Memory Representations in Visual Working Memory: Representational Quality and Memory Access[*]

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Previously, Shin and colleagues (2006) reported sequential deflections of encoding-related lateralization (ERL) waveforms in event-related potentials (ERPs). One of these deflections, observed at posterior electrode sites (P7/P8), started about 400 ms poststimulus, and was dependent on both memory set-size and the degree of matching between memory-sets and test probes. These suggest that there is a level at which relations among items and degree of memory access are important in visual working memory. Based on these findings the present study investigated representational quality and degree of memory access. It was hypothesized that representational quality could be lowered by competition between stimuli (local suppression), and that degree of memory access be lowered when probes only partially match memory-set stimuli (partial matching). The relative distance (close or far) and similarity (homogeneous or heterogeneous) between memory-set stimuli were varied. ERPs were recorded while participants made old or new responses to single probes preceded by memory-sets (of size 2 or 4). ERL results obtained from 33 participants showed (a) that large ERL effects were found at the P7/P8 sites with a latency of 400-700 ms from probe onset, similar to Shin et al. (2006); (b) that significant ERL activity was observed only for the homogeneous memory-sets presented far apart; and (c) that the heterogeneous memory-sets presented nearby showed significantly smaller ERL activity than set-size 2 memory-sets (representing no-suppression and complete matching). These results support a hybrid of the local suppression and partial matching hypotheses, suggesting that representational quality and degree of memory access can jointly influence visual working memory processing.

Key words : visual working memory, encoding-related lateralization (ERL), representational quality, degree of memory access, event-related potentials (ERPs)

In the past decades research on visual working memory has largely focused on revealing its storage capacity (e.g., Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007; Bays & Husain, 2008; Luck & Vogel, 1997). Studies have shown that the capacity is limited to a fixed number 3 or 4 items (e.g., Awh, Barton, & Vogel, 2007; Luck & Vogel, 1997). Yet, other studies have shown evidence against this idea, suggesting that the capacity can vary depending on some factors -- for instance, stimulus complexity (Alvarez & Cavanagh, 2004; Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2009), categorical distinctiveness of stimuli (Olsson & Poom, 2005), or choice of task (Awh et al., 2007; Olsson & Poom, 2005). Thus, how to view and measure the capacity of visual working memory has not been determined. In the midst of this heated debate over storage capacity, some researchers suggested to move beyond quantifying visual working memory capacity and to focus on the nature of memory representations (Brady, Konkle, & Alvarez, 2009, 2011; Brady & Alvarez, 2011), which is in fact the essential part of memory. Memory systems can be discussed in many aspects such as capacity, conscious access, memory representations, mechanisms of operation, and so on. When visual working memory is viewed as one of the memory systems, it is important to understand these various aspects. From this perspective, the current study sought to elucidate the nature of memory representations in visual working memory. Specifically, representational quality and degree of memory access were investigated by advancing previous results reported by Shin, Fabiani, and Gratton (2006).

Shin and colleagues (2006) investigated different levels of memory representation in visual working memory. They used some of the English alphabet letters, having different shapes but the same symbol such as G and g. A memory-set (of size 2 or 4) was presented and was followed by a single probe. These successive presentations of the memory-set and the probe yielded four conditions in which the probe matched or did not match the memory-set items in shape, symbol, and the number of memory-set items per hemifield. Distinct brain responses sensitive to the matching/mismatching between the memory-set and the probe in these dimensions were elicited across different time windows, suggesting the existence of physical, symbolic, and set-size dependent levels of representation.

These different levels were revealed through the encoding-related lateralization (ERL) method (Gratton, 1998). The ERL method uses divided-field paradigms in which a bilateral presentation of a memory-set is followed by a foveally presented probe that may or may not correspond to one of the items in the

memory-set. More specifically, as shown in Figure 1 half a set-size of memory items is presented in each hemifield. For example, in the case of a set-size 2 one item is presented in the left hemifield and the other in the right hemifield simultaneously. One probe item is then foveally presented. Following the contralateral organization of the visual system, it is expected that this divided-field presentation of a memory set leaves at least some of their memory representations lateralized. That is, contralaterally-biased memory representations are induced by this divided-field presentation. Also, as studies showed that the brain regions that were involved during encoding are activated at retrieval (Wheeler, Peterson, & Buckner, 2000), recognition of memory involves overlap between encoding and retrieval processes (Roediger, Weldon, & Challis, 1989). Thus, when the foveally presented probe matches one of the memory representations along different dimensions (e.g., shape, set-size), presumably the brain regions in which the lateralized memory traces were formed during encoding should reactivate. The shaded areas in Figure 1 show this logic. If foveally presented probes elicit asymmetric brain activity, this suggests the lateralization bias of the corresponding memory representation that was formed during encoding. Therefore, the extent to which a significant ERL is obtained can be taken to reflect lateralized

aspects of the encoded representation (referred to as the encoding-related lateralization). This ERL is derived from event-related brain potentials (ERPs, Fabiani, Gratton, & Federmeier, 2007), and is obtained only when the probe matches the memory-set. Thus, ERL activity is elicited only for old trials following probe onset.

