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Hitting the reset button: An ERP investigation of memory for temporal context

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ABSTRACT

This study explored how temporal context influences recognition. In an ERP experiment, subjects were asked to judge whether pictures, presented one at a time, had been seen since the previous appearance of a special reset screen. The reset screen separated sequences of successively presented stimuli and signaled a change in temporal context. A "new-repeat" picture was one that had been seen before but was to be called "new" because it had not appeared since the previous reset screen. New-repeat pictures elicited a more negative FN400 component than did "old" pictures even though both had seen before during the experiment. This suggests that familiarity, as indexed by the FN400, is sensitive to temporal context. A nearlier frontopolar old/new effect distinguished pictures that were seen for the first time in the experiment from all other pictures. The late positive component (LPC), which is typically greater for old stimuli, was smaller for new-repeat pictures than for pictures seen for the first time in the experiment. Finally, individual differences in task performance were predicted by the differences in amplitude of P3b that was evoked by the onset of the reset screen.

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1. Introduction

Studies of memory using event-related potentials (ERPs) have revealed two distinct ERP correlates of recognition. One of these is the FN400, a negative deflection at frontal sites from 300 to 500 ms, which is more negative for items judged new than for items judged old (Curran, 2000; Curran and Cleary, 2003; Duzel et al., 1997; Rugg and Curran, 2007; Rugg and Yonelinas, 2003; Tsivilis et al., 2001; Yovel and Paller, 2004). The other is the late positive component (LPC), a positive deflection at parietal sites from 400 to 800 ms, which is more positive for items judged old than for items judged new (Curran, 2000; Curran and Cleary, 2003; Duzel et al., 1997; Rugg and Curran, 2007; Rugg and Yonelinas, 2003; Tsivilis et al., 2001; Yovel and Paller, 2004). A common view in the literature is that these two components correspond to qualitatively distinct recognition memory processes (Rugg and Curran, 2007). The FN400 corresponds to a familiarity process that provides information about whether an item has been seen, but not the context in which it appeared. In contrast, the LPC corresponds to a recollection process that does involve retrieval of

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http://dx.doi.org/10.1016/j.brainres.2016.04.047 0006-8993/© 2016 Published by Elsevier B.V. contextual information (Curran, 2000; Duzel et al., 1997; Rugg and Yonelinas, 2003).

In most dual-process models of recognition memory, familiarity is not sensitive to the context in which an item appeared (e.g. Diana et al., 2007; Eichenbaum et al., 2007; Jacoby, 1991; Montaldi and Mayes, 2010; Parks and Yonelinas, 2007; Reder et al., 2000; Yonelinas, 2002). However, there is some debate, even among dual-process theorists, about whether contextual information might contribute to familiarity in some circumstances. Some have suggested, for example, that familiarity is sensitive to the slowly changing global context defined by the experimental setting (Mandler, 1980). In most studies of recognition memory, participants are asked to judge whether commonplace items were encountered during the experiment. Familiarity judgments along with the FN400 differ for old and new items, though *all* of the items have likely been encountered many times before the experiment.

Behavioral work has shown that familiarity is also sensitive to local context (i.e., features that may vary from trial to trial). Presenting contextual features at test that have been seen repeatedly with other items during study increases spurious familiarity judgments (Diana et al., 2004). Additionally, instructing people to encode contextual information along with items in a way that promotes unitization increases the impact of context on familiarity judgments (Diana et al., 2008, 2011).



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The ERP methodology has been used to provide converging evidence that local context impacts familiarity. According to one theory (Ecker et al., 2007a, 2007b), intrinsic (intra-item) contextual features such as object color are automatically processed and bound to object tokens, whereas extrinsic features such as background shape are not (for a review, see Zimmer and Ecker (2010)). The absence of a match between the current stimulus and stored object tokens produces an FN400. Consequently, the FN400 is only sensitive to intrinsic local context. In an experiment that tested this theory, participants studied items presented in various colors (Ecker et al., 2007a). At test, items appeared in the same color or in a different color. Subjects were asked to judge whether they had studied the object, ignoring its color. The FN400 was more negative when objects appeared in a different color than when they appeared in the same color. In a second condition of the experiment, participants studied items presented on different background shapes. The manipulation of item-shape match during the test phase did not affect the FN400. Ecker et al. interpreted these results in terms of the differential impact of intrinsic and extrinsic local context on familiarity processing.

Subsequent studies have identified other contextual features that do and do not affect familiarity. The FN400 is sensitive to changes from study to test in object color (Ecker et al., 2007a), word font color (Nyhus and Curran, 2009), and object screen location (Speer and Curran, 2007). The FN400 does not appear to be sensitive to the presence of a background shape (Ecker et al., 2007a), border color (Ecker et al., 2007a; Speer and Curran, 2007), or superposition of an object upon a background image (Ecker et al., 2007b). Some of these results can be understood in terms of the distinction between intrinsic and extrinsic local context. However, it is often difficult to define which features are intrinsic and extrinsic to a stimulus in advance.

