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The number of objects determines visual working memory capacity allocation for complex items



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ABSTRACT

The goal of the present study was to examine whether visual working memory (WM) capacity allocation is determined solely by complexity, with the number of objects being redundant, as suggested by flexible resource models. Participants performed the change detection task with random polygons as stimuli, while we monitored the contralateral delay activity (CDA), an electrophysiological marker whose amplitude rises as WM load increases. In Experiment 1, we compared the WM maintenance of one whole polygon to a single half of the polygon, equating the number of items but varying the complexity level. Additionally, we compared the whole polygon to two halves of a polygon, thus roughly equating perceptual complexity but manipulating the number of items. The results suggested that only the number of objects determined WM capacity allocation: the CDA was identical when comparing one whole polygon to one polygon half, even though these conditions differed in complexity. Furthermore, the CDA amplitude was lower in the whole polygon condition relative to the two halves condition, even though both contained roughly the same amount of information. Experiment 2 extended these results by showing that two polygon halves that moved separately but then met and moved together were gradually integrated to consume similar WM capacity as one polygon half. Additionally, in both experiments we found an object benefit in accuracy, corroborating the important role of objects in WM. Our results demonstrate that WM capacity allocation cannot be explained by complexity alone. Instead, it is highly sensitive to objecthood, as suggested by discrete slot models.

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Introduction

Visual working memory (WM) is the mechanism that stores and manipulates relevant visual stimuli. It is widely agreed that WM can only hold a limited amount of information, for example 3–4 simple objects (Cowan, 2001), but the nature of this limitation is at the heart of an ongoing debate between two general views, namely *slot models* and *resource models*.

Discrete slot models (Luck and Vogel, 1997; 2013; Zhang and Luck, 2008) describe WM as having 3–4 "slots", which function as placeholders. Maintaining an object in WM means allocating one of the slots to that object. Once all slots are allocated, any additional objects cannot be maintained in WM, so that no information regarding these extra objects is available. Supporting this idea, Zhang and Luck (2008) found that when subjects tried to maintain more than 3 items in WM, their accuracy could be modeled as a mixture of two types of responses. Some responses reflect retrieving the items that were stored in the WM

workspace, while others are completely random guesses, suggesting that some of the items did not enter WM at all. Furthermore, increasing the set-size from 3 to 6 (i.e., crossing the usual estimate of capacity limits) resulted in a decrease in the probability that an item would enter WM, but not in a decrease in the precision of the representations. Additionally, Both EEG (e.g., Vogel and Machizawa, 2004) and fMRI (e.g., Xu and Chun, 2006) studies have revealed a pattern of neural activity that increased as more objects were maintained in WM, until it reached a stable plateau at around 3–4 objects, at which point presenting more objects did not lead to a further increase in neural activity. This is consistent with the view that each item is given one slot, until no extra slots are left so that no additional items can enter WM.

Further research argued that although WM is limited in its capacity, adding extra features to the maintained items comes at no cost. For example, accuracy remains the same when WM maintains only the orientation of a tilted bar, or both its orientation and its color (Luck and Vogel, 1997; Luria and Vogel, 2011; Vogel, Woodman, and Luck, 2001; Woodman and Vogel, 2008; but see Fougnie, Asplund, and Marois, 2010, and Oberauer and Eichenberger, 2013, for important limitations to these findings). Thus, one slot can be allocated to one object regardless of the number of features, linking the number of slots to the number of integrated objects that are being represented in WM.

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According to flexible resource models (Bays and Husain, 2008; Fougnie, Suchow, and Alvarez, 2012; Ma, Husain, and Bays, 2014) WM can be adaptably shared between any number of objects or features. The limit is on the resolution of the items: the more items stored, the less precise their representations will be. Beside mathematical modeling (e.g., Bays and Husain, 2008; van den Berg, Shin, Chou, George, and Ma, 2012), the most compelling behavioral evidence supporting this notion came from experiments involving complex objects such as random polygons (e.g., Alvarez and Cavanagh, 2004; Gao, Li, Liang, Chen, Yin, and Shen, 2009). For example, Alvarez and Cavanagh (2004) found that as the complexity of the object increased, fewer items could be maintained in WM, which pointed towards a quantityquality tradeoff in allocating WM capacity. Several electrophysiological studies mirrored this result and reported greater neural activity for complex objects such as random polygons relative to simple objects such as colored squares (Allon, Balaban, and Luria, 2014; Gao, Ding, Yang, Liang, and Shui, 2013; Gao et al., 2009; Luria, Sessa, Gotler, Jolicoeur, and Dell'Acqua, 2010; Luria and Vogel, 2011).

In light of these findings, flexible resource models offer an appealing theory of WM capacity allocation, describing it solely in terms of resolution or complexity, with no need for the additional concept of objects (or slots). This flexible resource view can explain both evidence showing that a random polygon consumes more capacity than a simple color, and evidence showing that two colors consume more capacity than one, since in both cases information is added, and the overall perceptual complexity (i.e., the amount of relevant information) increases. The clear boundaries drawn between objects in discrete slot models are claimed to be redundant (Bays and Husain, 2008; Fougnie et al., 2012; van den Berg et al., 2012).

However, while an effect for complexity with the number of objects held constant (e.g., Gao et al., 2009) supports the influence of complexity on WM capacity allocation, it cannot be used to claim that objecthood has no influence. To argue that the objecthood notion is redundant in WM, one must compare conditions that are equal in perceptual complexity (i.e., have the same amount of relevant information) but differ in the number of objects. Current evidence leave open the possibility that over and above any effects of complexity, objecthood still plays an important part in the way in which WM represents complex items (see also Fougnie et al., 2010). In other words, it is possible that even a complex object is still an integrated object in visual WM. This would mean that not only the overall amount of information determines WM capacity allocation, as claimed by resource models, but also the distribution of that information among objects, echoing the basic view of slot models.