The present study focused on one of the ERL activities found in the previous study. This particular ERL activity emerged in a late time window, later than 400 ms after probe onset, and was evident at posterior electrode sites close to occipitotemporal areas of the brain, in which complex forms of objects such as faces (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999; Chong et al., 2013; Kanwisher, Chun, McDermott, & Ledden, 1996), houses (Epstein & Kanwisher, 1998), and letters (Allison et al., 1994, 1999; Flowers et al., 2004; Tarkiainen, Cornelissen, & Salmelin, 2002) are represented. This ERL was la rgest when the probe letter matched the memory-set letter by both shape and the number of items per hemifield. In other words, the ERL was largest when the memory-set item presented in one hemifield was identical to the probe, as shown in the upper panel in Figure 1. In addition, it was not until this time window when ERL amplitude was affected by the memory-set size, indicating that this particular ERL is set-size dependent. The
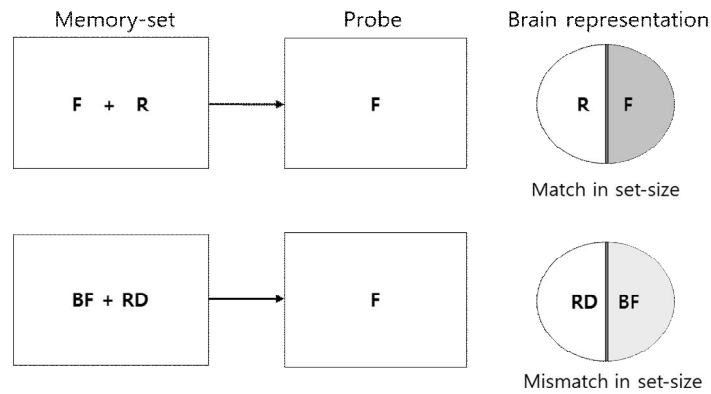
Figure 1. Illustration of a divided-field paradigm that provides the basis for the ERL method. The upper and lower panels show schematic descriptions of the difference in ERL activity found in Shin et al. (2006). They also show the complete and partial matching between the hemispherically-biased memory representation(s) and the probe, respectively. The darkness of the shades in the brain representation represents different ERL amplitudes.

current study tested two hypotheses, local suppression and partial matching, to account for this late, set-size dependent ERL effect. These hypotheses are intimately linked with representational quality and degree of memory access.

The local suppression hypothesis is based on the idea that this set-size dependent ERL effect might reflect a processing level in which a complex level of stimulus representation (e.g., relations among items) is achieved. Many visual cognition theories propose that in early processing stages features are rapidly and coarsely evaluated and in later stages multiple items demand attention and processing capacity is limited (Folk & Egeth, 1989; Treisman & Gelade, 1980). Some investigators have

postulated that the limited processing capacity may have a neurobiological basis, related to the changing sizes of receptive fields of neurons along visual pathways (Reynolds, Chelazzi, & Desimone, 1999). Results from brain imaging studies indicate that receptive fields typically increase as visual pathways progress from the posterior to the anterior areas (Kastner et al., 2001; Rousselet, Thorpe, & Fabre-Thorpe, 2004). This increasing receptive field sizes raise the likelihood of multiple stimuli falling within the same receptive field, leading to competition for neural representation among these stimuli and ultimately to lowing the quality of representation of each stimulus. In some studies, these degraded representations were reflected in suppressed functional magnetic resonance imaging

responses, which were scaled to the estimated receptive field sizes in the corresponding visual areas when multiple stimuli were shown in the same displays (Kastner, Weerd, Desimone, & Ungerleider, 1998, also see Kastner et al., 2001). Moreover, the magnitude of this suppression was inversely related to the extent to which stimuli were spatially separated (Kastner et al., 2001) as distancing stimuli from each other decreases the overlap in the receptive fields. In this context, the set-size dependent ERL effect may have occurred. Neural competition between the memory-set letters, caused by overlapped receptive fields, could have been greater in the set-size 4 than in the set-size 2 condition. As a result, in Shin et al. (2006) stimulus representation might have been more degraded when two letters were presented than when one letter was in the same hemifield.

The partial matching hypothesis is based on the idea that this late ERL effect may reflect a processing level in which the degree of matching between the memory representation and the probe is determined. In recognition memory the parietal ERP effect (see Rugg & Curran, 2007) is typically observed approximately at 400-800 ms poststimulus and reflects the degree to which specific information is recollected, as a larger ERP was observed for deeply studied items than for shallowly studied items (Rugg et al., 1998). Though it is not certain that the previous ERL

effect shares the same neural generator(s) responsible for this parietal ERP effect, it could have been produced due to the difference in accessing memory representations biased in the contralateral hemisphere. A full access should have facilitated a retrieval of more specific information than a partial access. As depicted in Figure 1, the upper panel shows the complete matching between the hemispherically biased memory representation and the probe (i.e., full access). The lower panel, however, shows the partial matching between the memory representations and the probe (i.e., partial access). Unlike in the complete matching condition, the degree of matching between the memory representations and the probe is low in half in the partial matching condition. This different degree of matching could have driven the different ERL effect in this time window. Namely, whether memory representations were accessed fully or partially may have been reflected in this late ERL activity. Pe rhaps, the partial match yielded a differential brain response from the complete matching because a smaller set of functional units (e.g., neurons) responded, and this was manifested in the amplitude difference between the complete and partial matching conditions.