1.1. Is the FN400 sensitive to temporal context?

Given that familiarity and the FN400 are influenced by at least some sources of contextual information, we asked whether the FN400 is sensitive to temporal context. We manipulated temporal context by presenting participants with sequences of images and occasionally inserting a boundary – in the form of a "reset" screen – between successive images. Participants were asked to judge whether each image had appeared since the last reset screen. Thus, the task involved location-based (i.e. temporal position relative to a boundary) rather than distance-based (i.e. elapsed time from present) judgments (Friedman, 1993).

Theories of episodic memory propose that episodes are bound with features of the context in which they appear, including temporal context (Tulving, 1983). Temporal context may change gradually over time, or with the insertion of pauses or boundaries between adjacent events. The insertion of such boundaries produces grouping effects in memory, whereby items that appeared before or after a boundary are grouped together more strongly than items that were separated by a boundary (for a review, see Farrell (2012)). Computational models that employ a multidimensional representation of temporal distinctiveness based on distance (i.e. elapsed time from present) and location (i.e. time relative to a boundary) can account for these results (Farrell, 2012; Lewandowsky et al., 2006). Based on the finding that inserting a boundary between adjacent events affects subsequent episodic recollection, we asked whether manipulating temporal context would impact familiarity processing and the FN400 as well.

To address this question, we modified a delayed-match-tosample task used with primates (Holscher and Rolls, 2002). Holscher and Rolls recorded from perirhinal cortex in macaques as they performed the task. Neurons in the perirhinal cortex reacted to the first presentation of each picture as if it were completely new, even if the picture had appeared several times in the previous block of trials. The perirhinal cortex is thought to be involved in familiarity processing (see Diana et al. (2007) and Eichenbaum et al. (2007) for reviews), and has been identified as a potential source of the FN400 (Curran et al., 2006; but see Rugg and Curran (2007) for an alternate view). On the basis of those results, we hypothesized that the FN400 in humans would also be sensitive to when a stimulus last appeared relative to a signal that denoted the start of a new block of trials.

In our modified version of the delayed-match-to-sample task, subjects viewed a series of pictures of everyday items, along with an occasional "reset" screen. With each presentation, they judged whether the picture had appeared since the most recent reset screen. The trials of greatest interest were those where a picture that had appeared before was shown for the first time in the current block of trials (i.e. new-repeats). The key question was whether the FN400 to new-repeats would differ from the FN400 to other pictures that had already appeared in the current block of trials (i.e. old pictures). Both types of pictures had appeared in the global context established by the experimental setting, but new-repeats had not appeared since the reset screen. Therefore, if the FN400 were more negative for new-repeat pictures than for old pictures, it would indicate that this component is sensitive to temporal context.

2. Results

2.1. Behavioral analyses

Response accuracy and correct response times are shown in Table 1. A repeated measures ANOVA revealed a significant difference in accuracy across the four picture types, F(3, 57)=30.50, p < .001. Subjects responded more accurately to new-first pictures than to all other pictures (all p < .001). Response accuracy did not vary across the remaining picture types (all p > .05). An ANOVA for correct response times also revealed a main effect of picture type F(3, 57)=15.28, p < .001. Responses to new-first and new-repeat pictures (all p < .01). Response durations did not different between new-first and new-repeat pictures, t(19)=.43, p > .1, nor between old-first and old-repeat pictures, t(19)=1.98, p > .05.

2.2. ERP analyses

2.2.1. Neural responses to picture stimuli

We performed a stimulus-locked analysis of ERP data from trials with correct responses. A preliminary analysis showed no main effect of block length, and no significant interactions involving block length. We collapsed data across blocks of different lengths, and generated stimulus-locked waveforms for the four types of pictures: new-first, new-repeat, old-first, and old-repeat.

2.2.1.1. 176–260 ms. We began by examining possible perceptual priming effects evident in the early ERPs (Fig. 2). To do so, we

Table 1	l											
Mean c	correct	RTs (i	in ms)	and	mean	accuracy	(as %)	with	SEMs	in	parenthe	eses

Trial type	RT	Accuracy
New-first	1125 (56)	.99 (.01)
New-repeat	1143 (57)	.85 (.01)
Old-first	943 (25)	.88 (.02)
Old-repeat	974 (37)	.88 (.02)
Reset	1129 (154)	-
Distractor	1048 (102)	-



Fig. 1. Simplified diagram showing distractor and reset screens, and different picture types.



Fig. 2. Stimulus-locked waveforms for new-first, new-repeat, old-first, and old-repeat pictures. Gray regions show time intervals containing the P2, the FN400, and the LPC.

analyzed mean ERP amplitudes from 176 to 260 ms (Curran and Dien, 2003). A 4 (condition) × 3 (region: Frontal, Central, Posterior) ANOVA revealed main effects of condition, F(3, 57)=15.27, p < .001, and region F(2, 38)=49.49, p < .001. The interaction between condition and region was significant, F(6, 114)=6.07, p < .001. Voltages were more negative for new-first pictures than

Table 2

Mean amplitude of ERP responses to picture stimuli from 176 to 260 ms with SEMs in parentheses.

