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ERPs and alpha oscillations track the encoding and maintenance of object-based representations in visual working memory

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Abstract

When memorizing an integrated object such as a Kanizsa figure, the completion of parts into a coherent whole is attained by grouping processes which render a whole-object representation in visual working memory (VWM). The present study measured event-related potentials (ERPs) and oscillatory amplitudes to track these processes of encoding and representing multiple features of an object in VWM. To this end, a change detection task was performed, which required observers to memorize both the orientations and colors of six "pacman" items while inducing configurations of the pacmen that systematically varied in terms of their grouping strength. The results revealed an effect of object configuration in VWM despite physically constant visual input: change detection for both orientation and color features was more accurate with increased grouping strength. At the electrophysiological level, the lateralized ERPs and alpha activity mirrored this behavioral pattern. Perception of the orientation features gave rise to the encoding of a grouped object as reflected by the amplitudes of the Ppc. The grouped object structure, in turn, modulated attention to both orientation and color features as indicated by the enhanced N1pc and N2pc. Finally, during item retention, the representation of individual objects and the concurrent allocation of attention to these memorized objects were modulated by grouping, as reflected by variations in the CDA amplitude and a concurrent lateralized alpha suppression, respectively. These results indicate that memorizing multiple features of grouped, to-be-integrated objects involves multiple, sequential stages of processing, providing support for a hierarchical model of object representations in VWM.

KEYWORDS

grouping, lateralized alpha suppression, lateralized ERPs, object-based representation, visual working memory

1 | INTRODUCTION

When perceiving meaningful visual objects in our cluttered environment, the visual system has to integrate disparate component parts into coherent wholes, as demonstrated, for example, by Kanizsa-type illusory figures (Kanizsa, 1955). For instance, as depicted in Figure 1a (left panel), a configuration of six "pacman" elements generates the perception of a star-shaped illusory object (a so-called "Kanizsa" figure) with sharp boundaries that are perceived as lying above the inducing circular elements. The perception of such an illusory object is usually referred to as "modal completion" (see Michotte et al., 1991). Recent neuroimaging studies showed activations in the lateral occipital complex (LOC) to be linked to the processing of Kanizsa figures, with closed shapes being represented via feedback signals from mid-level visual areas to lower-level striate and extrastriate areas (Altschuler et al., 2012; Chen et al., 2020; Chen, Weidner, et al., 2021; Lee & Nguyen, 2001; Murray et al., 2002; Stanley & Rubin, 2003).

The operation of binding smaller units into integrated whole objects not only supports the structuring of perceptual input for more efficient orienting and action in the environment, but also reduces capacity limitations in visual working memory (VWM; Delvenne & Bruyer, 2006; Morey, 2019; Morey et al., 2015; Nie et al., 2017; Peterson & Berryhill, 2013; Woodman et al., 2003; Vogel et al., 2001). For instance, when remembering the orientation of a gap in various disks, memory performance improves when neighboring disks are grouped to form an illusory rectangle, thereby effectively doubling the maximum number of reportable items in VWM (Diaz et al., 2021; Gao et al., 2016). It has also been suggested that individual, nonspatial features (such as color and orientation) might be represented as bound objects in VWM (e.g., Luck & Vogel, 1997; Luria & Vogel, 2011; but see Gao et al., 2011;

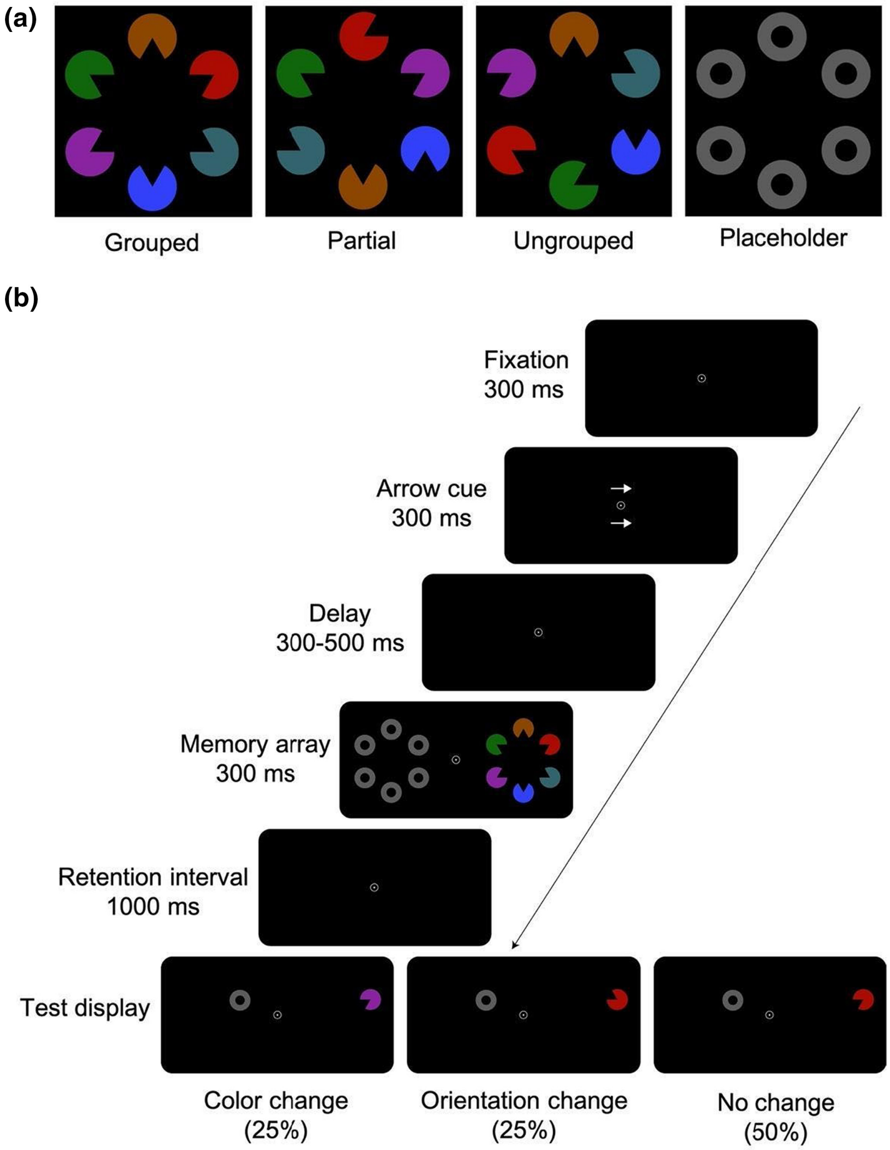

FIGURE 1 (a) Examples of the memory configurations in the grouped, partially grouped, and ungrouped conditions and for the placeholder configuration presented on the unattended display side. Note that each memory configuration presented exactly six different colors and orientations, such that the overall physical stimulation was identical in all three memory configurations. Moreover, the physical stimulation of the placeholder was in critical respects (including the size and positions) comparable to the memory configurations, without however providing relevant color and orientation information. (b) Example trial sequence, depicting a memory array that presents a grouped configuration on the right side of the display (as indicated by the preceding, 100% valid, arrow cue) and a to-be-ignored placeholder configuration of six gray circles on the left side. Following a retention interval, the test display is presented, which would reveal a probe item on the cued side (and a placeholder circle on the uncued side). The probe would either depict a color change (left), an orientation change (middle), or no change (right).

Ma et al., 2014). For instance, Luck and Vogel (1997) showed that VWM performance was essentially independent of the number of to-be-memorized features that constituted a given object; instead, memory capacity depended primarily on the number of individuated objects that had to be retained (see also Delvenne & Bruyer, 2004; Vogel et al., 2001; but see Wheeler & Treisman, 2002). Recently, Chen, Kocsis, et al. (2021) combined manipulations of spatial grouping with a concurrent manipulation of feature binding (see also Ecker et al., 2013; Fougnie et al., 2013; Luck & Vogel, 1997; Luria & Vogel, 2011; Olson & Jiang, 2002; Xu, 2002). In their study, a change detection task was used, which required participants to memorize six pacman elements, each depicting a unique color and orientation as presented in an initial memory display. The oriented pacmen could be grouped to form a complete illusory star, render a partially grouped triangle, or, respectively, an ungrouped configuration—thus gradually manipulating the strength of the complete-object representation (see examples in Figure 1a). Following a brief delay after the memory display offset, a single pacman probe item appeared at one of the locations that had been occupied by an item in the memory display. The task was to decide whether the probe item was the same as or different from the pacman presented previously at the same location in the memory display. Importantly, the change could occur for *grouping*-relevant features (orientation), or for *grouping*-irrelevant features (color). Thus, by systematically varying the amount of closure in the Kanizsa-type configuration (from a complete grouping through a partial grouping to an ungrouped configuration) by variations in orientation, memory performance for individual features (orientation and color) could be assessed relative to the presented grouping that was displayed. The results showed that the grouped object enhanced both the (grouping-relevant) orientation and (grouping-irrelevant) color representations when both features were task-relevant (for the same/different judgment), demonstrating that memory for various features can be improved by encountering them in a spatial grouping.