Letter distance and letter similarity were manipulated to test the local suppression and the partial matching hypothesis, respectively. As

shown in Figure 2, both distance and similarity were manipulated for the set-size 4 trials, in which the distance and similarity of two letters were varied within each hemifield. For letter distance, letters were presented close to or far from each other. In this case, the quality of letter representations should be lower for the near letters than for the distant letters. Thus, the local suppression hypothesis predicted that a smaller lateralization should be observed in the close condition than in the far condition. In addition, the far condition should elicit an ERL more similar to the set-size 2 condition than the close condition because the letters in the set-size 2 condition presumably have least neural

competition. Moreover, degraded representations can be reflected in the form of lower accuracy and/or slower reaction time (RT) as found in some studies (Bahcall & Kowler, 1999; McCarley & Mounts, 2007; Mounts & Gavett, 2004). The close condition in the current study may show such results.

For letter similarity, the two letters presented within the same hemifield were either identical -- homogeneous condition -- or different -- heterogeneous condition. Unlike the homogeneous condition (complete matching), the heterogeneous condition matches the probe only in half (partial matching). In other words, whereas the memory representations are fully accessed in the
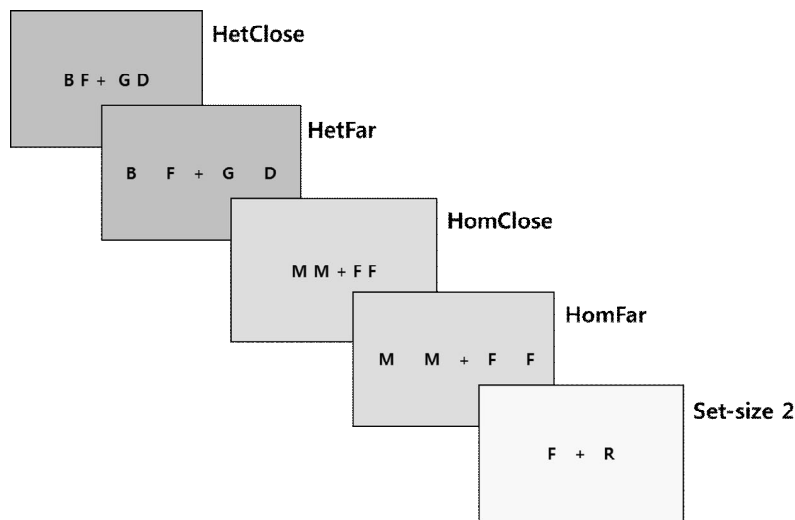

Figure 2. Examples of different memory-sets. If "F" (the probe) is preceded by these memory-sets, it will result in partial matching for the HetClose and HetFar and in complete matching for the HomClose, HomFar, and the set-size 2 trials. Note that the HetClose condition mimicked the set-size 4 condition in Shin et al. (2006) because the set-size 4 condition displayed stimuli that differed in shape and were close to each other.

homogeneous condition, they are partially accessed in the heterogeneous condition. Thus, the partial matching hypothesis predicted that a smaller lateralization should be observed for heterogeneous memory-set trials than for homogeneous memory-set trials. It was also expected that the set-size 2 and homogeneous conditions would show similar ERLs because the memory-sets in both conditions completely match the probe letters.

It is important to note that the local suppression hypothesis is concerned with encoding and maintenance stages and the partial matching hypothesis is with memory comparison and retrieval stages. Because these two hypotheses are directed to different stages in memory and are not mutually exclusive, a hybrid of the two hypothesis (referred to as the hybrid hypothesis) can exist. Thus, a mixture of results supporting the hybrid hypothesis can also be observed.

Four set-size 4 conditions and one set-size 2 condition were generated for old and new trials (see Figure 2). The set-size 4 conditions were: homogeneous letters presented adjacent to each other (HomClose); homogeneous letters presented far apart (HomFar); heterogeneous letters presented adjacent to each other (HetClose); and heterogeneous letters presented far apart (HetFar). Following the divided-field paradigm, two of the four letters were presented in the left and the right hemifield, respectively. Letter similarity was

manipulated only for the letters presented in the same hemifield, with the constraint that the letters in the two hemifields were always different. The set-size 2 condition was included to compare with ERLs elicited in the four experimental conditions and those obtained in Shin et al. (2006).

