of currently active task goals on the format of visual WM representations. Here, visual sample objects were composed of dissociable component shapes, and had to be memorized in tasks that encouraged observers to represent these objects either in a part-based or in an integrated fashion.

We employed lateralised change detection tasks where observers had to memorize sample objects on one task-relevant side (left or right) and match them with subsequent test objects that were presented at fixation. Sample and test displays were separated by a delay period of 850 ms, and match and mismatch trials were equally likely. The task-relevant side of the memory sample display (left versus right) was changed between successive blocks. In different task conditions, memory sample displays contained either simple shapes or compound-shape objects that were composed of two spatially aligned shape parts (see Figure 1). We assessed the maintenance of task-relevant sample objects in WM by measuring CDA components during the delay period between sample and test displays in four different blocked task conditions. The two critical conditions were the Whole and Parts tasks. In these two tasks, the memory sample displays were identical, and contained objects composed of two vertically aligned compound shapes on either side (see Figure 1). To facilitate the activation of part-based WM representations of these compound-shape sample objects in the Parts task, and of integrated object-based WM representations in the Whole task, different test displays and task instructions were used in these two tasks. In the Whole task, test displays contained a single compound-shape object at fixation, and participants had to report on each trial whether this object was exactly identical to the memorized sample object. On half of all mismatch trials, the test object was composed of one matching and one mismatching shape. On the other half, both shapes matched the memorized sample shapes, but appeared in the reverse spatial configuration (e.g., circle-above-hourglass when hourglass-above circle was the memorized sample object). Because activating part-based WM representations of sample objects would not enable participants to distinguish fully matching from inverted mismatching test objects, the inclusion of these objects should encourage participants to generate integrated object-based WM representations in the Whole

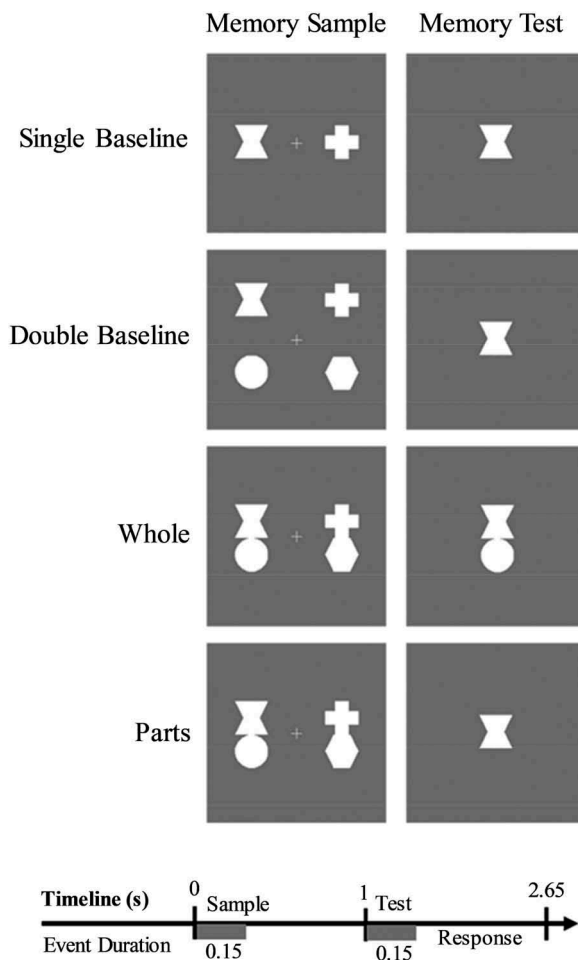


Figure 1. Example memory sample and test displays shown in the four different task conditions. These examples show sample-test match trials where the stimuli on the left side of the sample displays were task-relevant. In the Single and Double baseline tasks, participants memorized one or two simple shapes on the task-relevant side, and reported whether a memorized shape was repeated in the test display. In the Whole and Parts tasks, compound-shape objects on the relevant side had to be memorized, and memory was tested either for the whole object or for an individual shape part. The bottom panel shows the time course of events in individual trials.

task. This task was contrasted with the Parts task, where test displays contained a single basic shape at fixation. On match trials, this shape was identical to one of the two shapes of the memorized sample display object. On mismatch trials, the test shape matched neither of the two relevant sample shapes. In this task, participants were expected to activate separate WM representations of the two component shapes on the task-relevant side of the sample displays, as either shape was equally likely to reappear in the subsequent test display. They had no incentive to form object-based WM representations that integrated across these two shapes, because employing such

an encoding strategy might actually make it harder to detect matches between individual sample and test shapes.