	Frontal	Central	Posterior
New-first	-6.99 (1.11)	-5.89 (0.98)	$\begin{array}{c} -0.14 \ (0.64) \\ 1.57 \ (0.64) \\ 1.60 \ (0.65) \\ 3.24 \ (0.70) \end{array}$
New-repeat	-5.35 (1.00)	-4.01 (0.81)	
Old-first	-4.06 (0.99)	-3.37 (0.87)	
Old-repeat	-3.81 (1.01)	-2.32 (0.88)	

for all others (Fig. 2). These effects were greatest over the frontal region (Table 2). We therefore performed an additional 2 (Old, New) × 2 (First, Repeat) ANOVA using data from frontal region. Both main effects were significant (Old/New: F(1, 19)=19.67, p < .001; First/Repeat: F(1, 19)=28.54, p < .001), as was the interaction, F(1, 19)=7.70, p < .05. Paired contrasts confirmed that voltages were more negative for new-first pictures than for all others (all p < .001).

2.2.1.2. 300–500 ms. We then analyzed the ERP data during the time window of the FN400, from 300 to 500 ms (Mollison and Curran, 2012; Speer and Curran, 2007). A 4 (condition) × 3 (region: Frontal, Central, Posterior) ANOVA revealed main effects of condition, F(3, 57)=36.58, p < .001, and region F(2, 38)=41.89, p < .001. The interaction between condition and region was significant, F(6, 114)=6.72, p < .001. Voltages were most negative for new-first pictures, followed by new-repeat pictures, old-first pictures, and old-repeat pictures (Figs. 2 and 3). These effects were greatest over the frontal region (Table 3) consistent with the FN400.

We performed an additional 2 (Old, New) × 2 (First, Repeat) ANOVA using data from frontal region. Both main effects were significant (Old/New: F(1, 19)=52.597, p < .001; First/Repeat: F(1, 19)=17.68, p < .001), as was the interaction, F(1, 19)=8.71, p < .01. Paired contrasts showed that voltages were more negative for new-first pictures than for all other types of pictures (all p < .001). Voltages were also more negative for new-repeat pictures than for old-first and old-repeat pictures (all p < .01). Voltages did not differ between old-first and old-repeat pictures, t(19)=.89, p > .3.

It is possible that these effects depended on the number of trials between successive repetitions of the stimulus rather than the primary manipulation of interest (i.e. whether the stimulus had appeared since the previous reset screen). To test this possibility, we replicated these analyses on the subset of trials where the stimulus had last appeared within the previous 10 trials. Voltages remained more negative for new-repeat than for old-first pictures, t(19)=2.22, p < .05, or old-repeat pictures, t(19)=3.36, p < .01.¹

¹ New-repeats and old-firsts provide an interesting additional contrast since the stimuli in the former case occur before and after the reset screen, whereas the stimuli in the latter case occur only after the reset screen. A 2 (condition; New-first, Old-Repeat) × 2 (number of intervening items; 10 or fewer, 10 or more) revealed a main effect of condition, F(1, 19)=9.50, p < .01, but not of number of intervening items, F(1, 19)=.17, p > .5. The interaction was also not significant, F(1, 19)=.12, p > .5. New-firsts were accompanied by a uniformly more negative FN400 across

176 to 260 msec



Fig. 3. Headplots for new-first, old-first, new-repeat, and old-repeat pictures from 176 to 260 ms (top), 300 to 500 ms (middle), and 400 to 800 ms (bottom).

Table 4

in parentheses.

New-first

Old-first

Old-repeat

New-repeat

Table 3

Mean amplitude of ERP responses to picture stimuli from 300 to 500 ms with SEMs in parentheses.

	Frontal	Central	Posterior
New-first	-6.99 (1.11)	-5.89 (0.98)	$\begin{array}{c} -0.14 \ (0.64) \\ 1.57 \ (0.64) \\ 1.60 \ (0.65) \\ 3.24 \ (0.70) \end{array}$
New-repeat	-5.35 (1.00)	-4.01 (0.81)	
Old-first	-4.06 (0.99)	-3.37 (0.87)	
Old-repeat	-3.81 (1.01)	-2.32 (0.88)	

2.2.1.3. 400–800 ms. Next, we analyzed the ERP data during the time window of the LPC (Mollison and Curran, 2012; Speer and Curran, 2007), from 400 to 800 ms. A 4 (condition) × 3 (region: Frontal, Central, Posterior) ANOVA revealed a main effect of condition, F(3, 57)=4.73, p < .01, and region F(2, 38)=55.24, p < .001. The interaction was not significant, F(6, 114)=1.33, p > .2. Voltages were more positive for old pictures than for new pictures, and for first presentations than for repeat presentations (Figs. 2 and 3).

