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BRIEF REPORT

Using electrophysiology to demonstrate that cueing affects long-term memory storage over the short term

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Abstract As researchers who study working memory, we often assume that participants keep a representation of an object in working memory when we present a cue that indicates that the object will be tested in a couple of seconds. This intuitively accounts for how well people can remember a cued object, relative to their memory for that same object presented without a cue. However, it is possible that this superior memory does not purely reflect storage of the cued object in working memory. We tested the hypothesis that cues presented during a stream of objects, followed by a short retention interval and immediate memory test, can change how information is handled by long-term memory. We tested this hypothesis by using a family of frontal event-related potentials believed to reflect long-term memory storage. We found that these frontal indices of long-term memory were sensitive to the task relevance of objects signaled by auditory cues, even when the objects repeated frequently, such that proactive interference was high. Our findings indicate the problematic nature of assuming process purity in the study of working memory, and demonstrate that frequent stimulus repetitions fail to isolate the role of working memory mechanisms.

Keywords Cognitive neuroscience · Cognitive neuroscience of memory · Working memory · Long-term memory · Event-related potentials · Process purity · Object memory · Cueing

As psychologists, we often make implicit assumptions about the degree to which our tasks are pure measures of our process of interest. This issue of process purity is perhaps most critical in the study of human memory, where the same pattern of results can be interpreted as being due entirely to the storage of information in a permanent, long-term memory, or entirely to the storage of information in a temporary working memory (Baddeley, 1986; Crowder, 1982; Surprenant & Neath, 2009; Thorn, Gathercole, & Frankish, 2005). For example, from one perspective, our ability to remember a series of stimuli presented on a trial is due to how accurately each of the stimuli is represented in long-term memory, allowing for its retrieval at the time of test (Brown, Chater, & Neath, 2008; Polyn, Norman, & Kahana, 2009). However, from another perspective, our memory abilities in almost exactly the same task are interpreted as being due to the nature of storage in working memory (Endress & Potter, 2014). These conflicting perspectives cannot both be correct, but when using behavioral data alone, it is extremely difficult to determine whether the task that we are using relies on long-term memory, working memory, or both of these types of memory stores.

Many studies, including our own, have interpreted participants' ability to remember cued objects across short retention intervals as being due purely to the maintenance of those cued representations in working memory (e.g.,

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Griffin & Nobre, 2003; Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, 2007; Maxcey-Richard & Hollingworth, 2013; Sperling, 1960; Williams & Woodman, 2012). Our goal here was to determine whether we could use event-related potentials (ERPs) to empirically assess whether such tasks also draw on information represented in long-term memory or represent a process-pure measure of storage in working memory, as we had previously believed.

In the present study, we took the approach of using ERP components that previous work has suggested are sensitive measures of whether information is stored in long-term memory. The first ERP component, the anterior P1 (sometimes known as the P170), is a frontocentral positivity that is hypothesized to provide a measure of long-term memory either due to familiarity (Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Friedman, 2004; Voss, Schendan, & Paller, 2010) or the initiation of memory search (Diana, Vilberg, & Reder, 2005). This component is generally more positive when a given stimulus in long-term memory is correctly recognized (Tsivilis, Otten, & Rugg, 2001), or used to processes a new visual input (Reinhart & Woodman, 2014). The second component is the FN400 old/new effect, a midfrontal positivity elicited by familiar objects, even objects that participants cannot remember seeing (Rugg et al., 1998). Although research on both of these indices has purported to measure different aspects of long-term memory (Danker et al., 2008; Paller, Lucas, & Voss, 2012; Voss et al., 2010), all of the studies suggest that these components are indicative of long-term memory storage or the attempted use of that stored information. This means that these ERP components are believed to be more sensitive measures of long-term memory storage than are behavioral responses. We used both of these components elicited by the test objects in our explicit memory task, to assess whether long-term memory contributes to the pattern of performance typically attributed to working memory (e.g., Endress & Potter, 2014; Maxcey-Richard & Hollingworth, 2013).