It is important to note that the current investigation focuses only on the role of objects in WM. Thus, we contrasted models that posit a central role for objects with models that allow WM to be flexibly distributed among features with no regard to the objects to which the features belong. Notably, some flexible resource theories do posit a certain status for objects in WM maintenance (e.g., Brady, Konkle, and Alvarez, 2011), but the centrality of the concept of objecthood is not clear in these models. Flexible resource models, including those allowing for an influence of objects on capacity allocation, will need to be reframed if a strong influence for objecthood is found for complex items, which is considered to be the hallmark of resolution effects in VWM.

The goal of the present study was to test the idea that even complex objects are represented as integrated units in WM. To do so, we used random polygons, which could be broken in halves (see Fig. 1), enabling us to compare WM capacity allocation for a whole polygon to two control conditions. The first comparison was between one whole polygon and just a single half of the polygon, conditions that are equated in terms of the number of objects (one in both cases) but differ in terms of complexity. If indeed the sole factor determining capacity allocation is complexity, a whole polygon should consume more capacity than its half, since it is more complex. Alternatively, if WM capacity allocation is affected by the number of objects even for complex items,

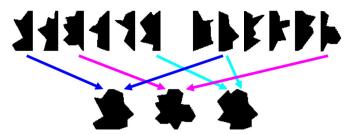


Fig. 1. The stimuli used in the present experiments. The top row presents the left-side halves of polygons (on the left), and the right-side halves (on the right). The bottom row presents 3 of the 36 possible polygons, created by randomly combining one left-side half with one right-side half.

the counterintuitive prediction is that the capacity consumed by a whole polygon should be similar to the capacity consumed by its half.

A second interesting comparison was between one whole polygon and two separately presented polygon halves. Although the two halves are not exactly as complex as the whole polygon, it can be asserted that these conditions are at least roughly similar in complexity, and critically, both are more complex than a single half. If WM capacity allocation is solely determined by complexity, both conditions should consume roughly the same amount of capacity. However, if objecthood determines WM capacity allocation, a whole polygon should consume less capacity than its two halves when presented separately.

The advantage of the current approach is that it provides a controlled way of examining the interplay between complexity and objecthood in WM representations, as it manipulates complexity without using items from different categories (e.g., colored squares versus random polygons; e.g., Alvarez and Cavanagh, 2004) or changing the number of relevant dimensions (e.g., only color or both color and orientation; e.g. Luck and Vogel, 1997), as was done in the past.

We used two different measures of capacity allocation to determine the influence of complexity and objecthood on WM. First, if objecthood does play a part in capacity allocation, we expect to find an object benefit in performance (e.g., Duncan, 1984), meaning that memory for a similar amount of information should be better when that information is distributed among fewer items. Hence, accuracy for a whole polygon should be higher than for two separately presented polygon-halves, although perceptual complexity is roughly equated between these conditions. In fact, if the centrality of objects view held by slot models is correct, and given that accuracy can faithfully reflect WM capacity allocation, performance should be the same for a whole polygon as for a single polygon-half.

However, it has been previously argued that behavioral effects found for complex items (e.g., Alvarez and Cavanagh, 2004) are strongly influenced by the comparison process, so that behavioral data do not necessarily reflect the WM representations (Awh, Barton, and Vogel, 2007). To avoid this problem, we used a second measure of WM employment, namely the contralateral delay activity (CDA; McCollough, Machizawa, and Vogel, 2007; Vogel and Machizawa, 2004; Vogel, McCollough, and Machizawa, 2005).

The CDA is a negative slow wave found at posterior electrodes following stimulus presentation and persisting throughout the retention interval. The amplitude of the CDA rises as more items are being held in WM, reaching an asymptote which is strongly correlated with the individual WM capacity (e.g., Vogel and Machizawa, 2004). Corroborating the reliability of the CDA as a measure of WM, it was recently reported that, similarly to the behavioral WM capacity, this electrophysiological marker itself has a direct correlation with fluid intelligence (Unsworth, Fukuda, Awh, and Vogel, 2015). Since the CDA is measured before the onset of the test array (i.e., before the initiation of the comparison process), it is not contaminated by the comparison process, and hence can be confidently attributed specifically to the WM maintenance period. Therefore, factors that influence behavioral performance but are external to WM maintenance, such as the difficulty of the

comparison process, do not affect the CDA (e.g., Ikkai, McCollough, and Vogel, 2010; Luria et al., 2010). The fact that the CDA exclusively reflects the employment of visual WM was successfully exploited to demonstrate WM involvement in tasks that are not classically classified as "short term memory" paradigms, such as visual search and multiple object tracking (e.g., Drew and Vogel, 2008; Woodman and Arita, 2011; Carlisle, Arita, Pardo, and Woodman, 2011).

It is important to note that the CDA amplitude does not reflect the number of maintained locations, even though most experimental setups present every object in a unique spatial position. Ikkai et al. (2010) presented two sets of items (colors) sequentially, and compared a condition in which the second set of items was presented at the same positions as the first set, to a condition in which the two sets of items were presented in different positions on the screen. Importantly, similar CDA amplitudes were found regardless of whether the stimuli were presented in different locations or at the same locations, indicating that the CDA does not simply reflect the number of attended locations. Additionally, it was recently demonstrated that two simple colors that shared the same spatial position had a higher CDA amplitude than just one color, as long as their movement history suggested that they were two separate items (Luria and Vogel, 2014). Moreover, even two simple items sharing a location and moving together for a full second can produce a CDA amplitude higher than one moving item, if the task encourages their individuation (Balaban and Luria, in press). Thus, the CDA does not simply track the number of attended locations.