While grouping benefited the storage of both grouping-relevant and -irrelevant features in VWM, it remains unclear which processes contribute to this benefit, as a facilitatory effect could emerge at various stages of processing. For instance, current models that link object perception, attention and memory (for reviews, see, e.g., Bundesen et al., 2011; Walther & Koch, 2007) would differentiate between a hierarchy of sequential processing stages that comprises differentiable computational mechanisms and neuronal sources of processing, which encompass the initial, early perceptual stimulus analysis, the subsequent allocation of attention to selected objects, followed by their maintenance in memory. The present study was designed to investigate these component processes by taking advantage of previously established event-related potential (ERP) and oscillatory markers associated with the encoding and maintenance of working memory contents, the aim being to identify critical processes that are influenced by object grouping. That is, we tracked the temporal dynamics of illusory figure processing in order to investigate how object integration impacts early perceptual, attentional, and memory-related processing stages.

The first series of lateralized ERP components of interest include the early positivity posterior contralateral (Ppc), the subsequent posterior N1pc, as well as the attention-related N2pc (also referred to as posterior contralateral negativity, PCN). In working memory tasks that intend to measure lateralized components, the to-be-memorized array is typically only presented in one hemifield which is prompted by an arrow cue (e.g. Vogel & Machizawa, 2004). In such a design, participants first use the cue to orient their attention to one side of the display, after which they select/encode the relevant items on the cued side. These two processes are supposedly reflected in the lateralized P1/N1 component (or Ppc/N1pc, respectively; Adam et al., 2018; Fortier-Gauthier et al., 2012; for a review, see Mangun (1995)) and the N2pc (e.g., Eimer, 1996; Luck & Hillyard, 1994), respectively. For instance, spatial cueing would typically give rise to a contralateral positivity in the P1 time range (which has—in this context—been referred to as the contralateral positivity, or CP), presumably due to an attentional boost of perceptual processing at the cued location (Fukuda & Vogel, 2009; Hoffmeister et al., 2022; Livingstone et al., 2017). Moreover, bottom-up differences in saliency may also give rise to a comparable contralateral positivity (that is usually labeled Ppc), which can occur in absence of any spatial cues (e.g., Barras & Kerzel, 2017; Fortier-Gauthier et al., 2012; Wiegand et al., 2015). For example, the Ppc has been reported to be modulated by spatial attentional requirements in a visual search task, e.g. when a to-be-attended target item on one side of the displays is presented together with to-be-ignored, yet salient distractors on the other side (e.g., Barras & Kerzel, 2017; Fortier-Gauthier et al., 2012; Wiegand et al., 2015). In the present study, we used the label Ppc for the contralateral positivity at posterior electrodes in the P1 range, but it should be noted that this component could also be referred to as a CP in spatial cueing studies (e.g., Hoffmeister et al., 2022; Livingstone et al., 2017).

Moreover, in non-spatial attention studies, the posterior P1 has also been linked to the difficulty of processing the presented stimuli (Kruggel et al., 2001; Taylor, 2002), revealing an enhanced P1 with increased complexity of the presented stimuli. In addition, the posterior N1 has been suggested to reflects endogenous processes relating to Gestalt perception (Herrmann & Bosch, 2001;

Kruggel et al., 2001; Slavutskaya & Mikhailova, 2011). For instance, Slavutskaya and Mikhailova (2011) found that processing of whole versus perceptually comparable, disintegrated images was reflected in amplitude changes in the posterior P1 and N1. A number of studies also found enhanced amplitudes in response to illusory figures, as compared to ungrouped baseline configurations, to reveal differential processing in the posterior N1 (e.g., Herrmann & Bosch, 2001; Kruggel et al., 2001; Murray et al., 2004; Proverbio & Zani, 2002; Senkowski et al., 2005; see also Murray et al., 2002, for even earlier effects).

In the subsequent time window, the actual spatial-attentional selection of grouped vs. ungrouped configurations is indexed by the N2pc (Conci et al., 2006, 2011; Eimer, 1996; Luck & Hillyard, 1994; Töllner et al., 2015). Previous work showed search to be more efficient for grouped, as compared to ungrouped, targets (Conci et al., 2007; see also Nie et al., 2016), and this is associated with larger N2pc amplitudes—which is indicative of the enhanced engagement of focal attention by the grouped target (Conci et al., 2011) as opposed to a broader tuning of attention by grouped, task-irrelevant distractors (Conci et al., 2006). Thus, previous evidence suggests that both the processing of grouped objects and the biasing of initial attentional priorities might be reflected in the Ppc and N1pc components and the subsequent allocation of (focal) attentional processing resources to the illusory figure is associated with the N2pc.

An additional component of interest is the contralateral delay activity (CDA), a sustained negativity during the delay period between the memory and test displays. The CDA has been found to monotonically scale with the number of items held in VWM up to the measured storage limit (of approximately 3–4 items; Fukuda et al., 2015; Luria et al., 2016; Vogel & Machizawa, 2004). The CDA amplitude has also been reported to decrease in some studies when to-be-remembered objects are bound or grouped into higher-order units (Luria et al., 2016; Luria & Vogel, 2011; Peterson et al., 2015), suggesting that it actually reflects the number of "integrated units" represented in VWM. For example, the CDA amplitude was comparable when memorizing only orientation features as opposed to both color and orientation features, which were presented on the same physical objects, whereas the CDA increased when the same orientation and color features were presented as separate objects (Luria & Vogel, 2011; Woodman & Vogel, 2008). The difference in the CDA amplitude thus appears to reflect the number of separable objects. Moreover, it has also been reported that similar colors may be compressed in VWM such that the CDA amplitude for these colors is essentially comparable to the amplitude for just one to-be-memorized color (Gao et al., 2011; Peterson et al., 2015). Finally, the CDA has also been shown to provide a characteristic, task-dependent signature of the active maintenance process, where a larger CDA amplitude is observed for identical stimuli when the task requires the encoding of objects with high (as opposed to low) precision (Machizawa et al., 2012). In agreement with this finding, Chen, Töllner, et al. (2018) investigated "amodal" completion (of occluded objects) in VWM and reported a sustained increase in the CDA amplitude for globally completed objects (as compared to uncompleted objects). For instance, when observers were required to memorize occluded parts of an object, persistent mnemonic activity (as indexed by an increased CDA amplitude) was required to generate complete-object representations from physically specified fragments and in order to maintain the resulting complete-object representations in a readily accessible form (see also Emrich et al., 2008; Ewerdwalbesloh et al., 2016; Pun et al., 2012). This suggests that the representation of a globally completed object may, in some cases, also require more (rather than less) mnemonic resources. Previous studies not only reported comparable behavioral dynamics (e.g., Chen, Glasauer, et al., 2018) but also partly overlapping neural mechanisms for amodal and modal completions (Murray et al., 2004). It might therefore be conceivable that modally completed, grouped vs. ungrouped variants of a Kanizsa figure reveal similar VWM storage properties and generate similar CDA patterns to shapes that are completed on the basis of amodal completion. In sum, the role of the CDA concerning object binding and grouping reveals a rather complex and seemingly flexible mechanism, which is not necessarily reflecting bottom-up objecthood cues on the basis of their salience alone (for a review, see Luria et al., 2016). Rather, the CDA appears to depend on specific stimulus characteristics in combination with the related task demands.