Although the current study was motivated by the late ERL results found in the previous study, the two studies are different in the following ways. First, whereas the previous study varied memory set-size (2 and 4) and letter-case match between the memory-set and the probe (case match and case mismatch), the current study varied the distance (close and far) and the similarity (homogeneous and heterogeneous) of the memory-set items. Moreover, unlike the previous study in which the number of the set-size 2 and set-size 4 conditions was equal, in the current study two memory-set items were presented in one condition (i.e., the baseline condition) and four memory-set items were presented in th e four conditions (i.e., HomClose, HomFar, HetClose, and HetFar). Among these set-size 4 conditions, the condition HetClose resembled the set-size 4 condition in the previous study, in which the distance between memory-set letters was close and the letters shown within each hemifield were different.

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Methods

Participants Thirty-five young adults (10 men) participated in the study after signing informed consent. Two of the participants were excluded from data analysis due to an ERP recording error, resulting in a total of 33 participants. All were right-handed (as assessed by Edinburgh Handedness Inventory, Oldfield, 1971) and had normal or corrected-to-normal vision. They reported themselves in good health and received monetary bonus for their participation.

Stimuli and Task The stimuli were made up of the same set of upper-case letters B, D, F, G, H, J, M, R, T used in the previous study (Shin et al., 2006). Each trial was initiated by the presentation of a memory set comprising two or four letters presented simultaneously for 250 ms. In the set-size 2 condition, a single letter was displayed 2.5° to the left and another at the same eccentricity to their right of fixation. In the set-size 4 "close" condition, two letters were displayed 2° and 3°, respectively, to the left and the right of fixation. In the set-size 4 "far" condition, the letter eccentricities were 1.3° and 3.8°, respectively. After an interval of 850 ms, a probe letter was displayed for 210 ms at the center of the screen, right above the fixation cross. The next memory-set was presented 1690 ms after the onset of the previous probe. A fixation cross remained on the screen throughout the experiment. The computer screen was located approximately 60 cm from the participants' eyes. Participants were asked to fixate their eyes on the central cross and to limit other body movements.

Participants were asked to respond to probes as quickly and accurately as possible by pressing one of two buttons on a response box. The probe letter membership in the memory set determined the hand to use for responding (i.e., old vs. new) with participant's preferred fingers. Hand assignments were counterbalanced across participants. Participants were given up to 1600 ms to respond to the probes.

The letters making up the memory-set were randomly selected from the set of letters listed above. On half of the trials, the probe was one of the letters in the memory-set, so that the ratio of "old" to "new" letter trials was 1:1. On 20% of the trials, the memory set-size was two, with one item presented in each hemifield. On the rest (80%) of the trials, the memory set size was four, with two items presented in each hemifield. Each of the set-size 4 conditions occurred on 20% of the trials. Finally, the ratio of the probe that was encoded in the left hemifield (old-left) to that encoded in the right hemifield (old-right) was 1:1. The stimulus conditions were randomly distributed across trials.

A total of 24 blocks of 40 trials each (960 trials in total) were run, with a 40-trial practice at the beginning of the experiment.

ERP Recording The electroencephalogram (EEG) was recorded from 22 scalp locations (10-20 Electrode System, Jasper, 1958) by means of an electrode cap (Neuromedical Supplies, Sterling, VA, USA). The left mastoid was used as an on-line reference, and the average of the left and right mastoids was derived as an off-line reference. The recording locations included 4 midline sites (Fz, Cz, Pz, and Oz), 9 sites to the left of the midline (Fp1, F3, F7, C3, T7, P3, P7, O1 and left mastoid) and their homologous sites to the right of the midline. Vertical and horizontal electrooculographic activity was recorded bipolarly. A 0.01- to 30-Hz bandpass filter was used for all electrophysiological recordings. Electrode impedance was kept below 10 kilo-ohms. EEGs and electrooculograms (EOGs) were sampled at 100 Hz.

Data Reduction and Analysis Ocular artifacts (blinks and saccades) in the raw EEG data were corrected according to a procedure developed by Gratton, Coles, and Donchin (1983). EEG and EOG were epoched starting 200 ms before the presentation of the probe and ending 1300 ms poststimulus. All trials with potentials exceeding 200 μV or with EEG exceeding the A/D range in any of the channels were considered to contain artifact-related activity and were excluded from further analyses. After these preliminary steps were completed, the average waveforms were obtained for trials on which the participants responded to the test probe correctly, separately for each subject, electrode and condition. Only trials in which the probe stimulus matched one of the memory set stimuli (i.e., old trials) were of interest and thus were analyzed in this study. Among these trials, the left- and right-hemifield encoding conditions were collapsed because only the relative side of the ERP effects at test in relationship to the stimulus side at encoding is relevant to the ERL waveforms. The ERL waveforms were derived from the ERP waveforms following a procedure analogous to the derivation of the lateralized readiness potential (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988; Gratton, 1998; Shin, Fabiani, & Gratton, 2004; Shin, 2012).

$$ERL = [(E_R - E_L)_{OLD\text{-}LEFT} + (E_L - E_R)_{OLD\text{-}RIGHT}] / 2$$

where E_L and E_R represent brain potentials recorded from homologous electrode sites on the left and the right scalp, respectively, and OLD-LEFT and OLD-RIGHT refer to the encoding side of a probe stimulus. The ERL was computed for each of the lateral EEG channels.