In the present study, participants viewed a series of objects that they needed to remember. At the end of each trial, their memory was tested for one object with a token discrimination test (i.e., deciding whether the test hammer was the same hammer that had been shown in the series). Participants responded whether the test object was “old” (an object presented during the trial) or “new” (an object not presented during the trial). On some trials, participants received an auditory cue indicating the object that was most likely to be tested. On a critical subset of trials, two objects were cued. On these two-cue trials, participants were told that the second cued object was most likely to be tested (the *cued* object) and that the originally cued object was least likely to be tested of all the objects (the *deprioritized* object). Previous work showed that participants were better at making token discrimination judgments at the end of each trial about the *cued* object than about the deprioritized object and uncued objects (Maxcey-Richard & Hollingworth, 2013). The dominant explanation of the results from this sequential-object paradigm in the literature has been that the deprioritized object and uncued objects were maintained in long-term memory, whereas the cued object was maintained in working memory (see also Hollingworth, 2004). However, this may not be a *process-pure* measure of working memory. Instead, long-term memory may influence, or even determine, the pattern of behavioral effects in this paradigm (e.g., Thorn et al., 2005). From this perspective, performance in the sequential-object paradigm could be reasonably accounted for with known long-term memory processes that allow for superior memory for particularly distinctive events (Nairne, Neath, Serra, & Byun, 1997; Neath, 1993), such as the most recently cued object.

If the hypothesis that long-term memory contributes to these cue benefits is correct, we should find that the long-term memory ERPs are modulated when the cued item is tested, relative to when uncued objects in the sequence are tested. If the hypothesis is correct that the cue benefits are process-pure in revealing the storage of these representations in working memory, then we should see that the long-term memory amplitude does not distinguish between cued and uncued items in the sequence. We tested this hypothesis in two experiments. In Experiment 1, we used a large stimulus set of pictures of real-world objects, whereas in Experiment 2 we used a small stimulus set.

Experiment 1

The goal of Experiment 1 was to test the prediction that long-term memory contributes to the cue benefits that have been attributed to working memory in the sequential-object paradigm. To do this, we measured accuracy and the amplitude of the ERPs indexing long-term memory. The stimuli consisted of 200 pairs of unique real-world photographs (Brady, Konkle, Alvarez, & Oliva, 2008). We used this large set of real-world stimuli to maximize the sensitivity of our procedure to reveal a role for long-term memory, if it exists. The large stimulus set with minimal repetitions across trials should minimize the proactive interference that could abate the contributions of long-term memory to this task (Maxcey & Woodman, 2014), a proposal that we then explicitly tested in Experiment 2.

Method

Participants Eighteen volunteers (18–35 years old) from Vanderbilt University and the surrounding community participated for payment. All reported normal or corrected-to-normal vision and provided informed consent.

Stimuli and procedure We presented stimuli using Psychophysics Toolbox (Brainard, 1997) in a dimly lit room, viewed from 140 cm. All images subtended 4.1° × 4.1° and appeared at the center of the screen. Responses were collected with a handheld gamepad (Logitech Precision).

The sequence of events in Experiment 1 is shown in Fig. 1. The objects were drawn from a set of 200 paired exemplars of common objects (Brady et al., 2008). Each trial began with an 800- to 1,600-ms fixation period consisting of a central black fixation that turned red 500 ms before the end of the fixation period. Participants were instructed that when the black fixation cross turned red, a stimulus was coming, and to refrain from blinking. The fixation period was followed by an object for 100 ms, then by another, 900-ms fixation display (400 ms of a black fixation cross, followed by 500 ms of a red fixation cross). The trials consisted of five or six objects (50 % five, 50 % six, randomly interleaved), so participants could not anticipate the end of the trial. After the last object in the sequence, a 900-ms red fixation cross indicated that the next object was the test object. At the end of the trial, participants were shown one object for 2,000 ms from the exemplar pair of one of the objects that had been presented in the trial (e.g., a polar bear image, but potentially not the exact same polar bear image) and were asked whether the exact same object had been presented. They pressed one of two different buttons on the handheld gamepad, using their right thumb, to indicate whether the test object was "new" or "old."