Apart from ERPs, the maintenance process can also be tracked with oscillatory markers. Several studies have demonstrated that posterior (putatively visual) alpha oscillations (8–12 Hz) in the retention interval are reduced in amplitude contralateral vs. ipsilateral to the retinotopic location of the to-be-retained items (e.g., Grimault et al., 2009; Lozano-Soldevilla et al., 2014), evidencing a relative amplitude difference between mnemonically relevant and irrelevant information. Accordingly, lateralized alpha-band activity has been taken to play a role in mnemonic retention (for a review, see van Ede, 2018; see also Erickson et al., 2017; Fukuda et al., 2015; Medendorp et al., 2007). Several studies have further demonstrated a link between alpha oscillations during retention and the concurrent location and orientation of to-be-remembered items (Foster et al., 2016; Fukuda et al., 2016), suggesting that alpha oscillations during VWM maintenance also track feature-specific identity information of the to-be-memorized items (Fukuda et al., 2016). Note that, posterior-occipital alpha has also been widely suggested to reflect an online index of top-down adjustments of attentional control (e.g., Murphy et al., 2020; Thut et al., 2006; Wang et al., 2019, 2021; Woodman et al., 2022), which is a critical factor contributing to effective VWM maintenance (Engle & Kane, 2004; Unsworth et al., 2014). Moreover, posterior-occipital alpha suppression has been shown to vary with changes in the attentional engagement (Boudewyn & Carter, 2018), with larger alpha suppression being evident when the attentional demands increase. Recall that VWM is usually considered to reflect a system that provides both short-term stores of representational formats and concurrent attentional, "executive" control structures that keep task-relevant information active and accessible during maintenance (Engle & Kane, 2004). The CDA and lateralized alpha may thus be mapped onto two separable cognitive mechanisms, relating to (i) the representation of individual objects and (ii) associated internal attentional control processes, respectively. That is, an increase in the lateralized alpha suppression for the to-be-remembered items might be directly associated with the increase in attentional control in particular when the number of items in the display exceeds the individual's capacity to select a manageable subset of items for efficient VWM storage (Fukuda et al., 2015).

In summary, the present study was designed to examine neural processing stages potentially implicated in the grouping benefits when memorizing individual features. Participants' (lateralized) electrophysiological brain activity was recorded while they performed a change detection task that presented a to-be-memorized configuration comprising six pacman items on one side of the display (that was cued with an initial arrow cue with 100% validity) and a to-be-ignored placeholder configuration of six gray circles on the other side. Participants had to memorize the color and orientation of pacman items that were presented either as a fully grouped, a partially grouped, or an ungrouped configuration. Note that the various pacman arrangements produced configurations differing in grouping strength, however without impacting the low-level properties of the image (see Figure 1a). That is, the number of items and their overall physical stimulation was identical for the grouped, partially grouped and ungrouped stimulus configurations (and for the task-irrelevant placeholders), and the three to-be-memorized types of configuration would therefore only differ in terms of grouping strength from each other. Subsequent to a retention interval, the test display was presented, which would reveal a probe item on the cued side (and a placeholder circle on the uncued side). The probe would either depict a color change, an orientation change, or no change (see Figure 1b). In this way, we were able to track at the neural level how the VWM representation of individual features is aided by grouping. We assessed behavioral performance measures (change detection accuracy) and lateralized ERP components, as well as oscillatory signals.

Based on our previous, related study (Chen, Kocsis, et al., 2021), we expected a grouping benefit in the change detection performance, that could in principle be mirrored in several lateralized ERP components and/or in corresponding oscillatory signals. We predicted that Ppc amplitudes which reflect the initial perceptual processing of the stimuli might be modulated by the grouping of the to-be-memorized configurations because of their inherent differences in the attentional requirements of initial visual processing. For instance, the less a given configuration is grouped, the greater the attentional requirements to process this stimulus, which should be reflected in the Ppc amplitudes. Variations in attentional selection should also be evident in the subsequent N1pc and N2pc components, revealing a more focused (and more strongly lateralized) shift of attention to the to-be-memorized configuration alongside with an increase in grouping strength. For the memory stage, orientation-based grouping might reduce the load by maintaining integrated, coherent shape representations, thus enhancing the VWM capacity for both color and orientation features, resulting in increased CDA amplitudes. At the same time, the generation of a global shape representation in the grouped Kanizsa figure might also be expected to require more mnemonic resources or, storage capacity than less grouped items in order to achieve a higher representational precision and this should also impact the CDA. Finally, lateralized alpha suppression contralateral to the to-be-remembered configurations was expected to reveal variations of cognitive control devoted to the memorized items in order to keep them active and accessible during the execution of complex cognitive tasks. There might be a larger alpha suppression for ungrouped relative to more grouped configurations thus reflecting greater executive attention (and increased difficulty) to hold the individual features for ungrouped configurations during maintenance.

2 | METHODS

2.1 | Participants

A total of 24 volunteers (12 females, mean age = 26.13 years; SD = 2.67 years, all were right-handed) participated in the experiment, for payment of € 9.00 per hour. All participants had normal or corrected-to-normal visual acuity and normal color vision. No subject reported mental or neurological diseases. All observers provided written informed consent, and the experimental procedure was approved by the ethics committee of the Department of Psychology at Ludwig-Maximilians-University, Munich. The sample size was larger than that of previous, similar studies (Chen, Kocsis, et al., 2021; Gao et al., 2016). A power analysis conducted with G*Power (Erdfelder et al., 1996) revealed that to detect a relatively large effect, $f(U) = 0.5$, of object configuration with a power of 95% and an alpha of .05, a sample of only 12 participants would be required. We further increased our sample to $N = 24$ observers to ensure sufficient statistical power in our analyses.

2.2 | Apparatus and stimuli

The experiment was programed in Matlab using Psychophysics Toolbox functions (Brainard, 1997). Stimuli were presented on a 19-inch computer monitor (1024 × 768 pixels screen resolution, 85-Hz refresh rate) against a black screen background (0.25 cd/m^2). Participants were seated at a distance of approximately 65 cm from the screen inside a shielded Faraday cage (Industrial Acoustics Company GmbH, Germany).

A bilateral version of the change detection task was adapted from previous studies, so as to be able to measure lateralized EEG components (e.g., Vogel & Machizawa, 2004). The to-be-memorized stimulus configuration (which was either presented on the left or right side of the screen) consisted of six items, presented on an imaginary circle (radius: 4° of visual angle), with all items arranged equidistantly to one another. Each item was a filled circle with a radius of 2.4° of visual angle and a 60° opening (1/6 of the overall area of the circle), thus forming a "pacman"-like figure. Each pacman was presented in a different color (all 5.0 cd/m^2; blue, RGB: 49,64,249; red, RGB: 172,11,2; green, RGB: 15,102,11; purple, RGB: 138,35,160; orange, RGB: 140,70,0, and mint, RGB: 50,99,109) and with a different orientation of its "mouth" (i.e., for a given pacman, the cut-out section could be rotated at an angle of 0°, 60°, 120°, 180°, 240°, or 300°, respectively). The distribution of the six colors among the six items was randomized on every trial. The distribution of the "mouth" orientations was determined by the three experimental conditions that were presented with equal probability throughout the experiment. In the "ungrouped" condition, the six possible mouth orientations were randomly assigned to the six display locations (Figure 1a, Ungrouped). In the "partial-grouping" condition, the openings of three items were oriented towards the center of the display, thus forming either an upward- or downward-pointing (illusory) triangle (Figure 1a, Partially grouped). The mouth orientations of the other three items were selected randomly from the remaining three orientations (without replacement of an already assigned orientation). Finally, in the "grouped" condition, the openings of all six items were oriented towards the center of the screen such that they formed an illusory star (Figure 1a, Grouped). In this way, a given memory display would always consist of six distinct colors and six distinct mouth orientations, irrespective of the grouping condition. Thus, for all three types of configuration, each display presented an equal number of (six) colors and orientations, such that the basic physical stimulation was identical across conditions. Of note, the ungrouped configuration served as a baseline: the pacman elements were randomly oriented (as well as randomly colored), making them unlikely to render any kind of grouped object, allowing us to assess whether change detection performance would be enhanced by any type of grouped structure. Finally, in the hemifield opposite to the memory array, a to-be-ignored placeholder configuration was presented, which consisted of six gray (RGB: 92,92,92) circles with a central hole (Figure 1a, Placeholder). These placeholders were similar in luminance to the memory items, and the size of the removed central circle corresponded to the size of the cut-out segment in the pacman items. This ensured that both display halves presented stimulus arrays with an identical physical stimulation, yet only the memory configuration provided task-relevant color and orientation information, while the placeholders remained constant throughout the entire experiment.