Average ERL waveforms were calculated for each participant, letter distance (close or far), letter similarity (homogeneous or heterogeneous), and set-size 2.

Large ERL effects were found at the electrode pair P7/P8[1], consistent with Shin et al. (2006). A time window between 400-700 ms was selected to calculate ERL mean amplitudes from this electrode pair. Three types of statistical analyses were performed: (a) to test whether the observed lateralization was significantly different from baseline (i.e., whether an ERL occurred within the time window), one-sample t tests were performed for the electrode pair location on the ERL measures, separately for the set-size 2 and the set-size 4 conditions (i.e, HomClose, HomFar, HetClose, and HetFar); (b) to evaluate whether the ERLs within the selected time

window systematically differed between conditions, a repeated measures analysis of variance (ANOVA) was performed with two factors (distance and similarity) submitted as within-subjects variables -- this analysis was conducted using the set-size 4 conditions only; (c) to test whether two selected conditions differed, paired t-tests were performed between the set-size 2 and the HetClose, between the HomFar and the HomClose, between the HetFar and HetClose, and between the HomFar and the average of the other three set-size 4 conditions (i.e., the average of HomClose, HetClose, and HetFar).

Results

Behavior   The old trials showed significantly lower accuracy and shorter RT than the new trials (89% and 596 ms for the old trials; 94% and 653 ms for the new trials), $F_s(1, 32) = 19.89$, $ps < 0.001$. For the remainder of this section, however, this behavioral report will be restricted on the results from the old trials as only they are relevant to ERL effects.

Table 1 shows mean accuracy and RT results in the old conditions. The HomClose, HomFar, and the set-size 2 conditions all were similar in both accuracy and RT, $F_s(2, 64) < 0.56$, ns. Accuracy and RTs were analysed separately by performing 2 (distance) X 2 (similarity) repeated

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1) Note that the electrode pair P3/P4 also showed ERL effects comparable to those at the electrode pair P7/P8. However, we focused our analysis on the P7/P8 sites. The reasons are as follows. First, the ERLs observed at the P3/P4 were very similar across the set-size 4 conditions (Ms = -0.50, -0.66, -0.40, -0.65 μV for the HomClose, HomFar, HetClose, and HetFar trials, respectively) unlike the P7/P8, leading to postulate that these ERLs may have different neural generators from the ERLs obtained at the P7/P8 sites. Second, given the occipitotemporal activation previously found with letter stimuli (e.g., Flowers et al., 2004; Tarkiainen et al., 2002), it appears that ventral locations are more reasonable locations to discuss than doral locations. To facilitate a more focused discussion, ERLs at the P3/P4 sites were not discussed further in the paper.

Table 1. Mean accuracy and RTs in the old conditions (n = 33). The units of accuracy and RT are proportions correct and milliseconds, respectively. Standard deviations are in parentheses

	Set-size 2	HomClose	HomFar	HetClose	HetFar
Accuracy	0.95 (0.04)	0.94 (0.04)	0.95 (0.04)	0.84 (0.10)	0.87 (0.09)
RT	562 (100)	564 (103)	565 (101)	645 (115)	645 (112)

measures ANOVAs. Accuracy was significantly higher in the far (91%) than in the close (89%) condition, $F(1, 32)$ = 49.07, p < 0.001, consistent with the idea that letter representations may have been degraded in the close condition due to competition between the letters. Accuracy was also significantly higher in the homogeneous (94%) than in the heterogeneous (85%) condition, $F(1, 32)$ = 9.21, p < 0.005. Moreover, accuracy rates differed by distance but this difference was more evident when the memory-set letters were heterogeneous than when they were homogeneous. This pattern was substantiated by a significant interaction between distance and similarity, $F(1, 32)$ = 4.87, p < 0.05, indicating the influences of both the representational quality and the degree of memory access on accurate responses. Responses were significantly faster in the homogeneous (564 ms) than in the heterogeneous (645 ms) condition, $F(1, 32)$ = 147.05, p < 0.001. No other significant results were found in the RT.

ERL   Figure 3 shows the grand-average ERP

waveforms from which the grand-average ERL waveforms were derived. Because we focused on the ERL effects observed in the P7/P8 electrode pair locations, Figure 3 also shows the grand-average ERP waveforms obtained in the P7 and P8 electrode sites. As displayed, the old-left and the old-right waveforms are reversed as a function of the electrode site. Consider the HomFar condition shown in Figure 3, for example. Whereas the old-right is more positive than the old-left in the P7 site, the old-left wave is more positive than the old-right in the P8 site. The average of this reversed difference between the left and right electrode sites is the ERL (shown in Figure 4), and this effect was visible for the set-size 2 and the HomFar trials, not for the other types of trials.