To find out whether the different demands imposed by the Parts versus Whole tasks determined whether visual objects are represented in a part-based versus integrated fashion in WM, we recorded and compared CDA components during WM maintenance in these two tasks. If compound-shape sample objects are always stored in an analogue image-based format, independent of task demands, CDA components should not differ between both tasks, as the sample display objects were physically identical. If task sets affect the way in which WM representations of these objects are formed, CDA amplitude differences between these two tasks should be found. More specifically, if sample objects are represented in an integrated fashion (as a single compound shape) in the Whole task, and as two separate basic shapes in the Parts task, these two tasks would differ with respect to their effective WM load (one object in the Whole task; two object in the Parts task). Because the CDA is sensitive to WM load, with CDA amplitudes increasing as the number of memorized objects increases (e.g., Vogel & Machizawa, 2004), CDA components should be reliably larger in the Parts as compared to the Whole task.

To confirm that the CDA was sensitive to WM load in the current experimental context, and to compare the effect of a direct manipulation of the number of memorized objects on CDA amplitudes with any CDA amplitude differences between the Parts and Whole tasks, we included two additional baseline tasks. In the Single baseline task, participants memorized a single simple shape on the task-relevant side. In the Double baseline task, they had to maintain two shapes on the relevant side, which were no longer vertically aligned (as in the Whole and Parts tasks), but spatially separated, in order to appear as two physically distinct objects (see Figure 1). Memory test displays contained a simple shape at fixation in both tasks. CDA components should be larger in the Double relative to the Single baseline task, reflecting an increase in WM load from one to two objects. If compound sample objects in the Whole and Parts tasks were represented in an integrated versus part-based fashion, the difference in the effective WM load in these two tasks (one versus two objects) should be analogous to the WM load difference between the Single and Double baseline tasks. In this case, the CDA amplitude increase for the Parts versus Whole task should be similar in size to the CDA amplitude difference between the Single and Double baseline tasks.

Methods

Participants

Sixteen participants were tested (mean age 29 years, 7 male, 1 left-handed). None of them had any visual or neurological impairments, and all gave informed written consent prior to testing. The experiment was approved by the Ethics Committee of the Department of Psychological Sciences, Birkbeck, University of London.

Apparatus, stimuli, and procedure

This experiment was programmed and executed using Matlab software (MathWorks, Natick, MA). Stimuli were presented on a 24-inch BenQ widescreen monitor (60Hz, 1920 × 1080 screen resolution) at a viewing distance of approximately 60 cm. On each trial, a memory sample display containing visual objects on the left and right side (at a horizontal eccentricity of 2.16° from central fixation) was followed after a delay period by a memory test display that included a single visual object at fixation. Sample and test displays were displayed for 150 ms, and the delay period between these two displays was 850 ms (see Figure 1). The interval between the offset of a memory test display and the onset of a sample display on the next trial was 1500 ms (i.e., there was no temporal jitter between successive trials). A grey fixation cross subtending 0.31 × 0.31 degrees of visual angle was present throughout each block. The memory test display object was superimposed on this fixation cross. Four different grey shapes (hexagon, circle, hourglass and cross) were used to generate sample and test display objects. All shapes were vertically and horizontally symmetrical and were equal in size (1.15 × 1.15°).