If WM capacity allocation is determined mainly by complexity, we should expect a whole polygon to produce the same CDA amplitude as two separately presented halves, since these conditions contain roughly the same amount of relevant information. In contrast, if objecthood affects WM capacity allocation even for complex items (as claimed by slot models), we should expect a whole polygon to produce a CDA amplitude similar to a single half, since these conditions have the same number of objects.

Materials and methods

Participants

All participants gave informed consent following the procedures of a protocol approved by the Ethics Committee at the Tel Aviv University. They were Tel Aviv University students who received course credit or 40 NIS (approximately \$10) per hour for participation. All subjects had normal or corrected-to-normal visual acuity and normal color-vision. Each experiment included 12 participants in the final analysis (7 females, mean age 25 in Experiment 1, 8 females, mean age 28 in the behavioral control experiment that followed Experiment 1, and 10 females, mean age 23 in Experiment 2). Subjects with a rejection rate of over 20% were replaced (two in Experiment 2).

Stimuli and procedure

Stimuli and procedure: Experiment 1

We used the bi-lateral version of the change detection task (e.g., Vogel and Machizawa, 2004). The stimuli were 6 right-side and 6 left-side halves of black random polygons (see Fig. 1). From a viewing distance of approximately 60 cm, each half of a polygon subtended approximately $1.6^{\circ} \times 0.8^{\circ}$ of visual angle. The left side of each right-side half and the right-side of each left-side half (meaning the "cropped" side) always subtended the full length of the shape, and hence each right-side half could combine with each left-side half to produce a whole polygon (see Fig. 1). The exact stimuli were randomly selected at the beginning of each trial, with the restriction that any stimulus could appear at most once (on each side). Stimuli appeared inside an imaginary $8.4^{\circ} \times 2.7^{\circ}$ rectangle (one in each side of fixation). Inside each rectangle, the exact positions of the stimuli were randomized on

each trial, with the constraint that the distance between the centers of each stimulus would be no less than 3.2°.

Each trial started with the presentation of a fixation point ("+") in the middle of the screen for 500 ms. Then, two arrow-cues were presented for 200 ms above and below fixation, indicating the to-beattended side for the upcoming trial (right or left, with an equal probability). Participants were instructed to memorize only the stimuli presented on the side indicated by the arrows. After a random interval (300, 400, or 500 ms from the cues' offset), the memory array was presented for 300 ms, followed by a retention interval (during which only the fixation point was presented) of 900 ms and then the test array (see Fig. 2). The test array remained visible until a response was emitted. Participants made an unspeeded response via button press (using the "Z" and "/" keys on a computer keyboard, indicating "same" and "different", respectively) to indicate whether the test array included only old items or one new item (with an equal probability for change and no-change trials; the test array at the uncued side was always identical to the memory array). On change trials, one of the halves in the cued side was replaced by a new half from the same side (i.e., a right-side polygon could only be replaced by a different right-side polygon, and a left-side polygon by a different left-side polygon). On the other half of the trials, the test array was identical to the memory array.

The experiment included 3 possible conditions that were randomly intermixed within each block. Here and throughout the paper, conditions are referred to in terms of the number of items presented in each hemifield instead of the total number of items appearing on the screen, because this is what subjects were asked to remember (since only one side was to be attended on each trial). In the single half condition, only one half of a polygon (either a right- or a left-side half, with an equal probability) was presented on each side. In the two separate halves condition, one right-side half and one left-side half of a polygon were presented on each side. In the whole polygon condition, one right-side half and one left-side half were presented next to each other, which created one whole polygon on each side (in this condition, each right-side half was equally likely to combine with each left-side half, meaning there were 36 possible polygons). Note that in every condition, including the whole polygon condition, only a single half could change shape in a given trial. Participants started with a practice block of 12 trials, followed by 12 blocks, each consisting of 60 trials, for a total of 720 experimental trials.

Following Experiment 1, we conducted a behavioral control experiment, which was identical to Experiment 1, except as noted below. EEG was not recorded, and hence the cueing stage was removed, and only one or two polygon halves were presented on the whole screen instead of in each side. In the single half and two halves conditions, only one polygon half could change between the memory and test array. In the whole polygon condition, however, a change occurred to the whole polygon, meaning both halves changed to different halves. Subjects completed 6 practice trials followed by 3 blocks of 60 trials each.

Stimuli and procedure: Experiment 2

Experiment 2 was identical to Experiment 1, except as noted below. The items in the memory array moved for $1000 \, \mathrm{ms}$ covering about 1.5° of visual angle, and then remained stationary for 300 ms before disappearing (for a total of 1300 ms, see Fig. 3). The items moved in straight lines and always stayed on the same side of the screen throughout their trajectory.

The experiment included 4 possible conditions. In the two conditions of separate movement (a single half or two separate halves), each half of a polygon moved in a different direction. In the whole polygon condition, one right-side half and one left-side half were presented adjacently (to create one whole polygon) and also moved together. In the two joining halves condition, one right-side half and one left-side half of a polygon moved separately for 600 ms, and then met to create one whole polygon, and moved together for 400 ms. Note again that in every condition (including the last two), only a single

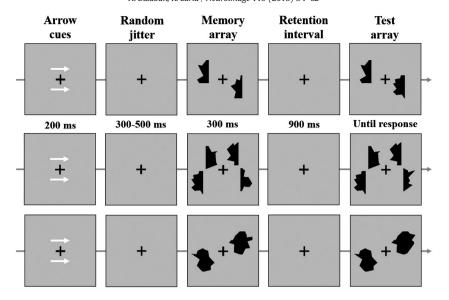


Fig. 2. An illustration of the different conditions in Experiment 1. The arrow cues indicate the relevant side for the upcoming trial, followed by a random jitter of 300–500 ms, the memory array of polygons (presented for 300 ms), a retention interval of 900 ms, and then the test array. The different conditions were (from top to bottom) a single half of a polygon, two separate halves of a polygon, and one whole polygon (as can be seen in the figure, in each condition items appeared on both sides of the screen, but subjects were asked to attended to only one side, indicated by the cues. We refer only to the number of items that were presented on the relevant side). In each condition, only a single half could change shape between the memory- and test-arrays.

half of a polygon could change shape in a given trial. Participants started with a practice block of 12 trials, followed by 15 blocks consisting of 60 trials each, for a total of 900 experimental trials.