To assess the magnitudes of these lateralizations, grand-average ERL waveforms were derived. Figure 4A shows the grand-average ERL waveforms for the close and far homogeneous memory-set trials. Figure 4B shows the corresponding waveforms for the heterogeneous memory-set trials. The set-size 2 ERL waveform is displayed in this figure for
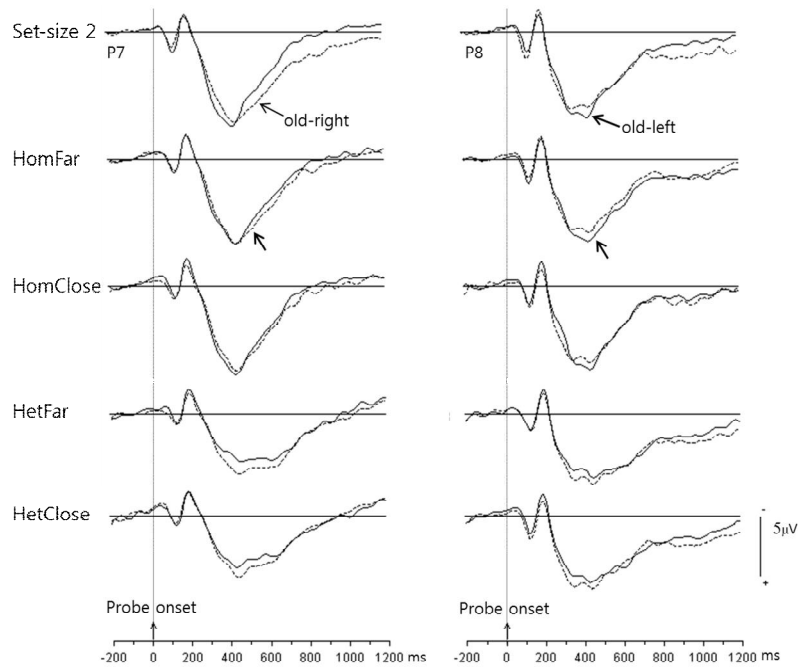
Figure 3. The grand-average ERP waveforms obtained from the P7 and P8 electrode sites for the five different types of trials. The old-left and the old-right indicate the hemifields in which a probe letter was presented during encoding and are represented by the solid and the dotted lines, respectively. The old-left and the old-right waveforms are visibly reversed between the left (i.e., P7) and the right (i.e., P8) channel for the set-size 2 and the HomFar trials (as indicated by the arrows). Note that negativity is plotted upward.
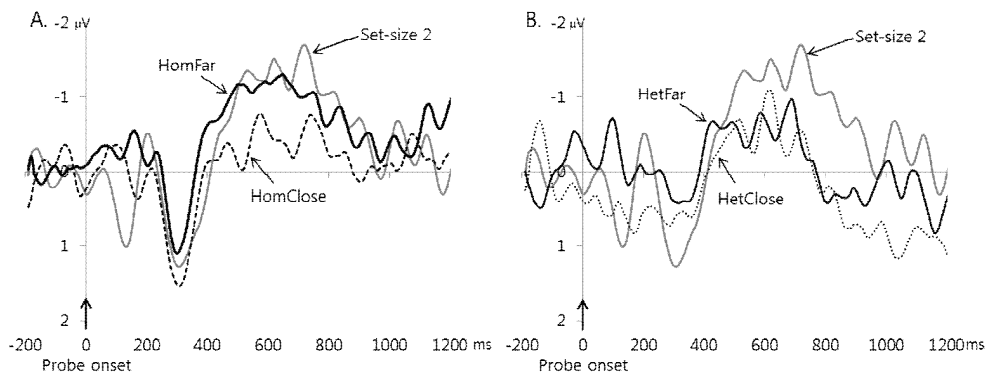

Figure 4. Grand-average ERL waveforms (n = 33) obtained at the electrode pair P7/P8 for the set-size 2, homogeneous (A), and heterogeneous (B) memory-set trials. Because these waveforms show lateralized activity, how largely they deviate from the baseline should be examined.

comparison purposes. One sample t-tests revealed that the late ERL activity observed in the HomFar (-1.06 μV) condition significantly differed from baseline, $t(32)$ = -3.21, p < 0.01, unlike that in the HomClose (-0.33 μV) condition, $t(32)$ = -1.09, ns. The ERLs in the HetFar (-0.62 μV) and HetClose (-0.47 μV) conditions were not reliably different from baseline, $ts(32)$ < -1.03, ns. The set-size 2 (-1.02 μV) condition showed a significant ERL effect $t(32)$ = -3.27, p < 0.01 as in Shin et al. (2006). The 2 (distance) X 2 (similarity) ANOVA conducted on the ERL measures did not yield any significant effect. A paired t-test performed on the set-size 2 and HetClose conditions showed a significant difference, $t(32)$ = -2.42, p < 0.05, similar to the set-size difference found in Shin et al. (2006). In addition, paired t-tests revealed that (a) in the homogeneous condition letter distance significantly affected the size of the ERLs, $t(32)$ = 1.74, p < 0.05 (one-tailed), but in the heterogeneous condition letter distance did not significantly affect the lateralization, $t(32)$ = 0.63, ns; (b) the HomFar and the average of the other set-size 4 conditions showed a significant lateralization difference, $t(32)$ = -1.80, p < 0.05 (one-tailed). Note that some of these significant results were obtained when directionality was assumed as a priori. Overall these results showed that both spatial closeness

and heterogeneity of the items elicited smaller ERLs, as predicted by the hybrid hypothesis considering both local suppression and partial matching effects.