We performed an additional 2 (Old, New) × 2 (First, Repeat) ANOVA using data from posterior region (Table 4). Both main effects were significant (Old/New: F(1, 19)=5.61, p < .05; First/Repeat: F(1, 19)=16.59, p < .001), but the interaction was not, F(1, 19)=16.59, p < .001, but the interaction was not, F(1, 19)=16.59, p < .001, but the interaction was not, F(1, 19)=16.59, p < .001, but the interaction was not, F(1, 19)=16.59, p < .001, but the interaction was not, F(1, 19)=16.59, p < .001, but the interaction was not, F(1, 19)=16.59, p < .001, but the interaction was not F(1, 19)=16.59, p < .001, but the interaction was not F(1, 19)=16.59, p < .001, but the interaction was not F(1, 19)=16.59, p < .001, P < 19)=1.17, p > .2. Paired contrasts showed that LPC was less positive for new-repeats than for all other picture types (all p < .05), and that the LPC did not vary among the other picture types.

Mean amplitude of ERP responses to picture stimuli from 400 to 800 ms with SEMs

Frontal

-2.66 (.73)

-3.06(.68)

-2.10 (.63)

-2.70(.72)

Central

-0.97 (.59)

- 1.58 (.57)

-0.51 (.53)

-1.09(.68)

Posterior

2.41 (.39)

1.38 (.49)

2.84 (.47)

2.30 (.58)

The timing of the LPC appeared to vary by condition (Fig. 2). This raises the possibility that mean amplitude measured over a fixed time window could obscure differences among conditions. To address this concern, we determined when the LPC was maximal over the posterior region for each participant and in each condition. There was a significant effect of condition on peak latency, *F* (3, 57)=4.37, p < .01, with shorter latencies for old-repeat pictures than for any other type of picture (Table 5; all p < .05). Peak latencies did not differ among the remaining picture types (all p > .1). To control for differences in peak latency, we calculated the peak amplitude of the LPC over the posterior region during this time window (Table 5). The effect of condition was significant, *F*(3, 57).

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Peak latency (in ms) and amplitude of LPC with SEMs in parentheses.

Trial type	Latency	Amplitude
New-first	589 (11)	5.82 (.49)
New-repeat	569 (23)	4.56 (.55)
Old-first	582 (14)	6.32 (.64)
Old-repeat	521 (12)	6.04 (.73)



Fig. 4. Stimulus-locked waveforms for reset and distractor screens. Gray regions show time interval containing the P3b.

57)=6.38, p < .001, owing to the smaller LPC for new-repeat pictures versus all other pictures (all p < .05). The LPC was numerically, but not significantly, smaller for new-first pictures than for old-first and old-repeat pictures. Thus, the results were largely consistent with the earlier analysis of mean amplitude from 400 to 800 ms.

2.2.2. Neural responses to distractor and reset screens

We compared stimulus-locked waveforms for reset and distractor screens (Figs. 4 and 5). The P3b was analyzed over the time window of 300 to 500 ms. There were significant main effects of condition, F(1, 19)=7.09, p < .05, and region, F(2, 38)=19.22, p < .01. The interaction between condition and region was also significant, F(2, 38)=3.26, p < .05. The P3b was larger for reset screens than for distractor screens, and the difference was greatest over the posterior region (Table 6).

We examined how the amplitude of the P3b, measured over the posterior region, correlated with task accuracy. P3b amplitudes following reset and distractor screens were positively associated with overall accuracy (reset screen: r=0.46, p < .05; distractor screen: r=0.36, p < .1). Table 7 shows correlations broken out by trial type. Of the various trial types, P3b amplitude following reset and distractor screens was most predictive of response accuracy to old-first and old-repeat pictures.

3. Discussion

This study yielded several quite clear results. First and foremost, the FN400 for repeated pictures that appeared for the first time in a block of trials (new-repeat) was of intermediate value: it was more positive than for pictures that appeared for the first time in the experiment (new-first), but more negative than for pictures that were repeated within a block (old-first and old-repeat). Second, an earlier frontopolar old/new effect distinguished between pictures seen for the first time in the experiment and all other pictures. Third, the amplitude of the LPC for new-repeat pictures was more negative than for all other pictures, including those not previously seen in the experiment. Fourth and finally, the reset screen produced a greater P3b compared to the distractor screen, and P3b amplitude was positively associated with participants' performance. We discuss each of these findings in turn.

3.1. FN400

The main purpose of this experiment was to determine whether the FN400 is sensitive to temporal context. To vary temporal context, we intermittently inserted boundaries between sequences of successively presented images. Inserting such boundaries produces groupings among items in episodic memory. Computational models account for these groupings in terms of the distinct temporal contexts bound to each episode (Farrell, 2012; Lewandowsky et al., 2006). In addition to affecting subsequent recollection, the change in temporal context might also impact familiarity processing and the FN400. We found that the FN400 was indeed sensitive to temporal context. This is consistent with, and goes beyond earlier studies showing that the FN400 is sensitive to associative recognition, item color, font color, and screen location (Ecker et al., 2007a; Mollison and Curran, 2012; Nyhus and Curran, 2009; Speer and Curran, 2007).