Following the 100-ms presentation of each object, a 100-ms tone indicated the prioritization status of each object during the first 100 ms of the 900-ms fixation period. Participants were instructed that memory for any object may be tested, but they were most likely to be tested on cued objects. The auditory tone cue differed in pitch from the tone presented with all other objects. Three cueing conditions occurred during the experiment. On *one-cue* trials, only one object in the sequence was cued. On *two-cue* trials, a second

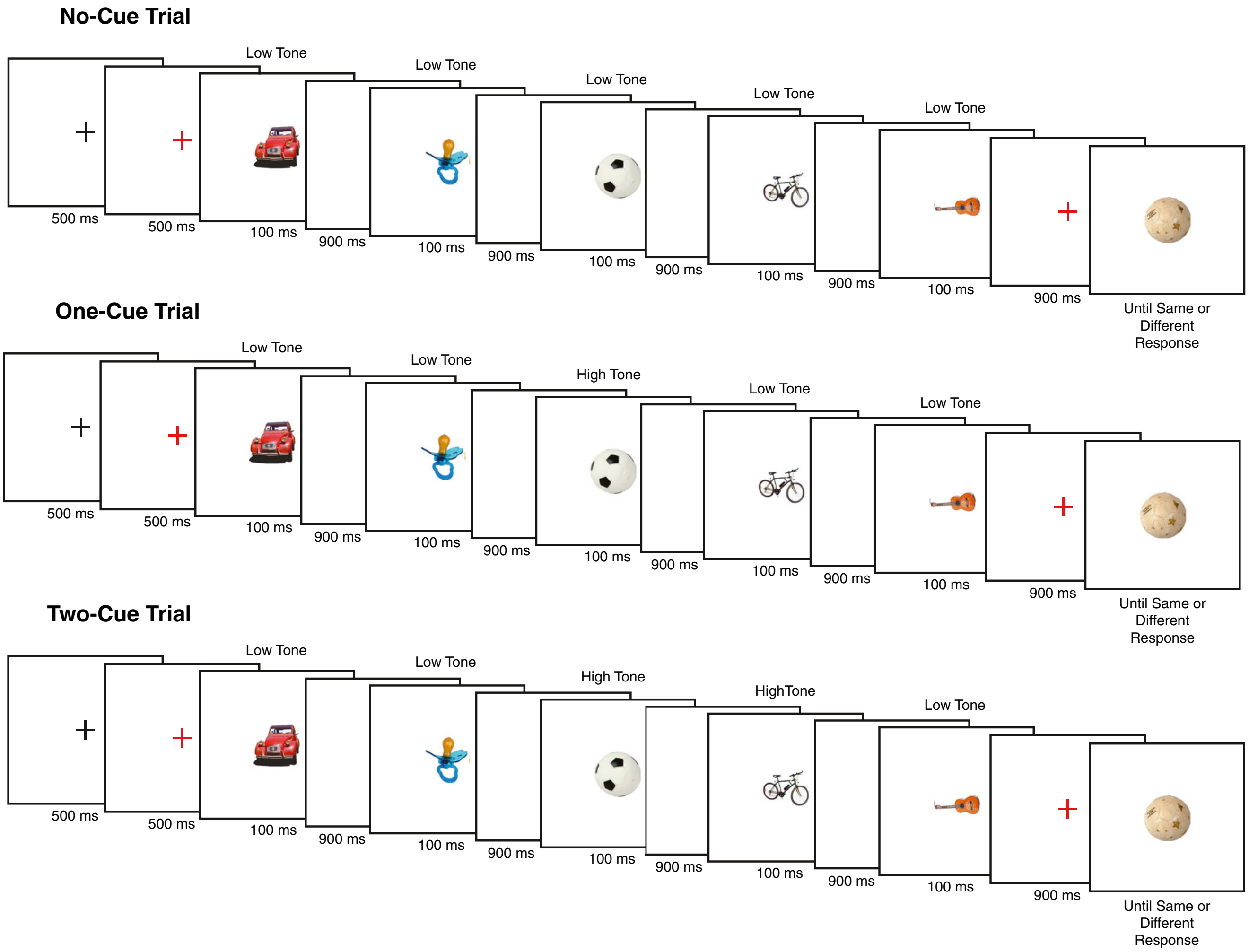

Fig. 1 Examples of the stimulus sequences used in the different trial types. These examples show trials in which the high-pitch tone served as the memory cue (the other half of the participants had low-pitch tones serve as the cues). Note that the two-cue trial shows a case in which the deprioritized object was tested, as is shown in subsequent figures. Most of these two-cue trials would have tested the second object cued (i.e., here the bicycle)

object, presented after the first cued object, was cued. In this case, participants were instructed that the most recently cued object was most likely to be tested, and that the originally cued object was least likely to be tested. Finally, on *no-cue* trials none of the objects were cued. The tone was either a high-pitched tone for cued objects and a low-pitched tone for all other objects, or vice versa. The meanings of the tones were counterbalanced across participants.