Discussion

The present study aimed at investigating the nature of memory representation in visual working memory. Using ERPs we investigated the degree to which stimuli are represented in degraded quality and that to which memory representations are accessed at retrieval. Previously Shin and colleagues (2006) used the ERL method and found ERL activity, occurring at posterior regions (P7/P8 electrode sites) in a late time window (> 400 ms poststimulus). This ERL activity was sensitive to both set-size and the degree of matching between memory representations and test probes, indicating that there is a level of memory representation at which representational quality and the degree of memory access become important. Local suppression, partial matching, and a hybrid of these two hypotheses were proposed to probe this particular ERL.

The local suppression hypothesis noted competitive relations among items. Studies have shown that multiple items compete for selection and this competition is modulated as a function of the overlap in receptive fields of neurons to

which these items fall (Folk & Egeth, 1989; Kastner et al., 1998, 2001; Reynolds et al., 1999; Treisman & Gelade, 1980). Following the hierarchy of visual pathways and their respective receptive field sizes (Kastner et al., 2001; Rousselet et al., 2004), this competition is more likely to occur for spatially close stimuli in higher visual areas rather later in time. To test this idea, distance was varied between two memory-set letters. It was predicted that an ERL should be elicited in the posterior regions in a late time window and be smaller in the close than in the far condition because of a degraded representational quality of each item. The partial matching hypothesis, a data-driven hypothesis, focused on the degree of matching between memory representation and probe. The previous late ERL was largest when the test probe matched the memory set in both shape and set-size (i.e., complete matching). This indicates that the complete match condition reflects a successful matching process, which in turn directs to the idea that ERL amplitude reflects the extent to which memory representations are accessed. To test this idea, two memory-set letters were varied to be homogeneous or heterogeneous. It was predicted that an ERL, observed in the posterior regions in a late time window, should be smaller in the heterogeneous condition than in the homogeneous condition because of lesser memory

access. A hybrid of these two hypotheses (i.e., the hybrid hypothesis) was also considered because the local suppression and partial matching hypotheses were not mutually exclusive. Thus, a mixture of results supporting these two hypotheses was expected as a possible outcome.

Behaviorally, accuracy was lower in the close than in the far condition, but this effect was more evident for the heterogeneous memory-set trials than for the homogeneous memory-set trials. Electrophysiologically, largest ERL effects were observed in the electrode pair P7/P8 after 400 ms poststimulus, similar to the previous study. A significant ERL difference was found between the set-size 2 condition and the HetClose condition (equivalent to the set-size 4 condition in Shin et al., 2006), replicating some of the findings in Shin et al. (2006). The overall ERL results were in line with the accuracy results. A significant distance effect was found in the homogeneous condition, with the ERL significantly larger for the HomFar than for th e HomClose memory-sets. Moreover, a significant ERL activity was found only in the HomFar condition among the four set-size 4 conditions, and the comparison of the HomFar condition with the average of the other set-size 4 conditions resulted in a significant difference.

These results indicate that both letter distance and letter similarity jointly played a role in generating the late ERLs, favoring the hybrid

hypothesis. This joint influence explains the ERL difference found between the set-size 2 and set-size 4 conditions in the previous study, which now is interpreted that the smaller ERL in the set-size 4 condition had occurred due to both local suppression of the stimuli and partial matching between memory representations and test probes. In the current study, the set-size 2 condition was included for comparison purposes. It properly served its purposes by showing a significant ERL difference between the set-size 2 and HetClose conditions and similar ERLs between the set-size 2 and HomFar conditions. These results suggest requirements for a large lateralization. They are: (a) stimuli to be encoded should be displayed with least interference from neighboring stimuli; and (b) a stimulus to be compared with encoded stimuli should be identical to the encoded stimuli, leading to complete matching. These requirements shed light on visual working memory research, such that visual stimuli can be represented in degraded fashions depending on their relative distance and also that degree of memory access jointly influences on this distance effect.