These results are partially consistent with a study by Holscher and Rolls (2002) where macaques performed a delayed-match-tosample task. Neurons in the perirhinal cortex responded to the first presentation of each picture in a block as if it were new. The FN400 to new-repeats in our subjects was in the direction of responses to pictures that were entirely new. The partial reset of the FN400 could indicate that the signal arises from a heterogeneous population of neurons in the perirhinal cortex with different response properties (Xiang and Brown, 1998). Alternatively, the FN400 could arise from other prefrontal regions that are impacted in part by earlier familiarity processing in the perirhinal cortex (Rugg and Curran, 2007). Both accounts permit the FN400 to be simultaneously sensitive to temporal context and other sources of

300 to 500 msec



Fig. 5. Headplots for reset and distractor screens from 300 to 500 ms.

Table 6

Mean amplitude of ERP responses to distractor and reset screens with SEMs in parentheses.

	300–500 ms			
	Frontal	Central	Posterior	
Reset Distractor	6.11 (1.15) 5.17 (0.74)	9.02 (1.06) 7.18 (0.92)	12.02 (1.15) 9.70 (1.21)	

Table 7

Correlations between P3b amplitude and task performance.

Trial type	Reset	Distractor
New-first	.23	05
New-repeat	.17	03
Old-first	.49	.49
Old-repeat	.46	.42

contextual information. We interpret the intermediate FN400 for new-repeats in our experiment in terms of their match to the global experiment context but not to the local temporal context. Old-firsts and old-repeats matched both contexts and were most positive during the time window of the FN400, whereas new-firsts matched neither and were most negative during the time window of the FN400.

The perirhinal cortex contains a heterogeneous population of neurons with distinct response properties (Xiang and Brown, 1998). Some are sensitive to the very first presentation of a stimulus (i.e. novelty), others are sensitive to stimuli that repeat after a brief delay (i.e. recency), and still others are sensitive to stimuli that appear more often (i.e. familiarity). The FN400 in our experiment showed something of a novelty response: it was most negative for items when they appeared for the very first time in the experiment. The FN400 was less sensitive to recency. When dividing trials by condition and number of intervening items, the effect of condition was significant but the effect of number of intervening items and the interaction were not. Lastly, the FN400 was sensitive to familiarity, defined as whether an item had appeared since the reset screen (c.f. Holscher and Rolls, 2002) rather than the lifetime frequency of an item (c.f. Xiang and Brown, 1998).

Several computational models of the parahippocampal cortices – including the perirhinal cortex – have been proposed. Some hold that the perirhinal cortex performs strictly acontextual processing (Bogacz et al., 2001), whereas others allow varying degrees of contextual or associative processing (Meeter et al., 2005; Norman

and O'Reilly, 2003). Our results, and the results of Holscher and Rolls (2002), are most consistent with a model by Meeter et al. (2005) in which parahippocampal nodes integrate contextual and stimulus information. Stimuli are represented along with contextual elements. The response to a stimulus is modulated by whether it has appeared before in the current context, which shifted with the reset screen in our paradigm.

3.2. Early frontopolar old/new effect

Shifting focus to the time before the FN400, we obtained a somewhat different old/new effect from 176 to 260 ms. Waveforms over the frontopolar scalp were more negative for new-first items than for all other items. Curran and Dien (2003) reported a similar effect for novel words presented in the visual modality. No such effect was obtained for words presented in the auditory modality. Tsivilis et al. (2001) also reported an early frontopolar old/new effect for images of novel scenes and objects. The effect was obtained only when the displayed scene and image were both new, and did not distinguish between studied and rearranged pairs of scenes and images. In line with those reports, we interpret the early frontopolar effect as relating to a visually specific perceptual priming mechanism.

3.3. Late positive component (LPC)

Although the primary goal of this study was to explore whether familiarity (and the FN400) is sensitive to temporal context, we also examined the LPC, the component most linked to recollection. The LPC is typically more positive when people retrieve detailed information about the stimulus, including contextual information. To correctly respond to new-repeat pictures in our task, subjects needed to know when the picture appeared relative to the reset screen. As such, we expected that the LPC would be more positive for new-repeat pictures than for new-first pictures. Contrary to this expectation, the amplitude of the LPC was *more negative* for new-repeat pictures than for new-first pictures.

Our interpretation of the LPC result is somewhat speculative. One explanation for the lower LPC amplitude for new-repeats versus new-firsts involves a phenomenon called the "reversed old/ new" effect (Nowicka et al., 2009). When people were instructed to try to forget words as they first studied them, LPC amplitudes during a later recognition test were lower for successfully forgotten words than for words that had not been studied (Nowicka et al., 2009). The authors attributed this "reversed old/new effect" to active inhibition of the to-be-forgotten word (see also Epstein (1972), Geiselman et al. (1983) and Van Hooff et al. (2009)). Likewise, subjects in our experiment may have needed to inhibit information about having previously seen new-repeat pictures in order to correctly identify them as "new". An alternate explanation is that the lower amplitude for new-repeat pictures was driven by subjects' lower confidence. Accuracy was lowest in that condition, and response durations were longest. Previous studies show that the LPC is smaller when people are not confident in their responses (Woodruff et al., 2006). Additional research is needed to distinguish between these explanations of the LPC effect in our experiment.