All trial types were randomly intermixed (no-cue, one-cue, and two-cue trials), with 120 one-cue trials (~15 %), 428 two-cue trials (~53 %), and 260 no-cue trials (~32 %), for a total of 808 trials. Across one-cue trials, the test object probed the cued object on 80 trials (~67 %) and the other objects on 10 trials apiece (~8 %) across each lag. In the event of a two-cue trial, the test object probed memory for the second cued object on 248 trials (~58 %), the deprioritized object on 80 trials (~19 %), and the objects at the other lags on 100 trials (~23 %). Across no-cue trials, the test object probed the lags on which cues were possible (i.e., matched-object lags) on 80 trials each (~31 %), and the other lags on 10 trials (~4 %) each. We weighted the trial numbers on no-cue trials to more heavily sample matched-object lags for comparison purposes. This weighting should only work against observing a difference between cue and no-cue trials.

ERP recording and analysis We recorded participants' electroencephalograms using our standard methods (Carlisle, Arita, Pardo, & Woodman, 2011). Five participants were replaced due to excessive artifacts, identified using a previously described two-step procedure (Woodman & Luck, 2003). The family of ERP components indexing long-term memory processes was measured from 170 to 400 ms after test object onset at the frontocentral electrode site, Fz (Reinhart & Woodman, 2014; Voss et al., 2010). The data were collapsed across the high- and low-tone variable due to the absence of a significant effect of tone pitch.

Results

Behavioral results The mean accuracies of participants' old-versus-new judgments across the critical trial types are shown in Fig. 2. These means indicate that participants used the cues to better remember the items that were marked as most relevant for the immediate memory test. In addition, participants showed flexibility in the use of these cues. That is, when an item was initially cued but was then followed by a second cued item, indicating that this second cued item was then likely to be tested (the first item then becoming "deprioritized"), the participants were able to track this dynamic shift in the behavioral relevance of these cued items.

Consistent with the results that are described above and unfolded in the planned comparisons below, an analysis of variance (ANOVA) with the factors Cue (cued vs. uncued) and Matched-Object Lag from no-cue trials (one-cue lag vs. two-cue lag) resulted in a significant main effect of cue, $F(1, 17) = 13.93$, $p = .0017$, and neither a reliable main effect of matched-object lag, $F(1, 17) = 0.45$, $p = .5135$, nor an interaction, $F(1, 17) = 1.22$, $p = .2849$. Participants exhibited superior memory performance for the cued object on the one-cue trials (85 %) relative to the matched-object lag (60 %), $t(17) = 3.97$, $p < .001$. On the two-cue trials, participants showed better memory for the second cued object (85 %) than for the matched-object lag (63 %), $t(17) = 3.30$, $p = .004$. On two-cue trials, performance for the deprioritized object (70 %) was reliably worse than memory for the second cued object (85 %), $t(17) = 2.32$, $p = .033$, but was not reliably better than performance for the matched-object lag (60 %), $t(17) = 1.57$, $p = 1.35$.

These findings replicate previous behavioral work (Maxcey-Richard & Hollingworth, 2013), demonstrating that participants remembered the cued object better than the uncued objects, and when two cues were presented, they effectively deprioritized the previously cued object. Now we turn to the ERP findings, to determine whether long-term memory representations contributed to these behavioral effects.

Electrophysiological results The ERP results from Experiment 1 are shown in Fig. 3. The amplitude of the long-term memory ERPs (i.e., the anterior P1 and subsequent FN400) elicited by the immediate memory test items tracked the relevance of the items indicated by the cues. The uncued items exhibited the most negative potentials, the deprioritized item a relatively more positive potential, and the cued items exhibited strongly positive potentials. Thus, the pattern of amplitudes shows the same pattern as performance during the immediate memory task, as would be expected if the long-term memory representations indexed by these ERP components were contributing to performance.