There were four task conditions, each delivered in four successive blocks. In all tasks, participants were instructed to memorize the memory sample display object(s) on one task-relevant side (left or right), and to match them to the subsequent test display object. Memory-test match and mismatch trials were equally likely in all four tasks, and the task-relevant side for the sample displays was blocked and changed from left to right, or vice versa, in each successive block (similar to our previous work on multi-modal WM where we measured visual and tactile CDA components concurrently, e.g., Katus & Eimer, 2019). There were two baseline tasks (Single and Double) where participants had to memorize either one or two simple shapes on one side, and to report whether there was a match between sample and test display shapes. In the *Single Baseline task*, the sample shape on each side was vertically aligned with the fixation cross. The memory test shape either matched or did not match the memorized sample shape. In the *Double Baseline task*, sample displays

included vertically two shapes on each side, which were separated by a distance of 3.17° (measured relative to the lower and upper edges of both shapes). The memory test shape either matched one of the two memorized sample shapes or neither of these shapes. The two critical tasks (Whole and Parts) included physically identical memory sample displays with two vertically arranged and spatially aligned shapes on either side (see Figure 1). These two tasks differed only with respect to the memory test displays shown on every trial. In the *Whole task*, test displays included an object consisting of two spatially aligned component shapes at fixation. Here, participants had to report whether this compound test object exactly matched the memorized compound-shape sample object. On half of all mismatch trials, one component shape differed between the memorized sample and test display object, while the other shape appeared in the same location in both objects. On the other half, the test display object contained both memorized shapes, but in the incorrect spatial configuration (e.g. cross above hexagon instead of hexagon above cross). These configural mismatch trials were included to discourage participants from encoding the two component shapes of the relevant sample object in an exclusively part-based fashion. In the *Parts task*, the test displays contained a single shape, which was either identical to one of the two memorized component shapes (match trials), or differed from both of these shapes (mismatch trials). Responses were recorded with a BlackBox Toolkit button system. Participants pressed the top button to report a sample-test match, and the bottom button to report a mismatch.

In all tasks, the assignment of different shapes to locations on the left and right side of the memory sample displays was randomly determined on each trial, without replacement. As a result, all four possible shapes appeared in each memory sample display in the Double Baseline, Whole, and Parts tasks, whereas only two of these four shapes were shown in sample displays in the Single Baseline task. There were 16 blocks in total (four blocks for each task), each consisting of 36 trials. The order in which the four tasks were delivered was counterbalanced across participants in the form of a size four Latin square (e.g. ABCD, CDAB, DCBA, BADC).

EEG recording and data analysis

EEG was DC-recorded from 27 scalp electrodes on an elastic cap at sites Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, Pz, PO7, PO8, PO9, PO10, and Oz. Sampling rate was 500 Hz, and a low-pass filter of 40 Hz was used during recording. No other filters were applied following EEG acquisition. Channels were referenced online to an electrode on the left earlobe,

and re-referenced offline to the average of the left and right earlobes. Trials were rejected from EEG analyses when an incorrect response was recorded, as well as when eye-blinks ($> \pm 60 \mu\text{V}$ at Fpz), eye-movements ($> \pm 30 \mu\text{V}$ in the HEOG channels), or muscle movement artefacts ($> \pm 80 \mu\text{V}$ at all other channels) were detected. The remaining trials were segmented into epochs from 100 ms before to 1000 ms after the onset of each memory sample display, separately for the four tasks and blocks where the left or right side of the memory sample display was task-relevant. ERP waveforms were then computed, and CDA components were measured on the basis of ERP mean amplitude values obtained between 350 and 950 ms after memory sample display onset at lateral posterior electrode sites PO7 & PO8 contralateral and ipsilateral to the currently task-relevant sample display side. CDA amplitude differences between tasks were then assessed with planned paired *t*-tests which compared CDA components between Parts versus Whole tasks, and between the Single and Double Baseline tasks. Additional analyses performed with a 200 ms baseline prior to sample display onset obtained virtually identical results.

To confirm that CDA components did not differ between blocks where the left versus right sample side was task-relevant, CDA difference values were analysed with the factors Task and Block (attend left versus right). There was no main effect of Block ($p > 0.4$), and no interaction with Task ($p > 0.1$). To assess possible pre-stimulus drifts of eye position towards the blocked relevant side, averaged HEOG waveforms measured during the 600 ms interval prior to sample display onset in attend-left and attend-right blocks were analysed for all four tasks. There was no effect of Attended Side ($p > 0.4$), and no interaction with Task ($p > 0.3$), confirming the absence of preparatory drifts of eye gaze.