2.3 | Procedure and design

Figure 1b illustrates an example trial sequence. Each trial started with the presentation of a central white fixation circle (0.6° × 0.6°), which remained on the screen for the entire trial. After 300 ms, two white arrows (1.1° × 1.1°) appeared above and below the fixation circle for 300 ms, with both arrows pointing either to the left or to the right (with equal probability). After a short delay period (that lasted for a random interval between 300 and 500 ms), the memory display appeared for 300 ms, presenting an ungrouped, partially grouped, or grouped configuration on the cued side (i.e., as indicated by the initially presented arrows, note that these arrow cues were 100% valid) together with a gray placeholder configuration on the uncued side. This was followed by a 1000-ms retention interval during which a blank screen was presented. Next, a test display appeared consisting of a single gray circle on the uncued side and a single pacman item—each positioned randomly at one of the six possible item locations (that had been occupied in the memory array) on the cued (and uncued) side. The probe display was presented until the participant issued a response: pressing the left or, respectively, the right mouse key to indicate whether the probe item was the same as or different from the pacman at the same location in the preceding memory display. Participants were instructed to respond as accurately as possible. In half of the trials, the probe on the cued side was identical (in terms of both color and gap orientation) to the item presented at that particular location in the previous memory display (no-change condition). In the other half of trials, the probe item was changed in either color or orientation (with equal probability) relative to the probed item in the memory array. The change was realized by presenting the probed item in either the color or the orientation of one of the other five items (randomly selected) in the memory display, thus encouraging observers to memorize individual items as conjunctions of color and orientation (rather than just independent sets of orientations and colors).

Trials were presented in randomized order such that all conditions, that is, the possible configurations (grouped, partially grouped, and ungrouped) and change types (no change, color, or orientation change), were presented randomly intermixed across trials. This ensured that observers were required to memorize both the color and orientation features in the memory displays. All participants performed 9 practice blocks of 64 trials each on the day before the experiment, to become familiar with the (rather demanding) task. The experiment itself then consisted of 18 blocks of 64 trials each, amounting to 1152 experimental trials. After each block, participants had the opportunity to take a short break.

2.4 | EEG recording

The EEG data were continuously recorded and digitized at 1000 Hz using a 64 channel Ag/AgCl active electrode system connected to a polyester elastic head-cap (EasyCap64, Brain Products, Munich, Germany). The electrodes were positioned in accordance with the international 10-10 system. The horizontal electrooculogram (EOG) was recorded from electrodes placed at the outer canthi of the eyes (F9 and F10). The vertical EOG was recorded from an electrode beneath the left eye (VEOG; positioned at the same distance from the center of the eye as the Fp1 electrode), in order to detect blinks and vertical eye movements. The electrode signals were amplified using a wireless amplifier system (BrainAmp, Brain Products, Munich, Germany) with a 0.1- to 250-Hz bandpass filter. During data acquisition, all electrodes were referenced to FCz and re-referenced offline to averaged mastoids. All electrode impedances were kept below 5 kΩ.

2.5 | Artifact rejection

Offline signal processing was performed using the Brain Vision Analyzer software (BrainProducts, Munich, Germany). The raw data were inspected visually to manually remove nonstereotypical noise. Next, an infomax independent component analysis was carried out to identify components representing blinks and/or horizontal eye movements and to remove these artifacts before back-projection of the residual components (1% of all trials were removed because of eye-movement artifacts). Prestimulus baseline correction (−200 ms to 0 ms before memory display onset) was performed on the raw voltages. ERPs were calculated time-locked to the onset of the memory display, with segments extending from 200 ms before memory display onset until 1300 ms afterwards. All epochs that contained artifacts were rejected and removed from the data proper [on average, 1.3% of all trials, where artifacts were defined as any signal exceeding ±60 μV, bursts of electromyographic activity (the maximum voltage step allowed per sampling point was 50 μV) and activity lower than 0.5 μV within intervals of 500 ms (indicating dead channels)]. Artifact-free epochs were averaged together to create ERP waveform.

2.6 | ERP data analysis

We included 6 parieto–occipital electrodes chosen a-priori and based on previous findings (e.g., Adam et al., 2018; Fukuda et al., 2015): PO3, PO4, PO7, PO8, O1, and O2. Specifically, we subtracted ERPs from parieto–occipital electrodes ipsilateral to the memory array's location from contralateral ERPs. Based on predictions drawn from previous work (see the Introduction section), we examined for an attentional modulation of modality-specific sensory responses in the visual Ppc, N1pc, N2pc, and CDA components (130–160 ms, 160–200 ms, 260–330 ms, and 350–1300 ms post memory display, respectively; in these time-windows, the respective components were clearly present in all conditions) at lateral parieto–occipital sites.

2.7 | Oscillatory amplitude analysis

To gain an overall picture of the frequency components, the pre-processed EEG time series data from each separate channel were Morlet-wavelet filtered into 31 frequency bands, $f_{\min} = 3$ Hz to $f_{\max} = 120$ Hz with the Morlet time–frequency compromise parameter m, being m = 5. For the time window between −200 and 1300 ms following stimulus onset, we extracted instantaneous amplitude values for the alpha band (8–12 Hz) and calculated the alpha amplitude for the same parieto–occipital electrodes as in the ERP analysis (PO3, PO4, PO7, PO8, O1, and O2). We calculated the mean amplitude over contralateral and ipsilateral posterior channels (PO3, PO4, PO7, PO8, O1, and O2) in the same way as for the ERP analysis (i.e., relative to the memory array). To compute the lateralization magnitude, we took the difference between the contralateral and ipsilateral alpha amplitude averaged over the specified time window (350–1300 ms) comparable to the procedure as described for the CDA.

3 | RESULTS

3.1 | Behavioral data

To determine whether there were differences in accuracy across the different experimental conditions, we performed a repeated-measures analysis of variance (ANOVA) with the factors object configuration (grouped, partially grouped, ungrouped) and change type (color, orientation). Greenhouse–Geisser-corrected values are reported when Mauchley's test of sphericity was statistically significant ($p < .05$). We additionally report Bayes factors (BF_{10}) for nonsignificant results to evaluate the evidence for the null hypothesis. The Bayes factor provides the ratio with which the alternative hypothesis is favored over the null hypothesis (values below 1/3 may be taken to support the null hypothesis, whereas values greater than 3 would provide evidence in favor of the alternative hypothesis; see Jeffreys, 1961; Kass & Raftery, 1995). As we had a-priori hypotheses about the direction of effects (we predicted grouping to lead to increased memory performance), one-tailed paired samples *t* tests (along with one-tailed Bayesian paired samples *t* tests) were used for comparisons between the various object configurations.

Figure 2a presents the percentage of correct responses as a function of object configuration, separately for color and orientation changes. The object-configuration by change-type repeated-measures ANOVA yielded significant main effects of object configuration, $F(2, 46) = 70.97$, $p < .001$, $\eta_p^2 = .76$, and change type, $F(1, 23) = 4.63$, $p = .04$, $\eta_p^2 = .17$. There was a graded effect of object configuration, with the highest accuracy for grouped configurations (73%), followed by partially grouped (66%) and ungrouped (63%) configurations (all p's $< .001$, d_zs > 0.88 for the pairwise comparisons between configurations). In addition, accuracy was higher for color changes than for orientation changes (68% vs. 66%). Finally, the object-configuration × change-type interaction was statistically significant, $F(2, 46) = 30.47$, $p < .001$, $\eta_p^2 = .57$: the enhancement of performance with increasing grouping strength was several times larger for orientation changes (grouped vs. ungrouped: 16%, $p < .001$, $d_z = 2.11$; grouped vs. partially grouped: 12%, $p < .001$, $d_z = 1.70$; partially grouped vs. ungrouped: 5%, $p < .001$, $d_z = 0.82$) than for color changes (grouped vs. ungrouped: 4%, $p < .001$, $d_z = 0.87$; grouped vs. partially grouped: 2%, $p = .013$, $d_z = 0.48$; partially grouped vs. ungrouped: 2%, $p = .038$, $d_z = 0.38$). It should be noted, however, that both types of change benefited significantly (albeit to a differential degree) from the increase in grouping strength. Overall, the mean performance was around 67%, while decreasing in some conditions to ~60% (e.g., in the orientation change condition with ungrouped configurations). Importantly, though, the mean accuracies were significantly above the chance level in all conditions, $ts(24) > 11.61$, $ps < .001$, $ds > 2.37$.