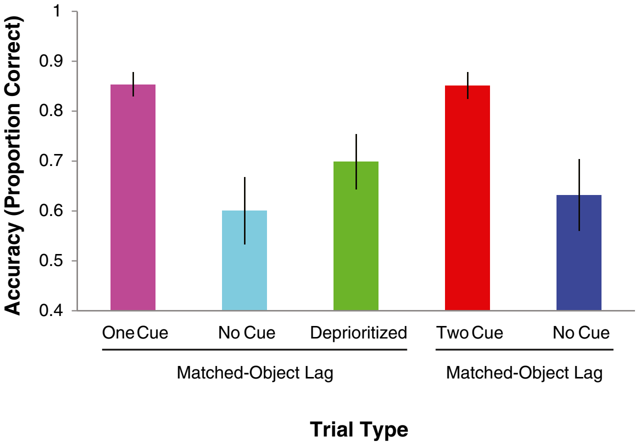

Fig. 2 Behavioral findings showing memory test accuracy across the trial types in Experiment 1. The error bars in this and subsequent figures show 95 % within-subjects confidence intervals (Cousineau, 2005)

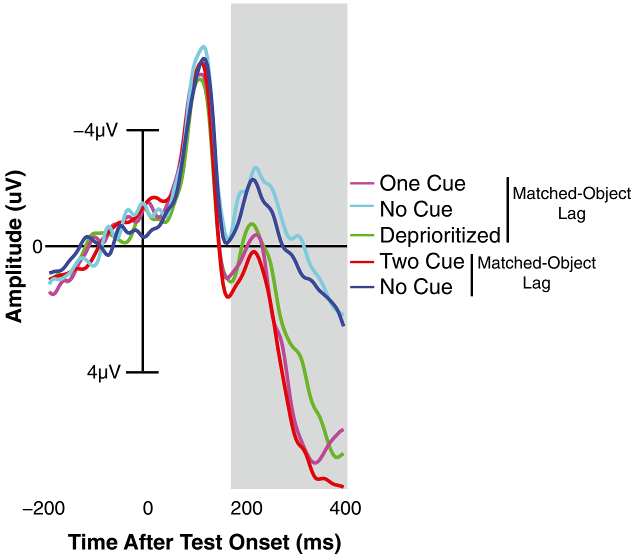

Fig. 3 Grand average waveforms time-locked to the onset of the memory test stimulus from the medial frontal electrode (Fz), where these long-term memory event-related potentials (ERPs) are maximal. The different traces show the findings from the trial types in Experiment 1. The gray region shows the measurement window of the ERPs

As we describe next, these observations and the planned comparisons described below were supported by an ANOVA with the factors Cue (cued vs. uncued) and Matched-Object Lag (one-cue vs. two-cue), which resulted in a significant main effect of cue, $F(1, 17) = 30.71$, $p < .001$, but neither a reliable main effect of matched-object lag, $F(1, 17) = 0.03$, $p = .8759$, nor a significant interaction, $F(1, 17) = 1.97$, $p = .1785$. On the one-cue trials, the amplitude of the long-term memory ERPs (the anterior P1 and subsequent FN400) elicited by the cued object was significantly more positive than that for the matched-object lag, $t(17) = 4.74$ $p < .001$. On two-cue trials, the amplitude elicited by the second cued object was also significantly more positive than the matched-object lag, $t(17) = 5.05$ $p < .001$. These results indicate that long-term memory amplitudes track performance in this sequential-object paradigm, as one would predict if these long-term memory representations contribute to the cue benefits often attributed to working memory storage.

Discussion

Experiment 1 demonstrated that under conditions in which cued objects are remembered more accurately, long-term memory ERPs track performance, appearing to contribute to the behavioral effects of superior memory for cued objects. These results cause concern for process-pure interpretations of the multitude of cueing studies that have attributed better memory for cued objects to their maintenance in working memory.

An important factor that we avoided with the design of Experiment 1 was proactive interference. Proactive interference occurs when memory for the information on a current trial is impaired because the information from previous trials makes it difficult to discern the previously relevant information from the relevant information on the current trial (Keppel & Underwood, 1962; Peterson & Peterson, 1959; Wickens, Born, & Allen, 1963). It has been proposed that the existence of proactive interference is one of the primary reasons that we require working memory, to suppress this competing previous information (Blalock & McCabe, 2011; Bunting, 2006; Hartshorne, 2008; Lin & Luck, 2012; Lustig, May, & Hasher, 2001; Makovski & Jiang, 2008; May, Hasher, & Kane, 1999; Unsworth & Engle, 2007).