3.4. P3b

The P3b was greater for the reset screen compared with the distractor screen. These ERP responses were particularly interesting in that they correlated positively with subjects' accuracy on the task. The most plausible explanation for this effect is that subjects differed in their attentiveness to the task, which correlated both with their P3b amplitudes and their accuracy. The P3 component is larger when people allocate more attention to a stimulus (Donchin, 1981; Kok, 2001; Polich, 2007; Wijers et al., 1989). The elevated P3b amplitudes may therefore have reflected the greater attentiveness of subjects who performed the task well. This is in line with a recent finding by Galli et al. (2013) showing that subsequent memory of a word could be predicted by ERP responses to a preparatory cue, but only when attention was not divided (see also Otten et al. (2006)).

A related set of findings come from the task-switching literature, where it has been found that ERP responses to a cue to switch tasks can be used to predict how quickly people will perform the new task in the upcoming block (Kieffaber and Hetrick, 2005; Li et al., 2012). In addition, a recent fMRI study (Manelis and Reder, 2015) found that when people were shown a cue indicating the upcoming difficulty level of an n-back task, neural responses to the cue predicted their ability to perform the task accurately. In these studies, as in ours, cues did not require distinctive behavioral responses, and yet neural responses to cues were still predictive of later performance.

4. Conclusion

This study most clearly demonstrates the effect of temporal context on the FN400, and it indicates an effect of inhibition and/ or confidence on the LPC. This study also provides support for the idea that neural processes occurring well in advance of a task can predict subsequent performance. The finding that the FN400 is sensitive to temporal context is consistent with, and goes beyond existing behavioral and neuroimaging studies of familiarity processing. In doing so, it provides new insight into the nature of recognition memory.

5. Methods

5.1. Subjects

Twenty volunteers (13 males) participated in the experiment. They ranged in age from 19 to 31, with a mean age of 23. They were recruited from the Carnegie Mellon University (CMU) subject pool and the Pittsburgh community. All subjects had normal or corrected to normal vision and were treated in accordance with CMU IRB guidelines. Following a debriefing at the end of the experiment, they received research experience credit or \$15.00 as compensation.

5.2. Stimuli and design

The stimuli were pictures of everyday items (squirrel, hammer, etc.) acquired from the Internet and displayed against a white background. A unique stimulus list consisting of 544 pictures with 28 reset screens and 28 distractor screens was generated for each subject. The background color of the reset and distractor screens were red and blue, with color assignment randomly determined for each subject. Every picture trial could be categorized by whether the picture had appeared since the previous reset screen, and whether the picture had appeared before during the experiment. There were four types of picture trials:

- 1. *New-first* when a picture appeared for the first time in the experiment, and the correct response was new;
- 2. *New-repeat* when a picture had last appeared before the reset screen, and the correct response was new;
- 3. *Old-first* when a picture had already appeared once since the reset screen, and the correct response was old;
- 4. *Old-repeat* when a picture had appeared before and since the reset screen, and the correct response was old.

A diagram of the different conditions is shown in Fig. 1.

Each subject's stimulus list consisted of four higher-order sets, each of which contained three short blocks, two medium blocks, and two long blocks. A block was defined as the period between the appearances of reset screens. We varied block length in order to make it difficult for subjects to anticipate when the next reset screen would appear. Short blocks consisted of 12 pictures, medium blocks of 20 pictures, and long blocks of 30 pictures. For each of the four higher-order trial sets, 34 picture trials appeared in each of the four conditions (new-first, new-repeat, old-first, and old-repeat).² Each set contained a distinct collection of pictures in order to separate any effects of task familiarity and practice with the conditions of interest. Distractor screens were inserted randomly into the stimulus list to provide a control condition against which to compare ERP responses to the reset screen.

5.3. Procedure

Subjects sat in an electrically shielded booth. Stimuli appeared on a CRT monitor placed behind radio-frequency shielded glass and set 50 cm from subjects. Some trials began with the presentation of a picture. Subjects were instructed to press the F key with their left index finger if they believed the picture had appeared since the most recent reset screen, and to press the J key with their right index finger if the picture had not. A buzzer sounded if the subject responded incorrectly. Other trials began with the presentation of a reset or distractor screen. Subjects were instructed to press the space bar to advance. The experiment was self-paced. Following all responses, a blank white screen appeared for 100–300 ms, after which the next trial began.