EEG recording: Experiments 1 and 2

The EEG was recorded inside a shielded Faraday cage using a Biosemi ActiveTwo EEG recording system (Biosemi B. V., Amsterdam, The Netherlands), and amplified with a bandpass of 0.16–100 Hz. Data

was recorded from 32 scalp-electrodes at a subset of locations from the extended 10–20 system (including mostly occipital and parietal sites, in which the CDA is usually most pronounced: Fp1, Fp2, AF3, AF4, F3, F4, F7, F8, Fz, FCz, C3, C4, Cz, T7, T8, P1, P2, P3, P4, P5, P6, P7, P8, Pz, PO3, PO4, PO7, PO8, POz, O1, O2, and Oz), as well as from 2 electrodes placed on the left and right mastoids. The horizontal electro-oculogram (EOG) was recorded from electrodes placed 1 cm to the left and right of the external canthi to detect horizontal eye movement, and the vertical EOG was recorded from an electrode beneath the left eye to

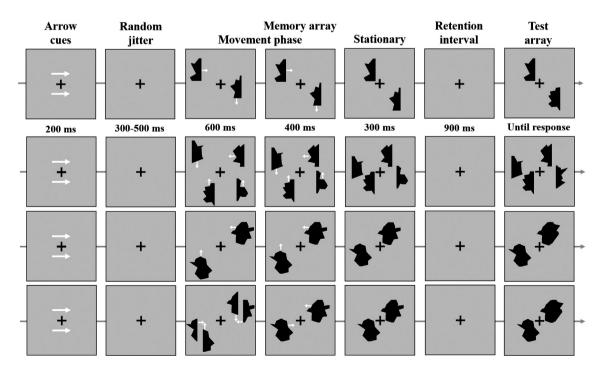


Fig. 3. An illustration of the different conditions in Experiments 2. The arrow cues indicate the relevant side for the upcoming trial, followed by a random jitter of 300–500 ms, and then the memory array of polygons was presented for a total of 1300 ms: 1000 ms of movement, and an additional 300 ms stationary display. Then a retention interval of 900 ms was presented, followed by the test array. The different conditions were (from top to bottom) a single half of a polygon, two halves of a polygon moving separately, one whole polygon, and the joining halves condition. In the joining halves condition, two halves of a polygon moved separately for 600 ms, and then met to create one whole polygon that moved for the remaining 400 ms. In each condition, only a single half could change shape between the memory- and test-arrays.

detect blinks and vertical eye movements. The single-ended voltage was recorded between each electrode site and a common mode sense electrode (CMS/DRL). Data was digitized at 256 Hz.

Offline signal processing and analysis was performed using EEGLAB Toolbox (Delorme and Makeig, 2004), ERPLAB Toolbox (Lopez-Calderon and Luck, 2014), and custom Matlab scripts. All electrodes were referenced to the average of the left and right mastoids. Artifact detection was performed using a peak-to-peak analysis, based on a sliding window 200 ms wide with a step of 100 ms. Trials containing activity exceeding 80 µV at the EOG electrodes or 100 µV at the analyzed electrodes (P7, P8, PO3, PO4, PO7, and PO8) were excluded from the averaged ERP waveforms. This procedure resulted in a mean rejection rate of 5% in Experiment 1, and 7.7% in Experiment 2.

The continuous data were segmented into epochs from -200 to +1200 ms relative to onset of the memory array in Experiment 1, and -200 to +2200 ms in Experiment 2 (until the end of the retention interval). The epoched data were then low-pass filtered using a non-causal Butterworth filter (12 dB/oct) with a half-amplitude cutoff point at 30 Hz. Only trials with a correct response emitted after at least 200 ms and at most 2000 ms after presentation of the test array were included in the analysis.

CDA analysis: Experiments 1 and 2

Separate average waveforms for each condition were generated, and difference waves were constructed by subtracting the average activity recorded at electrodes ipsilateral to the memorized array from the average activity recorded at electrodes contralateral to the memorized array. For statistical purposes, we used the mean amplitude found in the average of P7/P8, PO3/PO4, and PO7/PO8 electrodes. In Experiment 1 we used the average activity between 300 and 1200 ms, time locked to onset of the memory array.

The CDA can be monitored not only during the retention interval (when items are not visible), but also during visual tracking (e.g., Drew and Vogel, 2008; Drew, Horowitz, Wolfe, and Vogel, 2011; Drew Horowitz, Wolfe, and Vogel, 2012) and when the items are stationary but remain visible (Tsubomi, Fukuda, Watanabe, and Vogel, 2013). Thus, in Experiment 2, aside from analyzing the time window of retention (*Memory CDA*, between 1300 and 2200 ms after memory array onset), we could examine the formation of the WM representation, by analyzing the time window of the dynamic presentation of the items (*Tracking CDA*, between 500 and 1200 ms after memory array onset). Furthermore, due to the temporal dynamics of ERPs we could inspect the online updating of the representations in the joining condition. To that aim, for this condition we divided the Tracking CDA to *Early Tracking CDA*, between 500 and 900 ms after memory array onset, and *Late Tracking CDA*, between 900 and 1200 ms after memory array onset.