Accuracy and response times were higher and shorter for the homogeneous memory-set trials than for the heterogeneous memory-set trials. Perhaps this similarity effect was highly influenced by the number of verbal elements to hold in memory and to compare with the test probe. Although the homogeneous and heterogeneous memory-sets showed the same number of visual items (i.e., set-size 4), the verbal information in the heterogeneous memory-set is larger and thus more difficult to be held in memory than that in the homogeneous memory-set. This difference must have been reflected in the accuracy and RT results. In retrospect, using novel shapes (instead of well-learned letters) could have attenuated this sort of verbal influence on task performance and should have provided more convincing evidence of the nature of representation in visual working memory. Nonetheless, it should be noted that largest ERL effects were observed in the occipitotemporal regions where complex visual shapes are processed (Allison et al., 1994; Allison et al., 1999; Chong et al., 2013; Kanwisher et al., 1996; Epstein & Kanwisher, 1998; Flowers et al., 2004; Tarkiainen et al., 2002), and the ERLs showed the influence of distance in addition to similarity, suggesting that the E RLs discussed in this ppaper indeed reflect visual aspects of working memory. In behavioral measures accuracy rates seem to be more sensitive to the influence of these visual aspects than RT.

The fact that the ERL reflects how stimuli are represented during encoding provides important information, which is that the ERL

method can be used to investigate the nature of memory representations in visual working memory. Yet, one thing must be considered before making use of the ERL method in such investigation. The local suppression hypothesis postulated that a small ERL reflected a degraded stimulus representation and the reason for this degradation was competition for neural representation among stimuli that fall within the same receptive fields. This train of thoughts was supported by the distance effect showing that ERL activity was smaller in the close condition (where receptive fields were more overlapped) than in the far condition (where receptive fields were less overlapped). However, the current ERL results are still indirect evidence of representational quality. Whether the size of the ERL is an index of the quality of memory representation has to be determined in more direct ways in the future. It can be tested, for example, by physically degrading memory-set stimuli and correlating the levels of degradation with elicited ERL amplitudes. When this type of research is done, we now know that the test probe has to be identical to the memory-set to elicit a large ERL, given the ERL results in the two heterogeneous and the set-size 2 conditions in the current study. In other words, ERL results can differ depending on the degree of matching between memory set and probe. Thus, the degree of memory access should be kept constant when one uses the ERL method to investigate how stimuli are represented during encoding.

The set-size dependent ERL effect found in the previous study suggested that there is a processing level at which relations among items are represented in visual working memory. In the current study it seems that observers perceived the memory-set stimuli differently and encoded them into memory as either independent items or a unit depending on the relative distance between the stimuli. The idea that items are not represented in isolated fashions may be old. The phenomenon like perceptual grouping or chunking has long been discussed. However, in recent years studies have shown that observers form more efficient representations in visual working memory by making associations between items, finding regularities, and using redundancies based on the regularities found (Brady et al., 2009, 2011). These studies have paved the way for research focused more on elucidating the nature of memory represent ations in visual working memory than on determining memory capacity. The current study, showing brain evidence of relational memory representations, certainly agrees with such undertaking.

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시각 작업 기억에서의 기억 표상:
표상의 질과 기억 접근성

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Shin 등(2006)은 사건관련전위에서 도출한 부호화 관련 편측화(encoding-related lateralization, 이후 ERL)가 시간 창을 따라 순차적으로 나타난다고 보고하였다. 전극 위치 P7/P8에서 관찰된 ERL 활동 중에서 자극 제시 후 400ms부터 발달한 ERL은 기억세트의 크기와 기억세트와 검사자극 간의 일치 정도에 따라 영향을 받았다. 이것은 자극들 간의 관계와 기억된 표상에 접근하는 정도가 중요하게 작용하는 수준이 시각 작업 기억 과정 중에 있다는 것을 의미한다. 이러한 사실에 기초하여 본 실험에서는 표상의 질과 기억 표상에로의 접근성을 연구하였다. 자극 표상의 질은 자극들 간의 경쟁으로 낮아지고(국지적 억제 가설), 기억 표상에로의 접근성은 기억세트와 검사자극이 부분적으로만 일치할 때 낮아질 것이라고(부분적 일치 가설) 가정하였다. 두 가설을 검증하기 위해 네 글자로 제시되는 기억세트에서 글자 간의 상대적 거리(가깝거나 멀거나)와 유사성(같거나 다르거나)을 조작하였다. 사건관련전위 자료 수집 동안, 참가자는 검사자극이 바로 이전에 제시된 기억세트의 글자 중 하나인지 아닌지를 판단하였다. 33명에서 얻어진 ERL 결과는 다음과 같다. 첫째, Shin 등(2006)의 연구와 마찬가지로 P7/P8 위치에서 400-700ms의 잠재기로 큰 ERL 활동이 관찰되었다. 둘째, 같은 글자들이 멀리 제시되었을 경우에만 유의미한 ERL이 관찰되었다. 셋째, 다른 글자들이 가깝게 제시되었을 때가 한 개의 글자가 제시되었을 때보다 유의미하게 작은 ERL을 보였다. 이 결과들은 두 가설을 혼합한 가설을 지지하는 것으로서 표상의 질과 기억표상에 대한 접근 정도가 함께 결합하여 시각 작업 기억 과정에 영향을 끼침을 시사한다.

주제어 : 시각 작업 기억, 부호화 관련 편측화, 표상의 질, 기억 접근 정도, 사건 관련 전위