5.4. ERP recording

The EEG signal was recorded from 32 Ag-AgCl sintered electrodes (10–20 system). Additional electrodes were placed on the right and left mastoids. The right mastoid served as the reference electrode, and scalp recordings were algebraically re-referenced to the average of the right and left mastoids offline. The vertical EOG was recorded from electrodes placed above and below the orbit of

² This created a scenario where the correct response to 2/3 of previously seen pictures (new-repeat, old-first, and old-repeat) was "old". Equating the frequency of responses to pictures previously seen would have the undesirable consequence of creating an overall bias toward "new" responses.

the left eye, and the horizontal EOG was recorded from electrodes placed at the external canthi. Electrode impedances were kept below 5 k Ω . The EEG and EOG signals were amplified by a Neuroscan bioampliciation system (Neuroscan Inc., Sterling, VA) with a bandpass of .1–200 Hz and were digitized at 1000 Hz. The continuous data were filtered offline using a 70 Hz low-pass filter and down-sampled to 500 Hz.

The EEG recording was decomposed into independent components using the EEGLAB infomax algorithm (Delorme and Makeig, 2004). Components associated with eye blinks were visually identified and projected out of the EEG recording. The data were analyzed with respect to trial onsets (i.e. the appearance of pictures, reset screens, and distractor screens). Epochs of 1050 ms (including a 50 ms baseline) were extracted from the continuous recording and corrected over the prestimulus interval. Epochs containing voltages above $+100 \,\mu$ V or below $-100 \,\mu$ V were excluded from further analysis. In addition to creating topographical maps over the time windows of interest, we analyzed data from three regions of interest (ROIs): a frontal region (F3, FZ, F4), a central region (C3, CZ, C4), and a posterior region (P3, PZ, P4). For all analyses, we applied the Greenhouse-Geisser correction when factors had more than two levels.

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References

- Bogacz, R., Brown, M.W., Giraud-Carrier, C., 2001. Model of familiarity discrimination in the perirhinal cortex. J. Comput. Neurosci. 10 (1), 5–23.
- Curran, T., 2000. Brain potentials of recollection and familiarity. Mem. Cogn. 28, 923–938.
- Curran, T., Cleary, A.M., 2003. Using ERPs to dissociate recollection from familiarity in picture recognition. Cognit. Brain Res. 15 (2), 191–205.
- Curran, T., Dien, J., 2003. Differentiating amodal familiarity from modality-specific memory processes: an ERP study. Psychophysiology 40 (6), 979–988.
- Curran, T., Tepe, K.L., Piatt, C., 2006. ERP explorations of dual processes in recognition memory. In: Zimmer, H.D., Mecklinger, A., Lindenberger, U. (Eds.), Binding in Human Memory: A Neurocognitive Approach. Oxford University Press, UK, pp. 467–492.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods 134 (1), 9–21.
- Diana, R.A., Peterson, M.J., Reder, L.M., 2004. The role of spurious feature familiarity in recognition memory. Psychon. Bull. Rev. 11 (1), 150–156.
- Diana, R.A., Yonelinas, A.P., Ranganath, C., 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. Trends Cognit. Sci. 11 (9), 379–386.
- Diana, R.A., Van den Boom, W., Yonelinas, A.P., Ranganath, C., 2011. ERP correlates of source memory: Unitized source information increases familiarity-based retrieval. Brain Res. 1367, 278–286.
- Diana, R.A., Yonelinas, A.P., Ranganath, C., 2008. The effects of unitization on familiarity based source memory: testing a behavioral prediction derived from neuroimaging data. J. Exp. Psychol.: Learn., Mem., Cogn. 34 (4), 730–740.
- Donchin, E., 1981. Surprise! ... Surprise? Psychophysiology 18, 493-513.
- Duzel, E., Yonelinas, A.P., Mangun, G.R., Heinze, H.J., Tulving, E., 1997. Event-related potential correlates of two states of conscious awareness in memory. Proc. Natl. Acad. Sci. USA 94, 5973–5978.
- Ecker, U.K., Zimmer, H.D., Groh-Bordin, C., 2007a. Color and context: an ERP study on intrinsic and extrinsic feature binding in episodic memory. Mem. Cogn. 35 (6), 1483–1501.
- Ecker, U.K., Zimmer, H.D., Groh-Bordin, C., Mecklinger, A., 2007b. Context effects on familiarity are familiarity effects of context—an electrophysiological study. Int. J. Psychophysiol. 64 (2), 146–156.
- Eichenbaum, H., Yonelinas, A.P., Ranganath, C., 2007. The medial temporal lobe and recognition memory. Annu. Rev. Neurosci. 30, 123–152.