In Experiment 1, the objects were drawn from a set of 200 exemplar pairs, and each pair had to be sampled before sampling from the entire set restarted. Therefore, there was only a 7 % maximum likelihood that any object on any given trial had been involved in a preceding trial, creating a situation in which proactive interference was extremely low. We hypothesized that long-term memory may have played a role in prioritizing objects under conditions of low proactive interference, but this might not occur using a design in which objects repeated frequently across trials.

Experiment 2

In Experiment 2, we sought to determine whether we could diminish the role of long-term memory in our sequential-object paradigm by increasing proactive interference. To this end, the objects in the new experiment were drawn from a restricted set of only ten pairs of objects (e.g., Maxcey-Richard & Hollingworth, 2013). With this restricted set, the participant saw an object from the same exemplar pair over 440 times, and each exact image over 220 times. With such frequent object repetitions, the representations of all the objects in long-term memory would be expected to be sufficiently strong that proactive interference would be chronically high, leaving the long-term memory representations from the present trial difficult to distinguish from those of the previous trials. Thus, we predicted that performance in the sequential-object task would not be accompanied by enhanced long-term memory representations, due to high proactive interference requiring the use of working memory, consistent with the process purity account.

Method

The methods of Experiment 2 were identical to those of Experiment 1, with the following exceptions.

Participants A different group of 18 participants from the Vanderbilt University community took part in Experiment 2, after five had been replaced due to excessive artifacts.

Stimuli and procedure The stimuli consisted of ten pairs of objects drawn randomly from the full set of 200 object pairs used in Experiment 1.

Results

Behavioral results The mean accuracies of participants' old-versus-new judgments across the critical trial types are shown in Fig. 4. Although the overall levels of performance were reduced in Experiment 2 relative to Experiment 1, the pattern of effects resulting from the use of cues to indicate task relevance were strikingly similar.

Our planned comparisons described below were consistent with the results of an ANOVA with the factors Cue (cued vs. uncued) and Matched-Object Lag (one-cue vs. two-cue), which resulted in significant main effects of cue, $F(1, 17) = 17.94$, $p < .001$, and matched-object lag, $F(1, 17) = 33.88$, $p < .001$. The interaction was not significant, $F(1, 17) = 2.17$, $p = .1590$. On one-cue trials, participants exhibited superior memory performance for the cued object (74 %) relative to the matched-object lag (52 %), $t(17) = 4.45$, $p < .001$. On two-cue trials, participants also showed better memory for the second cued object (82 %) than for the matched-object lag (63 %), $t(17) = 3.68$, $p = .002$. On two-cue trials, performance for the deprioritized object (64 %) was reliably worse than memory for the second cued object (82 %), $t(17) = 3.72$, $p = .002$, but unlike in Experiment 1, was reliably better than performance for the comparison object in the matched-object lag (52 %), $t(17) = 4.01$, $p < .001$.

To further examine the effect of using a small stimulus set on our behavioral measures resulting from these immediate memory tests, we conducted a between-experiments ANOVA with Experiment (1 vs. 2), Cue (cue vs. uncued), and Matched-Object Lag (one-cue vs. two-cue) as factors. We found significant main effects of experiment, $F(1, 34) = 630.76$, $p < .001$, cue, $F(1, 34) = 30.56$, $p < .001$, and matched-object lag, $F(1, 34) = 16.27$, $p = .0003$, but no interactions of these terms were significant. Now we turn to the ERP findings, to determine whether long-term memory representations contributed to these behavioral effects under conditions of high proactive interference.