Statistical analysis: Experiments 1 and 2

In both experiments, we conducted a one-way analysis of variance (ANOVA) with condition as a within-subject variable on the CDA mean amplitude (in each time window, see above) as a dependent variable, and another one-way ANOVA with condition as a within-subject variable on accuracy as a dependent measure. All of these tests revealed a significant effect of condition, all Fs > 6, all ps < 0.01. We do not further report them, instead focusing on the comparisons between the different conditions.

Results and discussion

Experiment 1

Electrophysiological results

The CDA waveforms for the different conditions are presented in Fig. 4a. Our results indicate that the WM representations were not

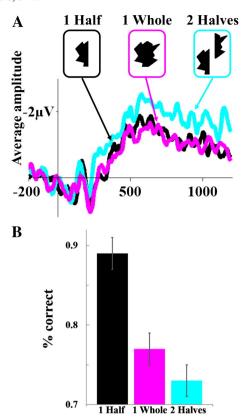


Fig. 4. The results of Experiment 1. A. The CDA amplitude for the different conditions, averaged across the P7/P8, PO3/PO4, and PO7/PO8 electrodes. The CDA amplitude in the one whole polygon condition was significantly lower than in the two halves condition, and similar to the single half condition. B. Accuracy rates for the different conditions, bars displaying standard error of the mean. Accuracy for one whole polygon was higher than for two halves. but lower than for a single half.

affected by the amount of information presented, but rather by the number of the presented objects. The CDA amplitude for the whole polygon condition (two adjacent halves of a polygon; M: $-1.05~\mu\text{V},$ SE: 0.25) was lower than for two halves of a polygon presented separately (M $-1.77~\mu\text{V},$ SE: 0.40), F (1, 11) = 7.42, MSE = 0.41, p < 0.05, even though both conditions were roughly as complex. Importantly, the CDA amplitude of a whole polygon was the same as that of a single half of a polygon (M: $-1.15~\mu\text{V},$ SE: 0.25), F (1, 11) < 1, MSE = 0.14, p = 0.53, despite the fact that a whole polygon has twice as much visual information, and hence is more complex. Replicating previous findings, the CDA amplitude for two halves of a polygon was higher than for a single half, F (1, 11) = 7.80, MSE = 0.29, p < 0.05.

Behavioral results

The accuracy for the different conditions is presented in Fig. 4b. Interestingly, the results revealed an object benefit when displaying the same amount of information within one object relative to two: accuracy for a whole polygon (M: 0.78, SE: 0.02) was higher than for two halves of a polygon presented separately (M: 0.73, SE: 0.02), F (1, 11) = 13.95, MSE = 0.00, p < 0.005. Accuracy for a whole polygon was lower than for a single half of a polygon (M: 0.89, SE: 0.02), F (1, 11) = 52.46, MSE = 0.00, p < 0.00005, indicating that the object benefit was imperfect.

Notably, the object benefit we found was rather small in magnitude. Accuracy for the whole polygon was more similar to 2 halves than to a single half. We suggest that the lower accuracy for a whole polygon compared to its half is due, at least partly, to errors that arise during the comparison of the test array to the VWM representations of the items (Awh et al., 2007). Specifically, since the whole polygon contained two halves, each with a potential to change, subjects' decision had to rely on the comparison of more features, thus leading to a greater

probability for an error. Therefore, we claim that the large decrease in accuracy found for the whole polygon does not necessarily reflect an inherent property of the VWM capacity it consumes, and is instead related to the specific way in which memory was probed in Experiment 1.

In order to put this notion to the test, we conducted a behavioral control experiment with 12 fresh subjects, including the same stimuli and conditions as in Experiment 1. Critically, however, the test phase was different than in Experiment 1: here, if a change occurred in the whole polygon condition, the entire polygon changed to a different one, instead of only one of its halves. Since the change signal is much larger, the comparison process of a whole polygon should be easier than in Experiment 1, and hence we expected accuracy for the whole polygon to approach that of a single polygon-half. This was indeed what we found, with accuracy for the whole polygon (M: 0.91, SE: 0.02) being higher than for two halves (M: 0.75, SE: 0.02), F(1, 11) =58.36, MSE = 0.01, p < 0.00002, and importantly, not significantly different than for a single half (M: 0.93, SE: 0.02), F(1, 11) = 1.06, MSE = 0.01, p = 0.34. This supports the idea that factors related to the comparison process are responsible for the low accuracy when complex items are used (Awh et al., 2007). More specifically, the results suggest that in Experiment 1, the difference in accuracy between a whole polygon and its half probably reflects errors related to the comparison stage.

Discussion

The goal of the first experiment was to examine whether WM capacity allocation for a complex item is solely determined by complexity, as suggested by resource models, or also by the number of objects. Our results suggest that even complex items are treated as integrated objects in WM. The WM representation (as indicated by the CDA) of one whole polygon resembled that of a single half of a polygon, suggesting that increasing the perceptual complexity of the object (i.e., adding more relevant visual information to it) did not change WM capacity allocation. In contrast, in the two separate halves condition, presenting roughly the same amount of information among two objects rather than one dramatically changed WM capacity allocation. Our behavioral results revealed a somewhat different pattern. Accuracy for a whole polygon was somewhat better than for its separate halves, but still worse than a single polygon half (i.e., the same number of objects with a lower level of complexity). As was previously claimed (Awh et al., 2007), we speculated that the decreased accuracy for a whole polygon relative to one half was due to errors arising during the comparison stage. A control experiment we conducted supported this notion, showing similar accuracy for a whole polygon and its half once the change to-be-detected was more salient for a whole polygon. Hence, we believe that the finding of a lower accuracy for a whole polygon should be interpreted with caution. The overall pattern of behavioral and electrophysiological results, along with the characteristics of the comparison process, can be easily explained by positing a central role to objects in WM capacity allocation, even for complex items. This resembles previous experiments showing that adding more features to simple objects (for example, asking subjects to remember not only the orientation of a tilted bar, but also its color) comes at no cost in WM (e.g., Luck and Vogel, 1997; Vogel et al., 2001), which supports the number of objects view of slot models.