- Epstein, W., 1972. Mechanisms in directed forgetting. In: Bower, G.H. (Ed.), The Psychology of Learning and Motivation vol. 6. Academic Press, New York, NY, pp. 147–191.
- Farrell, S., 2012. Temporal clustering and sequencing in short-term memory and episodic memory. Psychol. Rev. 119, 223–271.
- Friedman, W.J., 1993. Memory for the time of past events. Psychol. Bull. 113, 44–66. Galli, G., Gebert, D., Otten, J.L., 2013. (Available) processing resources influence encoding related brain activity before an event. Cortex 49, 2239–2248.
- Geiselman, R.E., Bjork, R.A., Fishman, D.L., 1983. Disrupted retrieval in directed forgetting: a link with posthypnotic amnesia. J. Exp. Psychol.: General. 112, 58–72.
- Holscher, C., Rolls, E.T., 2002. Perirhinal cortex neuronal activity is actively related to working memory in the macaque. Neural Plast. 9, 41–51.
- Jacoby, L.L., 1991. A process dissociation framework: separating automatic from intentional uses of memory. J. Mem. Lang. 30, 513–541.
- Kieffaber, P.D., Hetrick, W.P., 2005. Event-related potential correlates of task switching and switch costs. Psychophysiology 42 (1), 56–71.
- Kok, A., 2001. On the utility of P3 amplitude as a measure of processing capacity. Psychophysiology 38, 557–577.
- Li, L., Wang, M., Zhao, Q., Fogelson, N., 2012. Neural mechanisms underlying the cost of task switching: an ERP study. PLoS One 7 (7), e42233. http://dx.doi.org/ 10.1371/journal.pone.0042233.
- Lewandowsky, S., Brown, G.D., Wright, T., Nimmo, L.M., 2006. Timeless memory: evidence against temporal distinctiveness models of short-term memory for serial order. J. Mem. Lang. 54, 20–38.
- Manelis, A., Reder, L.M., 2015. He who is well prepared has half won the battle: an fMRI study of task preparation. Cereb. Cortex 25 (3), 726–735.
- Mandler, G., 1980. Recognizing: the judgment of previous occurrence. Psychol. Rev. 87 (3), 252–271.
- Meeter, M., Myers, C.E., Gluck, M.A., 2005. Integrating incremental learning and episodic memory models of the hippocampal region. Psychol. Rev. 112 (3), 560–585.
- Mollison, M.V., Curran, T., 2012. Familiarity in source memory. Neuropsychologia 50, 2546–2565.
- Montaldi, D., Mayes, A.R., 2010. The role of recollection and familiarity in the functional differentiation of the medial temporal lobes. Hippocampus 20, 1291–1314.
- Norman, K.A., O'Reilly, R.C., 2003. Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. Psychol. Rev. 110 (4), 611–646.
- Nowicka, A., Jednorog, K., Wypych, M., Marchewka, A., 2009. Reversed old/new effect for intentionally forgotten words: an ERP study of directed forgetting. Int. J. Psychophysiol. 71, 97–102.
- Nyhus, E., Curran, T., 2009. Semantic and perceptual effects on recognition memory: evidence from ERP. Brain Res. 1283 (4), 102–114.
- Otten, L.J., Quayle, A.H., Akram, S., Ditewig, T.A., Rugg, M.D., 2006. Brain activity before and event predicts later recollection. Nat. Neurosci. 9 (4), 489–491.
- Parks, C.M., Yonelinas, A.P., 2007. Moving beyond pure signal-detection models: comment on Wixted (2007). Psychol. Rev. 114, 188–201.
- Polich, J., 2007. Updating P300: An integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128–2148.
- Reder, L.M., Nhouyvanisvong, A., Schunn, C.D., Ayers, M.S., Angstadt, P., Hiraki, K., 2000. A mechanistic account of the mirror effect for word frequency: a computational model of remember-know judgments in a continuous recognition paradigm. J. Exp. Psychol.: Learn. Mem. Cogn. 26, 294–320.
- Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. Trends Cognit. Sci. 11 (6), 251–257.
- Rugg, M.D., Yonelinas, A.P., 2003. Human recognition memory: a cognitive neuroscience perspective. Trends Cognit. Sci. 7 (7), 313–319.
- Speer, N.K., Curran, T., 2007. ERP correlates of familiarity and recollection processes in visual associative recognition. Brain Res. 1174, 97–109.
- Tsivilis, D., Otten, L.J., Rugg, M.D., 2001. Context effects on the neural correlates of recognition memory: an electrophysiological study. Neuron 31 (3), 497–505. Tulving, E., 1983. Elements of Episodic Memory. Clarendon Press, Oxford.
- Van Hooff, J.C., Whitaker, T.A., Ford, R.M., 2009. Directed forgetting in direct and indirect tests of memory: seeking evidence of retrieval inhibition using electrophysiological measures. Brain Cogn. 71, 153–164.
- Wijers, A.A., Mulder, G., Okita, T., Mulder, L.J., 1989. Event-related potentials during memory search and selective attention to letter size and conjunctions of letter size and color. Psychophysiology 26, 529–547.
- Woodruff, C.C., Hayama, H.R., Rugg, M.D., 2006. Electrophysiological dissociation of the neural correlates of recollection and familiarity. Brain Res. 1100 (1), 125–135.
- Xiang, J.Z., Brown, M.W., 1998. Differential neuronal encoding of novelty, familiarity and recency in regions of the anterior temporal lobe. Neuropharmacology 37, 657–676.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. J. Mem. Lang. 46, 441–517.
- Yovel, G., Paller, K.A., 2004. The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. NeuroImage 21 (2), 789–800.
- Zimmer, H.D., Ecker, U.K., 2010. Remembering perceptual features unequally bound in object and episodic tokens: neural mechanisms and their electrophysiological correlates. Neurosci. Biobehav. Rev. 34, 1066–1079.