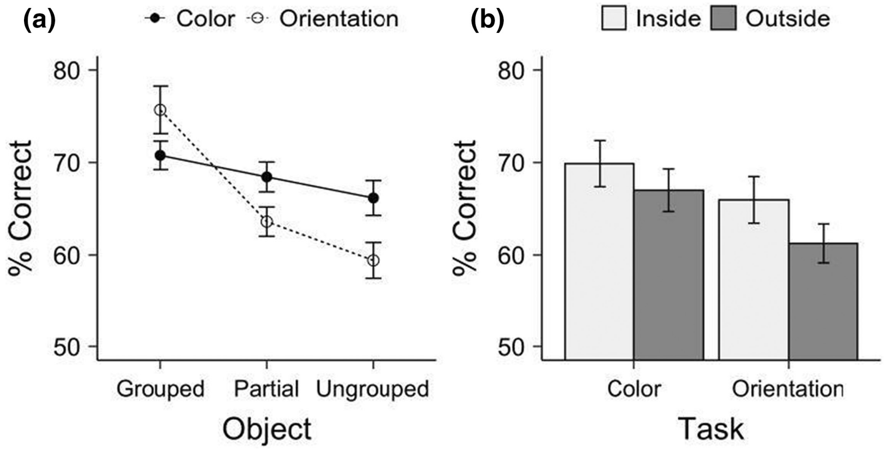

FIGURE 2 (a) The mean percentage of correct responses as a function of object configuration (grouped, partially grouped, and ungrouped) for the color and orientation changes (solid and dashed lines, respectively). (b) The mean percentage of correct responses as a function of change type (color and orientation) in the partially grouped triangle condition. Accuracies in b are plotted separately for trials on which the probe was one of the three pacmen that gave rise to the illusory triangle (inside), or, respectively, on which the probe was one of the three nongrouped pacmen (outside). Error bars denote the 95% (within-subject) confidence interval.

A subsequent analysis examined whether change detection performance was influenced by the probe location in partially grouped displays (with triangle groupings). Figure 2b presents the percentage of correct responses for color and orientation changes, separately for trials on which the probe was presented at one of the three pacman locations that formed the illusory triangle (inside) and, respectively, trials on which the probe appeared at one of the three other, "nongrouped" pacmen (outside). A corresponding two-way repeated-measures ANOVA of the accuracies, with the factors change type (color, orientation) and probe location (inside, outside), revealed both main effects to be statistically significant: change type, $F(1, 23)=15.96$, $p<.001$, $\eta_p^2=.41$; and probe location, $F(1, 23)=10.09$, $p=.004$, $\eta_p^2=.31$. Accuracies were higher for color changes (68%) than for orientation changes (64%), mirroring the analysis described above. In addition, the accuracies were increased when the probe was presented inside the partially grouped triangle (68%) as compared to an outside location (64%). The change-type × probe-location interaction was not statistically significant, $F(1, 23)=0.55$, $p=.47$, $\eta_p^2=.02$, $BF_{10}=0.34$. Thus, the behavioral results directly replicate our previous findings (Chen, Kocsis, et al., 2021) and show an object-benefit for both grouping-relevant *and* -irrelevant features.

Moreover, a final analysis was performed which computed an overall estimate of VWM capacity K (Cowan, 2001) in order to determine how the change in grouping strength across our stimulus configurations affected the capacity estimate. Each individual's memory capacity was computed using Cowan's formula: $K=(H-\text{FA})\times N$, where K is the memory capacity, H is the observed hit rate, FA is the false alarm rate and N is the number of (pacman) items presented. The resulting capacities for orientation and color change trials were then combined to yield an overall capacity estimate for a given configuration. Next, a one-way repeated-measures ANOVA was performed on the mean K estimates, which (again) revealed a reliable effect of Object Configuration, $F(2, 46)=70.97$, $p<.001$, $\eta_p^2=.76$. The K estimates were the largest for the grouped configuration (5.5), intermediate for partially grouped configuration (3.8), and smallest for the ungrouped configuration (3.0; all p's $<.001$, d_zs >0.65, for the pairwise comparison) between configurations). This shows that grouping can lead to a substantial enhancement of the overall VWM capacity beyond the usual capacity estimates of around 3–4 items (Luck & Vogel, 1997).

3.2 | ERP data

The corresponding ERP waves at parieto–occipital electrodes (averaged across electrodes PO3, PO4, PO7, PO8, O1, and O2) for the different object configurations are plotted in Figure 3a. Visual inspection of the ERP waves suggests that major differences between the different object configurations occurred in the Ppc, N1pc, N2pc, and CDA components. Statistical analyses confirmed this observation, showing significant contra/ipsilateral amplitude differences in the latency range of these components at parieto–occipital electrodes (see Figure 3b; all ps $<.05$, d_zs >0.39). Of note, the negative deflection that preceded the Ppc did not show any statistically significant difference across contra/ipsilateral amplitudes (all ps $>.05$, d_zs <0.34). For the subsequent analyses, we examined these amplitude variations across conditions separately for each component in a series of one-way repeated-measures ANOVAs with the within-subject factor Object Configuration (ungrouped, partially grouped, and grouped; see also Figure 3c).

First, the ANOVA of the mean Ppc amplitudes revealed the object-configuration effect to be statistically significant, $F(2, 46)=11.13$, $p<.001$, $\eta_p^2=.33$: there was a graded difference across object configurations, with the positive deflection being largest for the ungrouped (0.72 μV), intermediate for partially grouped (0.52 μV), and smallest for the grouped (0.36 μV) configurations (all p's $<.02$, d_zs >0.44, for the pairwise comparisons between configurations).

The analysis of the N1pc also yielded a significant configuration effect, $F(1.42, 32.59)=4.77$, $p=.025$, $\eta_p^2=.17$, with a larger negativity for the grouped (−0.61 μV) as compared to the ungrouped (−0.32 μV, $p=.004$, $d_z=0.59$) and partially grouped (−0.44 μV, $p=.004$, $d_z=0.60$) configurations, but no statistically significant difference between ungrouped and partially grouped configurations ($p=0.16$, $d_z=0.21$, $BF_{10}=0.56$).

For the N2pc, the Configuration effect was again statistically significant, $F(2, 46)=9.84$, $p<.001$, $\eta_p^2=.30$, due to more negative-going amplitudes for the grouped (−1.14 μV) as compared to the ungrouped (−0.77 μV, $p=.001$, $d_z=0.71$) and partially grouped (−0.82 μV, $p=.001$, $d_z=0.70$) configurations, but no reliable difference between ungrouped and partially grouped configurations ($p=.26$, $d_z=0.13$, $BF_{10}=0.38$).

Finally, the analysis of the CDA amplitudes also yielded an effect of object configuration, $F(2, 46)=5.72$, $p=.006$, $\eta_p^2=.20$. As depicted in Figure 3c, the mean CDA amplitude was more negative for the grouped (−1.45 μV) as compared to the ungrouped (−1.23 μV, $p=.003$, and $d_z=.62$) and partially grouped (−1.31 μV, $p=.005$, and $d_z=.57$) configuration. There was again no statistically significant difference between ungrouped and partially grouped configurations ($p=.14$, $d_z=.23$, and $BF_{10}=0.65$).

Moreover, when looking at the CDA in Figure 3a, it appears that object-specific variations were larger during the