It can be argued that in the whole polygon condition subjects simply ignored half of the polygon, despite the fact that either one of its halves could change. This can explain the lower CDA amplitude compared with two separate halves, since according to this view subjects only tried to maintain roughly half of the overall amount of information. However, our behavioral results speak against this idea: accuracy was better for two halves when they formed one whole polygon than when they were presented separately (albeit not to a great extent, presumably

due to comparison errors), although the same amount of information was needed to correctly identify the change. If our subjects ignored half of the information in the whole polygon condition, they should have been *less* accurate in this condition compared to the two separate halves condition. This means that the lower CDA amplitude in the whole polygon condition is not due to a difference in the amount of encoded information.

Since the present CDA results can be readily explained solely by objecthood, with no need for the concept of complexity, they seem at odds with the numerous reports, including ones relying on the CDA as an index of visual WM, suggesting that a complex item such as a random polygon consumes more WM capacity than a simple item such as a colored square (e.g., Gao et al., 2009; Luria et al., 2010). Importantly, we do not argue that perceptual complexity does not influence capacity allocation, but rather that objecthood is an important additional factor even for complex objects. Note that our results cannot be used to rule out the idea that the amount of information has an effect on WM representations, since in the current experiment even the condition with the lowest amount of information (i.e., half a polygon) can still be considered guite complex. It is possible that complex items consume an initial amount of extra capacity, but are still handled as objects afterwards. This notion is in line with the "slots + averaging" model (Zhang and Luck, 2008), in which certain items can be held in more than one slot. We return to these ideas in the General Discussion, but next we turn to put our claim to an even stronger test.

Experiment 2

The main goal of Experiment 2 was to offer an even stronger support for the argument that complex items are represented as integrated objects in WM. Here, we attempted to provide a demonstration that objecthood (i.e., the distribution of information within versus between objects) can dramatically change WM capacity allocation, even during the course of a trial. To this aim, we relied on recent findings showing that WM is sensitive to online objecthood cues and is able to update the status of the items accordingly. Namely, when separate simple items meet and move together, their WM representation is updated and they are treated as one unit (Luria and Vogel, 2014). Thus, in Experiment 2, we allowed the items to move on the screen in different ways. If random polygons behave like objects as we claim here, we should expect that two halves of a polygon meeting to create one whole polygon would be updated and treated as one object (as was found for simple objects), meaning that they should consume less WM capacity, despite the fact that perceptual complexity (i.e., the amount of relevant information) remained unchanged.

Again, we used two baseline conditions: a single half of a polygon or two halves of a polygon, moving independently. Critically, in the joining halves condition, two halves of a polygon started to move separately and then met to create one whole moving polygon. Thus, in this condition the exact same information was displayed first in two objects, and later on within a single object. If complex items behave like integrated objects, we would expect the CDA amplitude in the joining halves condition to be similar to two separately moving halves in the beginning of the trial (when the two halves are still separate), but then to decrease and approach the amplitude of one polygon as the WM representation is updated, similarly to what was found for simple objects such as colors (Luria and Vogel, 2014). In contrast, if only the amount of information determines capacity allocation in WM for complex items, we should expect the meeting of two separate polygon halves to have no effect on their WM representations, since the exact same information is presented throughout the trial.

To provide further support to the importance of objects in WM representation, we included a whole polygon condition, in which two halves of a polygon were presented adjacently to create one whole polygon that moved as a single unit throughout the trial. If the number of objects view of slot models is correct, this condition should produce

¹ We thank an anonymous reviewer for suggesting this experiment.

the same WM representation as a single half of a polygon, since a common motion is a strong objecthood cue (as has been demonstrated for simple objects, see Luria and Vogel, 2014). In contrast, if the amount of information view held by resource models is correct, this condition should be represented similarly to two separately presented halves.

Electrophysiological results: tracking CDA

The CDA waveforms for the different conditions are presented in Fig. 5a. Replicating the results of Experiment 1, we found that the WM capacity allocation for polygons was governed by the number of objects, rather than by complexity. First, the CDA amplitude for the whole polygon condition (M: $-1.05\,\mu\text{V}$, SE: 0.25) was lower than for two separately moving halves of a polygon (M: $-2.07\,\mu\text{V}$, SE: 0.29), F (1, 11) = 41.82, MSE = 0.15, p < 0.00005, despite the fact that perceptual complexity is roughly the same between these conditions. In fact, as in Experiment 1, the CDA amplitude of a whole polygon was the same as that of a single half of a polygon (M: $-1.23\,\mu\text{V}$, SE: 0.24), F (1, 11) = 1.27, MSE = 0.16, p = 0.28, a condition with half as much visual information, and hence less complexity. Replicating previous results, the CDA amplitude for two halves of a polygon was higher than for a single half, F (1, 11) = 24.78, MSE = 0.17, p < 0.0005.