Results

Behavioural performance

Figure 2 (top and middle panels) shows mean reaction times (RTs) and error rates for all four task conditions. For RTs, a one-way ANOVA with factor Task (Single Baseline, Double Baseline, Whole, Parts) showed a significant effect ($F(3,45) = 23.65, p < .001, \eta_p^2 = .70$). Responses were faster in the Single Baseline task (589 ms) relative to the Double Baseline task (704 ms; $t(15) = 9.08, p < .001, d = 0.87$), the Whole task (677 ms; $t(15) = 6.09, p < .001, d = 0.67$), and the Parts task (686 ms; $t(13) = 6.45, p < .001, d = .73$). There were no significant RT differences between any of the other three tasks (all $t(13) < 1.5$, all $p > .141$). Error rates also differed between the four tasks ($F(3,45) = 14.69, p < .001, \eta_p^2 = .495$). Errors were less frequent in the Single Baseline task (4%)

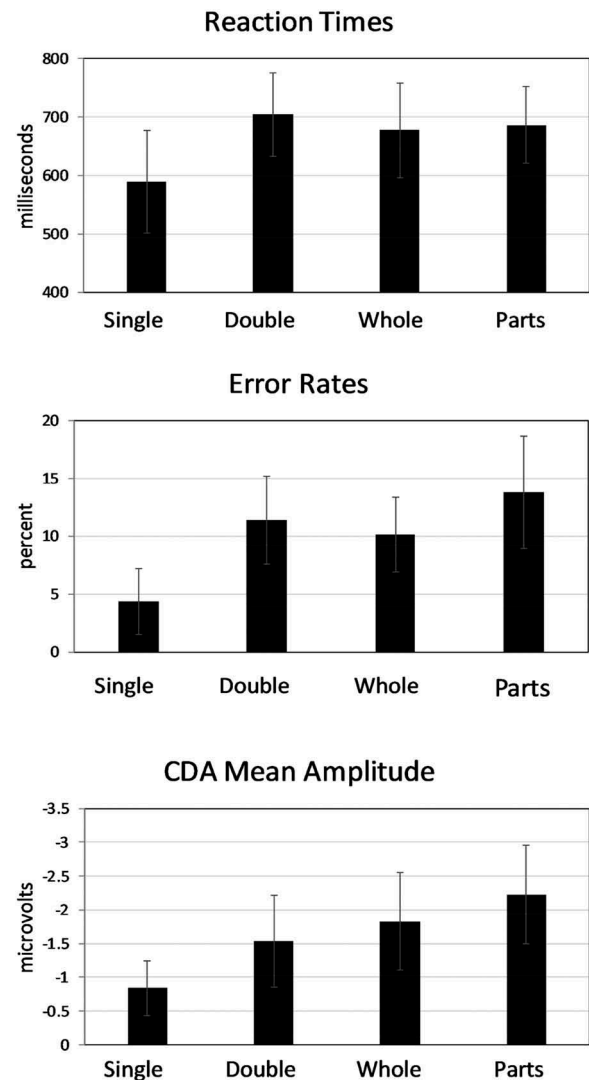


Figure 2. Mean RTs (top panel), error rates (middle panel), and CDA mean amplitudes obtained by subtracting ipsilateral from contralateral ERPs measured during the 350–950 ms interval after sample display onset (bottom panel), shown for all four task conditions. Error bars represent 95% confidence intervals.

than in the Double Baseline task (12%; $t(15) = 5.35, p < .001, d = 1.42$), the Whole task (10%; $t(15) = 4.02, p = .001, d = 1.14$), and the Parts task (13%; $t(15) = 4.44, p < .001, d = 1.34$). Errors were more frequent in the Parts to the Whole task ($t(15) = 2.65, p = .018, d = 0.45$). There were no error rate differences between the Double Baseline and Whole tasks ($t(15) = 1.91, p = .075, d = 0.32$) or between the Double Baseline and Parts task ($t(15) < 1$).