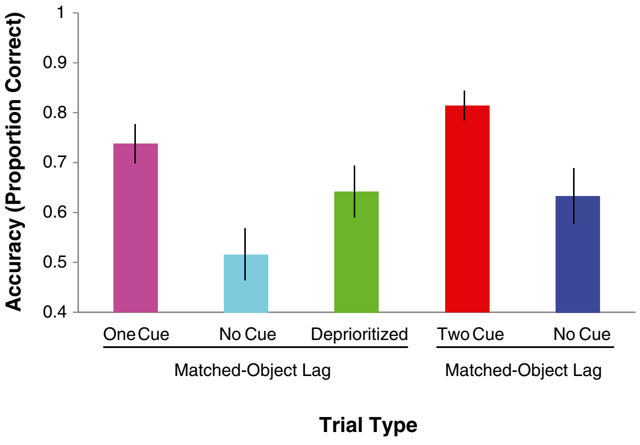

Fig. 4 Behavioral findings from Experiment 2, shown as in Fig. 2

Electrophysiological results The ERP results from Experiment 2 are shown in Fig. 5; Fig. 6 shows the mean amplitudes across Experiments 1 and 2. The overall amplitudes of the long-term memory ERPs were reduced in Experiment 2 relative to Experiment 1, a result similar to the overall reduction of mean performance between Experiments 1 and 2. But the remarkable finding is that the effects from our use of cues to indicate task relevance were strikingly similar in Experiment 2 and Experiment 1, even when we repeated the same ten object pairs hundreds of times.

An ANOVA with the factors Cue (cued vs. uncued) and Matched-Object Lag (one-cue vs. two-cue) resulted in a significant main effect of cue, $F(1, 17) = 27.30$, $p < .001$, and neither a reliable main effect of matched-object lag, $F(1, 17) = 2.54$, $p = .1294$, nor an interaction, $F(1, 17) = 0.09$, $p = .7695$, just as in Experiment 1. On one-cue trials, the amplitude of the long-term memory ERP components elicited by the cued object was significantly more positive than that from the object at the matched-object lag, $t(17) = 4.41$, $p < .001$. On two-cue trials, the amplitude elicited by the cued object was also significantly more positive than that from the object at the matched-object lag, $t(17) = 3.68$, $p = .002$. Despite the significant main effect of matched-object lag, we found no significant difference between the amplitudes elicited by the cued objects during one-cue and two-cue trials, $t(17) = 1.45$, $p = .166$. Replicating Experiment 1, these results indicate that

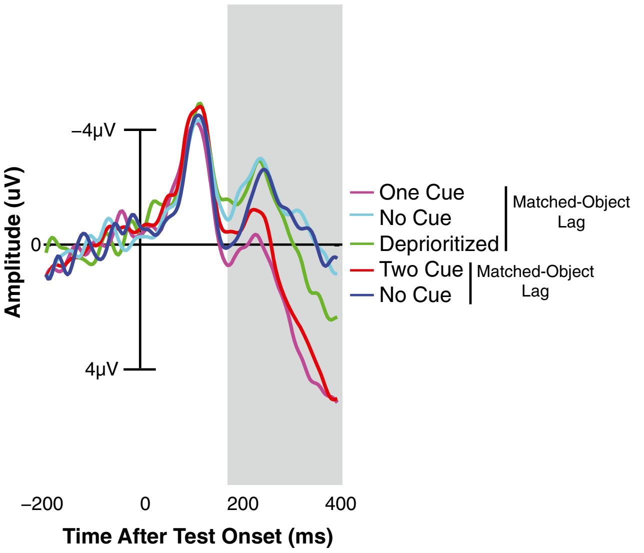

Fig. 5 Grand average waveforms from Experiment 2, shown as in Fig. 3

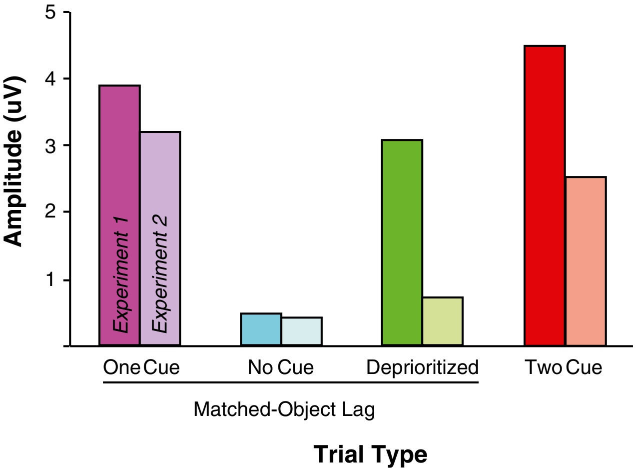

Fig. 6 Mean amplitudes of frontal waveforms from the shaded regions in Figs. 3 and 5, for direct comparisons across the corresponding trial types in Experiments 1 and 2. These amplitudes are subtracted from the no-cue baseline trials (i.e., the mean of no-cue trials at the two-cue object lag)

long-term memory ERP amplitudes tracked performance in this sequential-object paradigm, as would be predicted if these long-term memory representations contribute to the cue benefits often attributed to working memory storage, even when the stimuli are repeated again and again across trials.