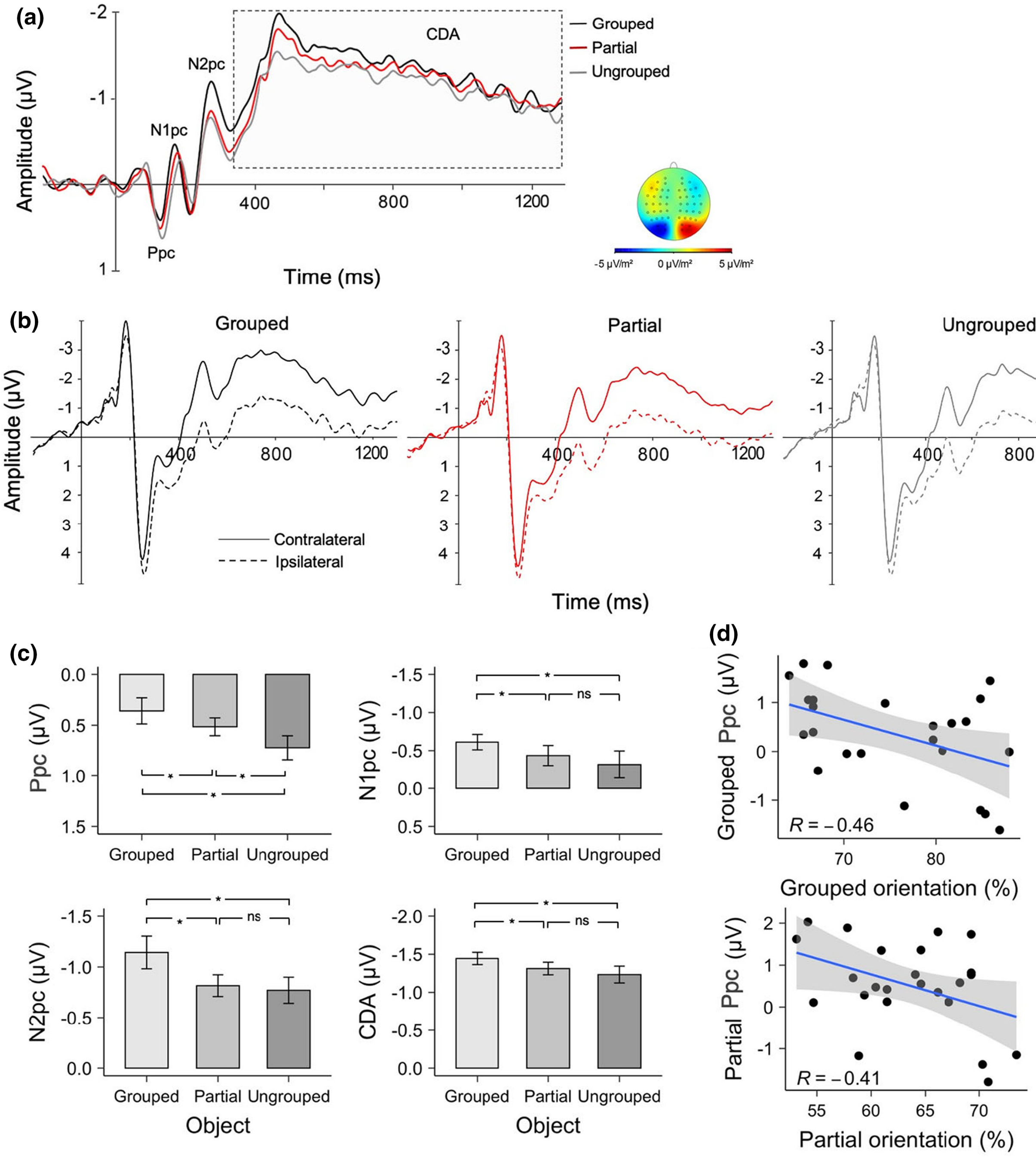

FIGURE 3 (a) Grand-average ERP difference waves (contralateral minus ipsilateral activity relative to the memorized display hemifield) time-locked to the onset of the memory display at parieto–occipital electrodes (PO3, PO4, PO7, PO8, O1, and O2) for the different object configurations. Scalp distribution maps were comparable across all components (Ppc, N1pc, N2pc, and CDA), we therefore chose to present the point in time at which the respective difference waves (between grouped and ungrouped configurations) reached their maximum. (b) Grand-average ERPs (a) at parieto–occipital electrodes (PO3, PO4, PO7, PO8, O1, and O2) contra- and ipsilateral to the object configurations. (c) The mean amplitudes of the Ppc, N1pc, N2pc, and CDA components as a function of object configuration. Error bars denote 95% (within-subject) confidence intervals. Statistically significant differences revealed by pairwise comparisons are indicated by asterisks; *$p < .05$. (d) Correlations. The scatterplots show the relationship between individuals' behavioral performance in grouped (upper panel) and partially grouped (lower panel) configurations and their corresponding Ppc amplitudes. Solid lines indicate the best-fitting regressions, shaded regions illustrate 95% confidence intervals.

initial parts of the retention period, while these differences then recede with increasing time. Given this, two further analyses on the early (350 ms to 800 ms) and late (800 ms to 1300 ms) CDA time windows were performed. These analyses showed a significant effect of Object Configuration in the early CDA amplitudes, $F(2, 46) = 10.12$, $p < .00$, $\eta_p^2 = .31$, with a larger negativity for grouped (−1.37 μV), than partially grouped (−1.19 μV), and ungrouped (−1.10 μV) configurations (grouped vs. ungrouped, $p < .001$, $d_z = .93$; grouped vs. partially grouped, $p = .003$, $d_z = .63$; partially grouped vs. ungrouped, $p = .085$, $d_z = .29$, $BF_{10} = 0.94$), thus mirroring the pattern reported for the overall CDA analysis. However, there was no comparable effect in the late CDA amplitudes, $F(2, 46) = 0.89$, $p = .42$, $\eta_p^2 = .04$, and $BF_{10} = 0.23$, which shows that the differences between object configurations indeed become smaller during the second half of the retention period. This gradual fading of object-specific variations may not primarily be associated with a specific functional cause, but could simply relate to the use of the high-pass filter of 0.1 Hz, which might have obscured some of our effects, especially in the slow potentials in the longer term (Tanner et al., 2015), albeit its beneficial effect of improving the signal-to-noise ratio.

The result patterns of the Ppc, N1pc, N2pc, and CDA mirror (at least to a large extent) the pattern of behavioral performance, evidencing an effect of Object Configuration, which was driven particularly by the fully grouped star object. Interestingly, this graded improvement in VWM performance with an increase in grouping strength (across all three configurations) was already evident at relatively early stages of perceptual processing, namely, in the Ppc component.

Moreover, the CDA results essentially mirrored the estimated VWM capacity scores (see above), thus supporting the view that the CDA corresponds to the number of effectively remembered items. In addition, the findings are also compatible with the view that the generation of a global shape (in Kanizsa figures) requires additional mnemonic resources, and this increase in the mnemonic activity may likewise be reflected in the increased negativity of the CDA.

Finally, additional correlational analyses between the individual behavioral performance and the corresponding ERP amplitudes revealed statistically significant negative relationships for the Ppc components in the grouped and partially grouped configurations for orientation changes (grouped: $r = -.46$, $p = .01$; partially grouped: $r = -.41$, $p = .02$; see Figure 3d), which was less pronounced with ungrouped configurations ($r = -.32$, $p = .06$, and $BF_{10} = 1.40$). That is, the Ppc amplitude scaled with behavioral performance in particular for the grouped (and partially grouped) memory configurations. The correlations thus show that larger performance benefits for the (partially) grouped memory configurations were associated with less positive Ppc amplitude deflections. No other statistically significant correlations between behavioral performance and ERP components were revealed. Statistical significance of the correlation coefficient was determined by comparing the observed correlations with results derived from 20,000 permutations of the two variables, thus excluding the influence from any outlier in the data.

3.3 | Oscillatory amplitude

Figure 4a shows the time–frequency profile across trials. As can be seen, variations of grouping strength modulated activations in the alpha band (8–12 Hz), with no other frequency ranges showing comparable changes in activity. Given this, we examined changes in the lateralized alpha amplitude (contralateral–ipsilateral) as a function of Object Configuration using a repeated-measures ANOVA with the within-subject factor Object Configuration (ungrouped, partially grouped, and grouped). The lateralized alpha during the *pre-stimulus* period (−200–0 ms) yielded no effect of configuration (−0.41 μV, −0.49 μV, and −0.37 μV for ungrouped, partially grouped, and grouped configurations, respectively), $F(2, 46) = 0.60$, $p = .55$, $\eta_p^2 = .03$, $BF_{10} = 0.18$, showing that alpha amplitudes were comparable across conditions before trial onset. However, during the *delay* period (350–1300 ms), there was a significant main effect of configuration, $F(2, 46) = 8.73$, $p < .001$, $\eta_p^2 = .28$, indicating that lateralized alpha is suppressed the most for ungrouped (−0.76 μV), followed by partially grouped (−0.69 μV), and least for grouped (−0.62 μV) configurations (all p's $< .02$, $|d_z|$s > 0.44, for the pairwise comparisons between configurations; see Figure 4b,c). Note that the observed differences in the lateralized alpha amplitudes were mainly associated with contralateral variations (which was strongly modulated by object configuration, $F(2, 46) = 7.71$, $p = .001$, $\eta_p^2 = .25$), thus reflecting processing of the task-relevant stimulus configurations rather than the inhibition of task-irrelevant placeholders (the latter being associated primarily with ipsilateral alpha activity, which was overall comparable for different configurations, $F(2, 46) = 0.12$, $p = .88$, $\eta_p^2 = .005$, $BF_{10} = 0.13$).