CDA components

Figure 3 shows ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to the task-relevant side of the memory displays, separately for each of the four tasks. CDA

difference waveforms obtained by subtracting ipsilateral from contralateral ERPs are shown in Figure 4 in different colours for each task. The corresponding grand-averaged CDA mean amplitude values for all four task conditions are shown in Figure 2 (bottom panel). Clear CDA components were present in all four tasks, and the expected load-dependent CDA amplitude increase was observed for the Double versus Single Baseline task. Critically, CDA amplitudes also appeared to be larger for the Parts as compared to the Whole task, in spite of the fact that memory sample displays were identical in these two tasks. These informal observations were confirmed statistically. An ANOVA of ERP mean amplitudes obtained at PO7/8 during the 350–950 ms interval after sample display onset with the factors Task (Single Baseline, Double Baseline, Whole, Parts) and Laterality (Contralateral, Ipsilateral) revealed a main effect of Laterality ($F(1,15) = 31.06$, $p < .001$, $\eta_p^2 = .674$), confirming the presence of reliable CDA components. Paired samples *t*-tests confirmed that significant CDA components were elicited in all four tasks (all *t*'s > 4.44 , all *p*'s $< .001$). An interaction between Task and Laterality ($F(3, 45) = 14.27$, $p < .001$, $\eta_p^2 = .487$) demonstrated that the size of CDA components differed between tasks. As predicted, CDA amplitudes were larger in the Double versus Single Baseline tasks (-1.53 μV versus -0.84 μV ; $t(15) = 2.46$, $p = .026$, $d = 0.65$), reflecting the expected effect of increased WM load. Critically, CDA components were also reliably larger in the Parts task than in the Whole task (-2.23 μV versus -1.83 μV ; $t(15) = 2.76$, $p = .015$, $d = 0.29$), indicating that effective WM load was higher in the former task. Notably, the CDA amplitude increase associated with having to memorize two rather than just one shape in the two Baseline tasks (0.69 μV) was numerically slightly larger than the CDA amplitude difference between the Parts and Whole tasks (0.40 μV), but this difference was far from significant ($t(15) = 1.16$, $p = .266$, $d = 0.33$).¹

Discussion

The goal of this study was to investigate whether top-down task settings can determine whether visual objects are represented in a part-based or integrated object-based fashion in WM. We employed a lateralised change detection task where compound objects composed of two basic shapes had to be memorized, and measured CDA components as electrophysiological markers of WM maintenance processes. In the two critical task conditions, identical memory sample displays were shown, but task demands were different. In the Parts task, only one of the two

spatially aligned component shapes of sample objects could re-appear in the subsequent test displays, which was expected to facilitate the formation of part-based WM representations of the two individual shapes. In the Whole task, memory test displays contained a compound-shape object. On half of all mismatch trials, these test objects included both component shapes of the memorized sample object, but in the reverse spatial configuration. This should have encouraged participants to activate a single object-based integrated WM representation of the memory samples.

The central result was that CDA components measured during the delay period in response to identical sample displays were reliably larger in the Parts task relative to the Whole task. If sample display objects had always been encoded and stored in an analogue pictorial fashion, irrespective of task instructions, no such CDA differences should have been observed. As CDA amplitudes are sensitive to the number of objects currently maintained in WM (e.g., Vogel & Machizawa, 2004), an obvious interpretation of the presence of larger CDA components in the Parts as compared to the Whole task is that effective WM load differed between these two tasks. In the Parts task, the compound-shape sample objects were stored in a part-based fashion, with two independent representations of their component shapes. In the Whole task, the same objects were instead encoded in an integrated fashion, as a single WM item that represented their overall shape, without individuating component parts. If the CDA amplitude difference between these two tasks reflects the difference between an effective WM load of one versus two items in the Parts versus Whole tasks, its size should be similar to the CDA amplitude difference between the Single and Double baseline tasks, where participants had to maintain one versus two spatially non-aligned basic shapes. This was indeed the case. CDA components were larger in the Double relative to the Single task, and this difference was only numerically but not reliably different from the CDA amplitude difference between the Parts and Whole tasks. Because test displays differed between the Parts and Whole tasks, the CDA difference between these tasks may reflect a modulation of WM storage that is task-dependent, but still tuned in a more bottom-up fashion to the anticipated perceptual properties of the test displays.