Our findings are inconsistent with our prediction that when the objects repeated frequently, long-term memory would no longer contribute to prioritize storage of the cued items across short retention intervals (Maxcey & Woodman, 2014). To further examine the effects of using a small stimulus set in Experiment 2, relative to Experiment 1, we conducted a between-experiments ANOVA on the mean ERP amplitudes, with Experiment (1 vs. 2), Cue (cue vs. uncued), and Matched-Object Lag (one-cue vs. two-cue) as factors. We observed a significant main effect of cue, $F(1, 34) = 56.90$, $p < .001$, but no reliable main effect of experiment, $F(1, 34) = 1.51$, $p = .2270$, or matched-object lag, $F(1, 34) = 0.62$, $p = .4364$. These statistical results confirm the observation that the patterns of effects were virtually identical across experiments, with only an overall difference in amplitudes between Experiments 1 and 2.

Discussion

As in Experiment 1, we found that the amplitude of the long-term memory ERPs tracked participants' behavioral reports of memory for the items on the different trial types. These findings indicate that when items repeat frequently across trials, long-term memory continues to contribute to performance in this memory task across short retention intervals, even when proactive interference should be extremely high. This finding is contrary to our prediction that under conditions of high proactive interference, long-term memory would no longer play a role.

General discussion

In Experiment 1, we showed that ERP components believed to be indices of long-term memory storage are sensitive to cues indicating the task relevance of items, tracking the behavioral report of participants' immediate memory tests. Our findings support the hypothesis that long-term memory contributes to the cue benefits that are often attributed to the selective storage of information in working memory. In Experiment 2, we showed that when the to-be-remembered objects are repeated frequently, saturating proactive interference with the representations previously stored in long-term memory, the amplitude of the putative ERP indices of long-term memory continued to track participants' behavioral reports. Our findings from Experiment 2 indicate that cue benefits cannot be confidently inferred as being due to preferential storage in working memory, even when short retention intervals are used and care is taken to eliminate the usefulness of long-term memory by turning up proactive interference between the items.

The assumption of process purity during memory tasks has been one that is particularly difficult to assess. Our findings speak strongly against the assumption of process purity—that is, that working memory is isolated by our paradigm. We have shown one way that concurrent recordings of participants' ERPs can be used to determine the nature of the memory representations supporting task performance. We believe that our general method can be useful for determining the locus of the memories driving performance across a range of paradigms (e.g., Reinhart & Woodman, 2014; Woodman, Carlisle, & Reinhart, 2013). Future work based on the present paradigm should examine the degree to which working memory plays a role in these tasks by simultaneously measuring the ERP components believed to index both long-term memory and working memory, such as the contralateral delay activity (Vogel & Machizawa, 2004).

At a theoretical level, our findings are consistent with perspectives that have proposed that attention and working memory are overlapping constructs that both operate within long-term memory (Cowan, 1999; Nee & Jonides, 2011; Norman, 1968). In the present study, these views could predict the pattern of ERP findings that we observed, and they are consistent with the interpretation that long-term memory processes operate to distinguish items of different task relevances within a short stream of stimuli, even when those items are repeated trial after trial and proactive interference should be maximal. This is because, according to these perspectives, the arena of long-term memory is where all of those items are represented, even when attention is focused on them to maintain a particularly high-fidelity representation. These findings could also be accounted for by other working memory models, though (Hutchinson & Turk-Browne, 2012). For example, the multiple-component framework of Baddeley and colleagues (Baddeley, 1986, 2007; Baddeley & Logie,

1999) uses a central executive component to shuttle representations to and from long-term memory, and this exchange might continue even when proactive interference is high.

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