4 | DISCUSSION

The present study examined a series of lateralized ERP components and the lateralized alpha-band suppression at parieto–occipital electrodes to elucidate the mechanisms involved in the representation of grouped features in VWM. The behavioral results revealed a large grouping benefit for detecting orientation changes; additionally, there was a smaller, but reliable benefit for color changes—thus directly replicating our previous behavioral study (Chen, Kocsis, et al., 2021). Analyses of the ERPs revealed that the Ppc, N1pc, N2pc, and CDA were all more negative when the pacmen formed perceptual groups

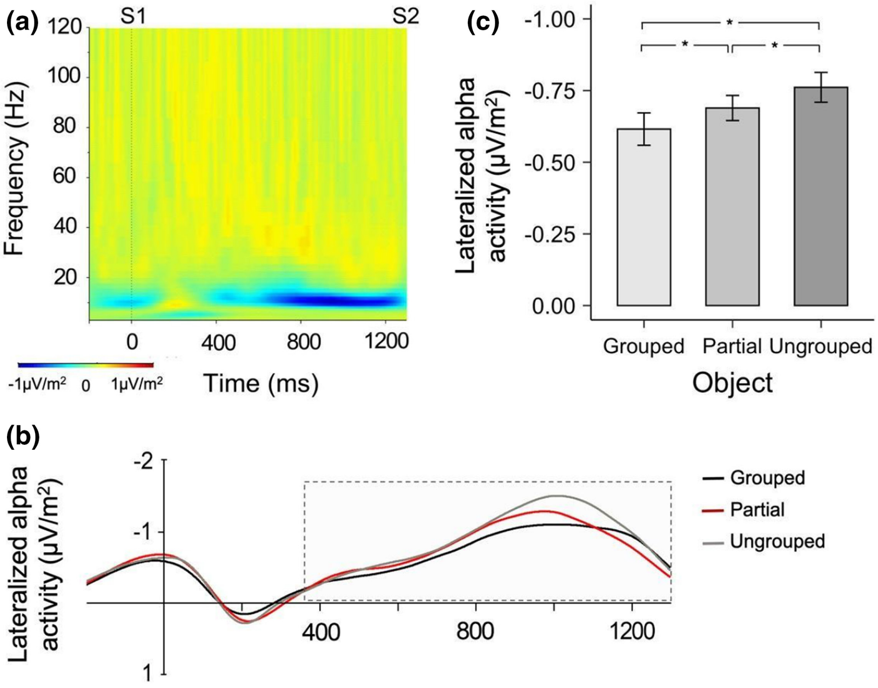

FIGURE 4 Analysis of alpha amplitudes. (a) Lateralized event-related amplitude changes in the frequency range between 0–120 Hz for the grouped configurations observed at the parieto–occipital channels (PO3, PO4, PO7, PO8, O1, and O2). In the figure, cold colors depict a reduction in power. The figure shows the strong decrease in power at frequencies around 8–12 Hz (in the alpha band) during memory retention. (b) Lateralized alpha amplitude, plotted as a function of time for grouped (black), partially grouped (red), and ungrouped (gray) configurations. The dashed rectangle denotes the time window during memory retention (350–1300 ms). (c) Mean lateralized (contralateral–ipsilateral) alpha amplitudes as a function of object configuration during the memory-retention time window (350–1300 ms); higher negative values reflect more reduced contralateral alpha activity. Error bars denote the 95% (within-subject) confidence interval. Statistically significant differences revealed by pairwise comparisons are indicated by asterisks; $^{*}p < .05$.

than when they did not. There was a single, longer-lasting change spanning the timing of the Ppc and N1pc. The early Ppc already mirrored the gradual variation of behavioral change-detection performance for grouped, partially grouped, and ungrouped configurations. Moreover, there was a significant negative relationship between behavioral accuracy and the Ppc in the grouped and partially grouped configurations, indicative of individual variations of grouping upon memory performance being already reflected in these early lateralizations. The Ppc component might be associated with an initial boost of perceptual processing (Fukuda & Vogel, 2009; Hoffmeister et al., 2022; Livingstone et al., 2017), but it was also found to be sensitive to object integration (e.g., Kasai et al., 2015; Nikolaev et al., 2008; Slavutskaya & Mikhailova, 2011). Of note, however, grouping was also found to influence subsequent attentional and memory processing stages, as evidenced by the modulations of the N1pc, N2pc, and CDA waves, which were driven in particular by the fully grouped star object. In addition, the lateralized alpha amplitude was gradually modulated by the presented object configurations, with most suppression occurring with the ungrouped, followed by partially grouped, and least suppression with grouped configurations. Taken together, these findings indicate that object integration at early perceptual stages influences processing at subsequent stages, thereby facilitating focal-attentional processing and the subsequent maintenance of individual objects and their constituent features, thus leading to enhanced precision of grouped representations stored in VWM.

Our results confirm that perceptual grouping provides an efficient means to combine multiple elements into higher-order units, consistent with previous reports of improved memory performance when multiple features can be represented as a coherent (grouped) object, as compared to the same set of features distributed across multiple, separate items (e.g., Chen, Kocsis, et al., 2021; Fougnie et al., 2013; Luria & Vogel, 2011; Olson & Jiang, 2002; Xu, 2002). In this view, grouping may enhance memory by providing an integrated, higher-order (superordinate) object representation (e.g., a “star” or a “triangle”), with this global object facilitating the comparison with the probe and thereby freeing VWM resources. This may explain why not only the grouping-relevant feature (orientation) but also the grouping-irrelevant feature (color) benefits from the superordinate object representation (at least when attention is set to process whole objects, that is, when both color and orientation are task-relevant, see Chen, Kocsis, et al., 2021). For instance, the improved VWM representation of orientation features with grouped configurations may free memory resources that are then available to also process the color features of the to-be-memorized objects in greater detail.

Going beyond previous findings, our results indicate that memorizing features (i.e., orientation and color) in grouped objects involves multiple, sequential stages of processing that can be traced using lateralized ERPs (see also Kasai et al., 2015). Interestingly, this benefit of grouping in VWM already arises at an early perceptual level of processing (as evidenced by the modulations in the Ppc component). In this regard, our study is the first to show that effects of grouping upon (higher-order) processing of visual information in VWM already originate at an early perceptual level of processing (i.e., in the Ppc). In earlier studies (e.g., Nikolaev et al., 2008; see also Esposito et al., 2023; Nikolaev et al., 2016), the P1 amplitudes were found to be affected by, and negatively correlated with, grouping sensitivity in a (perceptual) discrimination task. This is consistent with the present results that also showed negative correlations between the Ppc amplitudes and the (grouping-related) orientation detection performance. For instance, the larger the Ppc amplitude, the lower the orientation detection accuracies, suggesting that an increase in early visual processing demands (as indicated by a larger Ppc), coincides with comparably reduced performance for remembering the orientation features. The posterior P1 has also been found to reveal a systematic amplitude increase in relation to a progressive disintegration of objects into their constituent elements, with lower amplitudes to whole figures and larger amplitudes to their disintegrated parts (Slavutskaya & Mikhailova, 2011). Consistent with this result, the Ppc revealed the largest positivity for ungrouped, followed by partially grouped and least for grouped configurations, suggesting that the extraction of visual information is more demanding for ungrouped items relative to "more" grouped objects.

Preferential processing of a coherent grouped object (as compared to ungrouped fragments) was also evident in the N1pc (see also Herrmann & Bosch, 2001; Kruggel et al., 2001; Martinez et al., 2007; Murray et al., 2002). This effect was mainly driven by the large and reliable difference between grouped and partially grouped/ungrouped configurations, while revealing no statistically significant difference between partially grouped and ungrouped configurations. An obvious reason for the non-significant difference between ungrouped and partially grouped configurations could relate to overall task difficulty. For instance, our observers were required to memorize six different colors and six different orientations—which is clearly above the usual maximum VWM capacity estimate of three to four items (Luck & Vogel, 1997). ERP differences between the partially grouped and ungrouped configurations might thus be difficult to resolve given that performance clearly operates beyond the usual capacity limits. In the grouped condition, the performance improved quite substantially (revealing an orientation detection accuracy of 77% as compared to smaller differences for the partially grouped [65%] and ungrouped [60%] configurations). Due to this variation in the size of the behavioral effect, the N1pc results pattern could thus mirror the overall efficiency in selecting and representing the partially grouped and ungrouped configurations (the same might also be true for the subsequent N2pc and CDA effects, where the difference between partially grouped and ungrouped configurations was also non-significant). However, beyond these difficulties to resolve the gradual increase in grouping strength in some of the ERPs, the "overall" grouping modulations in the Ppc and N1pc together nevertheless clearly show that integrated objects modulate the bottom-up attentional deployment towards to-be-memorized items at early processing stages.

Following these, variations of grouping strength were found to also modulate the N2pc component, which—in the current study—likely reflects the engagement of focal attention (Eimer, 1996; Luck & Hillyard, 1994) by the to-be-memorized items. The current study yielded a larger N2pc for grouped relative to ungrouped and partially grouped configurations, which presumably reflects a more pronounced focus of (focal) attention towards more regular, grouped objects (see also Conci et al., 2006, 2011; Senkowski et al., 2005; Töllner et al., 2015). In previous visual search studies that employed Kanizsa-type configurations (e.g., Conci et al., 2006), the target was always defined as a Kanizsa figure while the distractors (in the opposite hemifields) varied in terms of grouping strength (alongside with a variation in target-distractor similarity). In these cases, stronger grouping in distractors would result in a broader attentional tuning, thus reducing the (focal) attentional engagement towards the Kanizsa target figure. In the current change-detection task, grouping strength was always manipulated in the task-relevant memory array (presented in one hemifield of the displays), which would conversely result in a larger N2pc for the grouped configuration relative to the less grouped configurations. These findings thus coincide in that grouping in distractors diverts attentions away from the target (see Conci et al., 2006), while enhanced grouping in the target configuration leads to an enhanced attentional focus (see Conci et al., 2011). Grouping thus appears to influence both early perceptual processes and the subsequent attentional selection and engagement, with attention being facilitated by the processing of the grouped items (e.g., Marini & Marzi, 2016; Rauschenberger & Yantis, 2001; Senkowski et al., 2005; Wiegand et al., 2015).