If two separate objects were stored in WM in the Parts and Double baseline tasks, and a single object in the Whole and Single baseline tasks, and if the CDA components observed in these tasks exclusively reflected this difference in effective WM load, CDA amplitudes should in principle

¹As can be seen in Figure 4, CDA amplitudes in the two baseline tasks were generally smaller than in the corresponding other task. This was the case both for the Single Baseline relative to the Whole task ($t(15) = 4.68$, $p < .001$, $d = 0.98$), and for the Double Baseline relative to the Parts task ($t(15) = 3.89$, $p = .001$, $d = 0.50$).

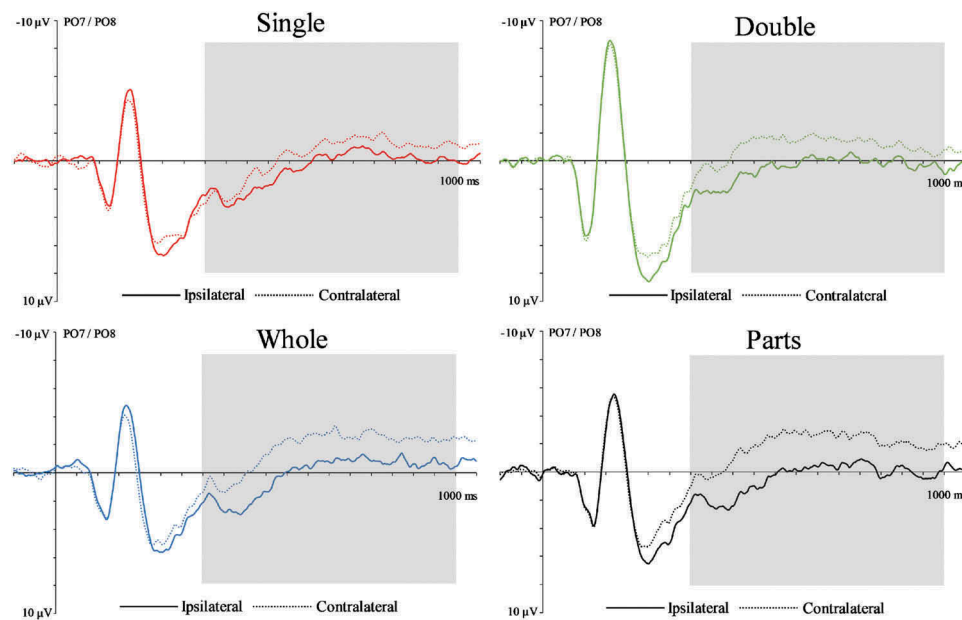


Figure 3. Grand-average event-related brain potentials (ERPs) measured during the 1000 ms interval after memory sample display onset at electrodes PO7/PO8 contralateral and ipsilateral to the task-relevant side of this display, shown separately for the four different task conditions. The shaded area marks the CDA analysis window.