Importantly, comparing the early (500–900 ms after memory array onset) and late (900–1200 ms after memory array onset) time windows of the display period for the joining halves condition revealed that objecthood changed the representations of the items online. This condition included two separately moving halves of a polygon that subsequently met and moved as one whole polygon for the rest of the trial. In the first stage of their movement in which they moved separately, the two halves (M: $-1.95\,\mu\text{V}$, SE: 0.34) were represented as two separate halves (M: $-1.99\,\mu\text{V}$, SE: 0.30), F (1, 11) < 1, MSE = 0.17, p = 0.80, producing a higher CDA amplitude compared with a single half (M: $-1.13\,\mu\text{V}$, SE: 0.24), F (1, 11) = 18.44, MSE = 0.22, p < 0.005. In contrast, during the later stage of the memory array presentation, we

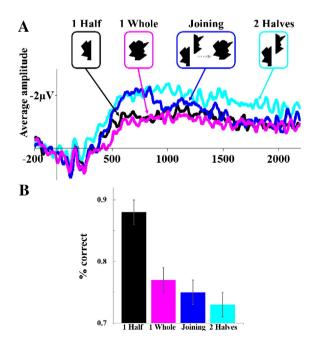


Fig. 5. The results of Experiment 2. A. The CDA amplitude for the different conditions, averaged across the P7/P8, PO3/PO4, and PO7/PO8 electrodes. The CDA amplitude in the one whole polygon condition was significantly lower than in the two separate halves condition, and similar to the single half condition. The CDA amplitude in the joining condition was significantly higher than a single half during the early part of memory array presentation (500–900 ms after memory array onset), but similar to a single half during the late part of presentation (900–1200 ms after memory array onset) and during the retention interval. B. Accuracy rates for the different conditions, bars displaying standard error of the mean. Accuracy for one whole polygon was higher than for two halves, but lower than for a single half. Accuracy for the joining condition was similar to two separate halves.

found evidence for the online integration of the two halves in the joining halves condition (M: $-1.65~\mu V$, SE: 0.27). Following the joint movement of the items, they were no longer represented similarly to two separate halves (M: $-2.18~\mu V$, SE: 0.29), F (1, 11) = 8.71, MSE = 0.19, p < 0.05, despite the fact that perceptual complexity is roughly the same between these conditions. Instead, the representation of the two joining halves was now updated and resembled that of a single half of a polygon (M: $-1.36~\mu V$, SE: 0.25), F (1, 11) = 2.83, MSE = 0.17, p = 0.12, a condition that carried half as much visual information, and hence was less complex.

Electrophysiological results: memory CDA

We found an identical pattern of results for the memory CDA as for the late tracking CDA, with the whole polygon and two joining polygons being represented similarly to a single half of a polygon, a condition which is less complex. Both the whole polygon (M: $-0.90~\mu\text{V}$, SE: 0.21) and the two joining halves (M: $-1.10~\mu\text{V}$, SE: 0.27) produced lower CDA amplitudes compared with two separate halves (M: $-1.70~\mu\text{V}$, SE: 0.26), F (1, 11) = 39.99, MSE = 0.09, p < 0.0001, and F (1, 11) = 14.21, MSE = 0.15, p < 0.005, respectively. The whole polygon, two joining halves, and single half (M: $-0.98~\mu\text{V}$, SE: 0.20) did not differ from each other, all Fs < 1.54, MSEs < 0.18, ps > 0.24. The CDA amplitude for two halves of a polygon moving separately was higher than for a single half, F (1, 11) = 15.95, MSE = 0.19, p < 0.005.

Behavioral results

The accuracy for the different conditions is presented in Fig. 5b. Replicating the results of Experiment 1, we found an object benefit, meaning an advantage for displaying the same amount of information in one object relative to two objects: accuracy for a whole polygon (M: 0.77, SE: 0.02) was higher than for two separate halves of a polygon (M: 0.73, SE: 0.02), F(1, 11) = 5.53, MSE = 0.00, p < 0.05, but lowerthan for a single half of a polygon (M: 0.88, SE: 0.02), F(1, 11) =71.75, MSE = 0.00, p < 0.000005. The joining halves condition did not produce a behavioral benefit: accuracy in this condition (M: 0.75, SE: 0.02) did not differ from two separate halves, F(1, 11) = 1.49, MSE = 0.00, p = 0.25, and was lower than for a single half, F (1, 11) = 91.1, MSE = 0.00, p < 0.000005. Once again, we suggest that the imperfect pattern of object benefits is due, at least partly, to errors occurring during the comparison of the test and memory arrays, an alternative supported by the results of the control experiment described above.

Discussion

Experiment 2 replicated and extended the findings of Experiment 1, with the CDA showing that WM capacity is mainly allocated to objects, even for complex items. The whole polygon condition produced CDA amplitudes similar to a single half of a polygon, despite carrying twice as much visual information, and hence being more complex. Once again, this cannot be explained by subjects ignoring half of the polygon in the whole polygon condition, since an object benefit in accuracy was found, meaning accuracy was better for a whole polygon than for two separately moving halves of a polygon (a condition involving roughly the same amount of task-relevant information). Similar to Experiment 1, the object benefit was quite small, and accuracy was lower for one whole polygon compared with its half, a pattern of results we attribute to mistakes arising during the comparison process.

Experiment 2 goes beyond Experiment 1 in demonstrating that the allocation of WM capacity between objects is done online, and can be updated dynamically as the items evolve. When two separately moving halves of a polygon met to create one whole polygon, their CDA amplitude, which started off similarly to two separately moving halves, gradually decreased until it approached the amplitude on a single moving half. Thus, once the two halves were associated with a single object, their maintenance in WM was equivalent to one object, as

suggested by the discrete slot approach, replicating similar evidence found for simple objects (Luria and Vogel, 2014).