Finally, the subsequent memory-maintenance stage exhibited a continuous grouping benefit, as revealed by an enhanced CDA for grouped, as compared to ungrouped and partially grouped, configurations. At first glance, this result seems inconsistent with previous evidence that suggested that perceptual grouping effectively reduces the effective number of "items" in the display, thereby leading to reduced CDA amplitudes (Anderson et al., 2013; Gao et al., 2011; Peterson et al., 2015). Of note, however, these previous studies usually manipulated grouping by means of item similarity, which is different from the current study, where disparate objects were bound into a unified global object by grouping on the basis of closure (and collinearity). For example, it was reported in previous studies that similar colors were compressed in VWM such that the CDA amplitude for these colors was reduced and essentially comparable in amplitude to just one to-be-memorized color (Gao et al., 2011; Peterson et al., 2015). In contrast, the six different colors and the six orientations used in the present study were maximally different from each other and they could therefore not be represented in a compressed format, which might then be seen in the CDA. Moreover, in the current study, the physical stimulation was always identical while only the grouping strength differed across conditions. The current study therefore provides evidence for an unconfounded influence of grouping upon VWM, while controlling other factors relating to the stimulus itself.

A major characteristic of the CDA is that its amplitude increases with the number of objects maintained in VWM (for a review, see Luria et al. (2016)), while usually reaching an asymptote at about 3–4 items, which reflects the maximum capacity (Cowan, 2001; Luck & Vogel, 2013). The current study presented 6 items (with 6 distinct orientations *and* 6 colors) in all conditions, which is clearly above the usual capacity limit. Interestingly, our results showed that grouping can lead to a substantial capacity enhancement up to an estimate of around 5.5 items with grouped configurations—relative to 3.8 and 3.0 items for partially grouped and ungrouped configurations, respectively. This increase in the overall K estimates was also mirrored in CDA variations, which suggests that the grouping-dependent increase in memory capacity is reflected in the CDA measure.

The CDA appears to not only represent the passive storage of individual items, but also reflects the active representation of globally completed objects in VWM, which may in turn require additional mnemonic resources. For instance, a sustained increase in the CDA amplitude (and a concurrent improvement in performance) was found to be associated with objects that are completed despite partial occlusion—as compared to physically identical, yet uncompleted object fragments (Chen, Töllner, et al., 2018). It is thus possible that "modal" completion of Kanizsa figures exhibits similar VWM storage properties and reveals comparable CDA modulations than objects that are integrated on the basis of "amodal" completion (e.g., due to partial occlusion), given that modal and amodal completions are associated with comparable behavioral patterns (e.g., Chen, Glasauer, et al., 2018) and partially overlapping neural mechanisms (Murray et al., 2004).

A complementary pattern of results was additionally revealed from the analysis of the oscillatory amplitudes. For instance, we found a graded, grouping-strength-related modulation in the lateralized alpha suppression during the maintenance phase, which was comparable to the observed Ppc variation during initial perceptual processing. Specifically, the observed differences in the lateralized alpha amplitudes that we observed were associated mainly with contralateral variations, that is, they reflect the processing of the task-relevant stimulus configurations rather than the inhibition of task-irrelevant placeholders (see also Bacigalupo & Luck, 2019; Noonan et al., 2016; Thut et al., 2006). Moreover, our findings show that the lateralized alpha suppression increased as grouping strength decreased, thus possibly reflecting the "effort" in representing individual features of less vs. more strongly grouped objects despite a constant number of to-be-encoded locations. Posterior-occipital alpha has been suggested to reflect top-down adjustments of attentional control (e.g., Murphy et al., 2020; Thut et al., 2006; Wang et al., 2019, 2021; Woodman et al., 2022). In agreement with this interpretation, the variation of lateralized alpha in the current study may index the larger attentional demands required to process the less (vs. more) grouped configurations. This may also explain the similarity of the result pattern revealed for the lateralized alpha suppression to concurrent variations in the Ppc component, with both components actually revealing a statistically significant correlation (grouped: $r = .41$, $p = .02$; partially grouped: $r = .32$, $p = .067$, $BF_{10} = 1.35$; ungrouped: $r = .37$, $p = .037$). These comparable modulations of the neuronal signatures might thus be associated with comparable (attentional) processing requirements (albeit at different levels of processing).

We would thus propose that the CDA and lateralized alpha suppression might be mapped onto two separable cognitive mechanisms of VWM, relating to (i) the representation of individual objects and (ii) associated attentional control processes, respectively (Unsworth et al., 2014; see also Fukuda et al., 2015). That is, the CDA effect as a function of grouping might be more consistent with mechanisms necessary for holding multiple individuated representations in an active state over the duration of the retention interval. And the increased lateralized alpha suppression for more ungrouped elements might in turn be directly associated with the increased attentional control demands for keeping the individual representations accessible during maintenance when the displayed stimulus configuration increases in perceptual complexity. In this view, the two neurophysiological signals might reflect manifestations of linked neural processes (see also Mazaheri & Jensen, 2008; van Dijk et al., 2010; but see Fukuda et al., 2015), with lower effort and higher precision in representing features of the grouped configuration as compared to higher effort and lower precision relating to ungrouped configurations. While being overall consistent with our current findings, admittedly, this interpretation of the relation between the CDA and alpha activity is, to a certain extent, still speculative and it might thus be necessary to consolidate these interpretations in future studies.

Our current findings may also be related to a theoretical framework that we proposed previously (Chen, Kocsis, et al., 2021), and according to which objects might be stored in VWM in terms of a hierarchical structure, comprising basic feature-level representations and associated higher-order, object-level representations (see also Brady et al., 2011; Nie et al., 2017). The representation of information at different levels in this hierarchy would jointly determine the capacity and quality of VWM representations. Moreover, depending on the current task, only to-be-remembered objects and associated features would be encoded and/or represented (Bocincova & Johnson, 2019; Chen, Kocsis, et al., 2021; Serences et al., 2009; Woodman & Vogel, 2008). In this view, the encoding of grouping-relevant (orientation) features would give rise to the encoding of the superordinate grouped object (which would in turn be represented at a higher level in the hierarchical memory structure, and which is reflected by the effects seen in the early Ppc). The superordinate object representation in turn strengthens the representation of the grouping-relevant features (via reciprocal-feedforward/feedback connections). Moreover, the superordinate object representation also enhances the attentional selection (as reflected by the enhanced N1pc and N2pc) of both grouping-relevant and -irrelevant features at the basic level of representation via a feedback connection as the complete object is brought into the “focus of attention” (see, e.g., Oberauer & Hein, 2012; Printzlau et al., 2022; Souza & Oberauer, 2017). In the subsequent retention stage, the number and precision of feature representations is improved by the (superordinate) grouped object representation which might be reflected by variations in the CDA amplitude, while concurrent alpha activity would index the attentional requirements to process these maintained objects (see Machizawa et al., 2012; Wang et al., 2019, 2021; Woodman et al., 2022).

5 | CONCLUSIONS

The present study shows that memorizing (grouping-relevant and -irrelevant) features in grouped objects involves multiple, sequential stages of processing that can be traced using lateralized ERPs and alpha activity. When multiple features of an object need to be encoded, the observed benefit of grouping arises already at an early, perceptual level, influencing subsequent processes of attentional selection, with attention conferring an advantage to grouped items during the encoding of the stimulus configurations into VWM and reinforcing the representations of individual features during the retention stage. The results provide support for a hierarchical model of memory representation, with the grouping-relevant feature establishing a superordinate object representation, which in turn enhances the representation of the basic-level grouping-relevant and -irrelevant features.

AUTHOR CONTRIBUTIONS

Siyi Chen: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft. **Thomas Töllner:** Conceptualization; methodology; resources; software; validation. **Hermann J. Müller:** Conceptualization; resources; validation; writing – review and editing. **Markus Conci:** Conceptualization; funding acquisition; methodology; project administration; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and materials have been made available via the Open Science Framework and can be accessed under this link: https://osf.io/3u96g/.

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