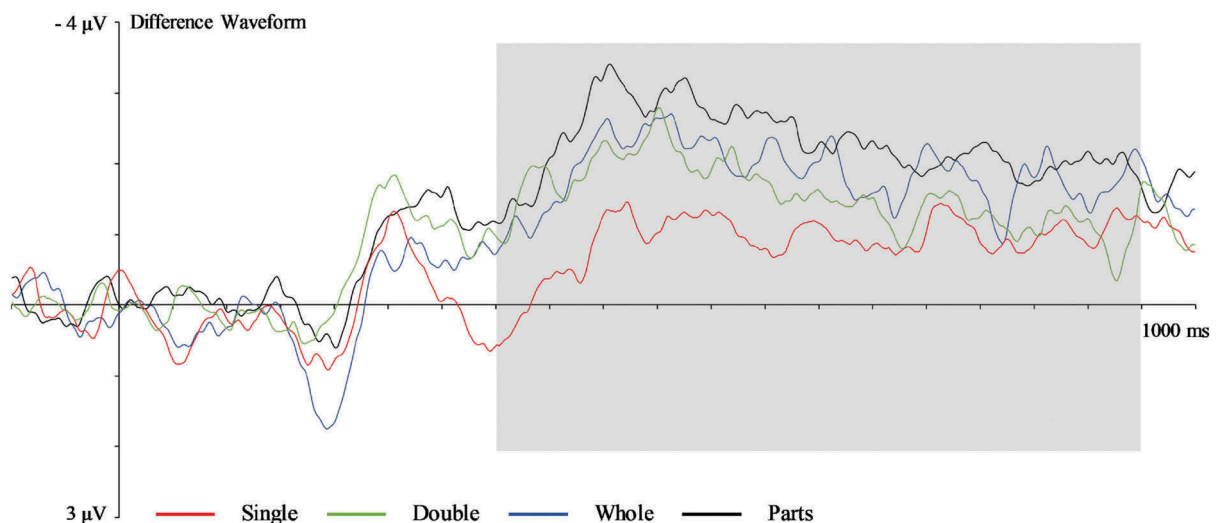


Figure 4. CDA difference waveforms obtained during the 1000ms interval after memory sample display onset at electrodes PO7/PO8 by subtracting ipsilateral from contralateral ERPs for all four different tasks conditions. The shaded area marks the CDA analysis window.

have been identical within these two pairs of tasks. However, this was not the case. CDA amplitudes were larger for compound-shape sample objects in the Parts and Whole tasks than for single-shape samples in the Double and Single baseline tasks (see Figure 4). The CDA difference between the Whole and Single baseline tasks is likely to be primarily due to the fact that memory sample objects were more complex in the former task (compound shapes versus simple shapes). Previous studies have found larger CDA

components in tasks where memorized objects were more complex (e.g., irregularly shaped polygons versus colours), even when WM load was held constant (e.g., Luria et al., 2010; see Luria, Balaban, Awh, & Vogel, 2016, for discussion). The presence of larger CDA amplitudes in the Parts task relative to the Double Baseline task is more difficult to explain. It is likely to be linked to the physical differences between the sample displays in these two tasks (see Figure 1). CDAs were reduced in size when sample

displays contained two vertically separated shapes (Double Baseline task) relative to displays with two spatially aligned shapes (Parts task). In a previous CDA study where observers memorized multiple coloured objects (Peterson, Gözenman, Arciniega, & Berryhill, 2015), CDA amplitudes also differed between sample displays with connected versus unconnected objects. However, these CDA amplitude modulations interacted with the similarity of sample display objects in a complex way, precluding a clear interpretation of this effect. One possibility is that generating separate WM representations of two connected shapes may have been more demanding than encoding and maintaining two unconnected shapes (see Luria & Vogel, 2011, Exp. 2, for the reverse case where the integration of shapes into a single object resulted in a reduction of CDA amplitudes). Such shape individuation costs may also have contributed to the CDA differences observed between the Parts and Whole tasks, as separate WM representations of component shapes were only required in the former task.

Overall, the current study provides novel evidence that the format in which identical visual stimuli are represented in WM can be flexibly controlled in line with current task demands. Previous CDA research by Woodman and Vogel (2008) has suggested that object colours and orientations can be represented separately and selectively in WM in tasks where only one of these features is task-relevant, even when they belong to the same object. Here, we demonstrate that the top-down control of WM maintenance is not limited to the selective encoding of object features from different dimensions, but can also result in qualitative differences in the way that visual objects and their component parts are stored. These objects can be represented in an integrated or in a part-based fashion, depending on whether memory is subsequently tested separately for individual shape components or for whole objects. The presence of larger CDA components in a task where component parts had to be maintained independently could either be a direct result of an increase in effective WM load, but could also reflect the demands of additional shape individuation processes (see above). These two possibilities need to be dissociated in future research. In either case, these CDA differences demonstrate that changes in task demands can alter how physically identical visual objects are represented in WM. These representations are not merely copies of the sensory information received by the visual system. Instead, this information is transformed into a representational format that is most useful for the task at hand. One possibility is that task goals directly modulate how visual objects and their parts are represented in WM. When integrated representations of whole objects are required, object-based WM representations are formed. When the component parts of visual objects are task-relevant, WM individuates and

retains separate representations of these parts. An alternative possibility is that representations of integrated objects and of their component parts co-exist, perhaps at different levels of the visual processing hierarchy, and that task goals operate through a separate pointer system that actively maintains specific representations (see Drew & Vogel, 2008, for possible links between the CDA and pointer system for WM in intraparietal sulcus). In this scenario, larger CDA amplitudes in the Parts versus Whole tasks would reflect the activation of two pointers to two component shapes in the former task and the activation of a single pointer to an integrated object representation in the latter task.