General discussion

The goal of the present study was to test the idea that WM capacity allocation is determined solely by complexity, with the number of objects being redundant, as suggested by flexible resource models (e.g., Bays and Husain, 2008). We used random polygons, since similar stimuli were extensively used in past research as an example of complex items. We monitored two measures of WM capacity allocation: accuracy, allowing us to detect object benefits (e.g., Duncan, 1984), and the CDA (e.g., Vogel and Machizawa, 2004), an electrophysiological marker sensitive to the online employment of WM resources. In order to isolate the potential role of the number of objects, we compared one whole polygon to two separately presented polygon halves, a condition with roughly the same amount of information distributed among two objects rather than one. In order to isolate the potential role of perceptual complexity, we compared one whole polygon to a single half of a polygon: both conditions have only one object, but a single polygon-half has half the amount of visual information, and is therefore less complex.

The main conclusion from Experiments 1 and 2 is that even complex items are represented as integrated units in visual WM, suggesting a key role for objecthood, in agreement with the basic view of discrete slot models (e.g., Luck and Vogel, 2013). A whole polygon consumed the same amount of WM capacity (as indicated by the CDA) relative to a single half of a polygon, even though half a polygon is much less complex. Additionally, an object benefit was found in the accuracy performance, meaning that accuracy was better in the whole polygon condition relative to the two halves. This behavioral benefit was not perfect, which could be due to the more difficult comparison process involved (Awh et al., 2007), as was supported by a separate behavioral control experiment.

In Experiment 2, by using displays of moving items, we could demonstrate that the capacity allocation of WM can be changed online, following the dynamics of objecthood cues. In the joining halves condition of this experiment, two polygon-halves moved separately and then met to create one whole moving polygon. We found that the WM representation of this condition started off similarly to two separately-moving halves, but throughout the trial the representations gradually became integrated and finally were similar to a single polygon-half. This resembles previous evidence from simple objects (Luria and Vogel, 2014), and provides compelling support to the notion that objecthood dynamically shapes WM capacity allocation, even with the overall amount of relevant visual information remaining constant.

Since we rely on the CDA as our main index of WM capacity allocation, it could be argued that the lack of an effect for complexity is due to an insensitivity of the CDA amplitude to complexity, instead of to inherent properties of WM. However, several studies did find robust effects of complexity on the CDA amplitude (Allon et al., 2014; Gao et al., 2009; Gao et al., 2013; Luria et al., 2010) by demonstrating that random polygons result in a higher CDA amplitude than simple shapes. Thus, WM capacity allocation, as indexed by the CDA amplitude, is indeed influenced by complexity (as argued by resource models). However, these findings still left open the possibility that objecthood also plays a part in WM capacity allocation, as was found in the current experiment.

While we argue that our results reflect the influence of the number of objects on WM capacity allocation, a possible alternative explanation is that the reduction in CDA amplitude found for a whole polygon compared to two separately presented halves can be attributed to a smaller number of *locations*, instead of a smaller number of *objects*. However, as was mentioned in the Introduction, several studies tested this alternative explanation, and rejected it. Specifically, it was demonstrated that displaying items sequentially at the same locations leads to a similar

CDA amplitude as when presenting each item in a unique location (Ikkai et al., 2010). Additionally, it has been recently shown that merely presenting items in a shared location does not result in a lower CDA amplitude compared to presenting the items separately (Luria and Vogel, 2014; Balaban and Luria, in press), for example if the meeting is brief and follows a history of independent movement, or if the task encourages individuation. Therefore, we believe the present findings cannot be reduced to a claim regarding locations, and instead they highlight the role objecthood plays in guiding WM representations.

How can the present results be reconciled with the previous finding demonstrating that perceptual complexity does influence WM capacity allocation? Specifically, it has been demonstrated that complex items such as random polygons consume more WM resources than the same number of simple objects (e.g., Gao et al., 2009; Luria et al., 2010). In contrast, using the CDA as a measure of WM capacity allocation and manipulating both objecthood and complexity with a single set of stimuli, we found complexity not to affect capacity allocation: a whole polygon was found to consume just as much capacity as its half. However, it is possible that we found no difference since even our most simple condition (i.e., a single polygon-half) was still quite complex. Hence, we do not argue against the established role complexity plays in WM capacity allocation, but simply claim that the importance of complexity cannot be regarded as evidence for the redundancy of objecthood, a factor we found to deeply affect WM capacity allocation.

To describe both our results and previous findings regarding complex objects, we suggest that complex items might initially consume extra capacity relative to simple objects, but once this initial capacity is allocated to them, they are treated as integrated objects just like simple items. This idea can be incorporated into an existing version of slot models, namely the "slots + averaging" model suggested by Zhang and Luck (2008). This model enables certain items to be given more than one slots, an idea originally used to explain why one simple item is associated with better performance than two simple items. Similarly, it is possible that complex objects such as random polygons are assigned more than one slot (explaining the difference between them and simple objects which are assigned only one slot), but from that point on, the items still behave as integrated objects, as we found. This speculative notion can be the target for future research.

Flexible resource models might also be able to incorporate our present findings, with one major adjustment. Namely, they would have to include some way of addressing the influence of objecthood on the way capacity is allocated. For example, it could be that capacity is initially allocated to objects, and is then distributed between the different features of an object in a flexible manner (e.g., "hierarchical structured feature bundles"; Brady et al., 2011; see also Fougnie et al., 2010; Suchow, Fougnie, and Alvarez, 2014). Such a model incorporates a certain role for objects, while still allowing for effects of information load. To account for our results, these models need to make objects a central factor in capacity allocation, similarly to the basic view of slot models.

Conclusion

We conclude that objecthood has an important influence on WM capacity allocation, even when it is tested in the natural environment of flexible resource models, namely using complex objects. To summarize, we suggest that any theory of WM cannot be complete without incorporating objects as a fundamental factor.

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