Acknowledgments

This research was supported by Grant ES/L016400/1 from the Economic and Social Research Council (ESRC), UK, and by Grant RPG-2015-370 from the Leverhulme Trust, UK.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Economic and Social Research Council [ES/L016400/1]; Leverhulme Trust [RPG-2015-370].

References

- Baddeley, A. (2012). Working memory: Theories, models, and controversies. *Annual Review of Psychology*, 63, 1–29.
- Balaban, H., & Luria, R. (2016). Object representations in visual working memory change according to the task context. *Cortex*, 81, 1–13.
- Behrmann, M., Peterson, M. A., Moscovitch, M., & Suzuki, S. (2006). Independent representation of parts and the relations between them: Evidence from integrative agnosia. *Journal of Experimental Psychology: Human Perception and Performance*, 32(5), 1169.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, 94(2), 115.
- Delvenne, J.-F., & Bruyer, R. (2004). Does visual short-term memory store bound features? *Visual Cognition*, 11(1), 1–27.
- Drew, T., & Vogel, E. K. (2008). Neural measures of individual differences in selecting and tracking multiple moving objects. *Journal of Neuroscience*, 28(16), 4183–4191.
- Emrich, S. M., Riggall, A. C., LaRocque, J. J., & Postle, B. R. (2013). Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory. *Journal of Neuroscience*, 33(15), 6516–6523.
- Katus, T., & Eimer, M. (2019). The sources of dual-task costs in multisensory WM tasks. *Journal of Cognitive Neuroscience*, 31(2), 175–185.

- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390(6657), 279–281.
- Luria, R., Balaban, H., Awh, E., & Vogel, K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience and Biobehavioral Reviews*, 62, 100–108.
- Luria, R., & Vogel, E. K. (2011). Shape and color conjunction stimuli are represented as bound objects in visual working memory. *Neuropsychologia*, 49(6), 1632–1639.
- Luria, R., Sessa, P., Gotler, A., Jolicoeur, P., & Dell'Acqua, R. (2010). Visual short-term memory capacity for simple and complex objects. *Journal of Cognitive Neuroscience*, 22(3), 496–512.
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, 6(6), 255–260.
- McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, 43(1), 77–94.
- Olson, I. R., & Jiang, Y. (2002). Is visual short-term memory object-based? Rejection of the “strong-object” hypothesis. *Perception & Psychophysics*, 64(7), 1055–1067.
- Peterson, D. J., Gözenman, F., Arciniega, H., & Berryhill, M. E. (2015). Contralateral delay activity tracks the influence of Gestalt grouping principles on active visual working memory representations. *Attention, Perception, & Psychophysics*, 77(7), 2270–2283.
- Poljac, E., de-Wit, L., & Wagemans, J. (2012). Perceptual wholes can reduce the conscious accessibility of their parts. *Cognition*, 123(2), 308–312.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139(1), 23–38.
- Ranganath, C., Cohen, M. X., Dam, C., & D'Esposito, M. (2004). Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *Journal of Neuroscience*, 24(16), 3917–3925.
- Riddoch, M. J., Humphreys, G. W., Akhtar, N., Allen, H., Bracewell, R. M., & Schofield, A. J. (2008). A tale of two agnosias: Distinctions between form and integrative agnosia. *Cognitive Neuropsychology*, 25(1), 56–92.
- Vergauwe, E., & Cowan, N. (2015). Working memory units are all in your head: Factors that influence whether features or objects are the favored units. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 41(5), 1404–1416.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428(6984), 748–751.
- Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General*, 131(1), 48–64.
- Woodman, G. F., & Vogel, E. K. (2008). Selective storage and maintenance of an object's features in visual working memory. *Psychonomic Bulletin & Review*, 15(1), 223–229.