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Biological Psychology 66 (2004) 235-255

BIOLOGICAL PSYCHOLOGY

www.elsevier.com/locate/biopsycho

Neural correlates of temporal context discrimination

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Received 16 March 2003; accepted 3 October 2003

Abstract

This study investigated event-related potential (ERP) effects when judgments about temporal context (recency judgments) required the retrieval of different amount of information. Subjects studied two consecutively presented word lists and at test made recency judgments to word pairs composed of two previously studied words, one drawn from each list ('Old + Old different' pairs), both drawn from the same list ('Old + Old same' pairs), or two unstudied words ('New + New' pairs). A frontopolar old/new effect was elicited by correct recency judgments which did not differ between both 'Old + Old' pairs. This finding suggests that the generators of the frontopolar old/new effect are not sensitive to the differing retrieval demands required here. However, an old/new effect over left inferior temporal electrodes was larger for 'Old + Old same' than for 'Old + Old different' pairs. The significance of these old/new effects are discussed in relation to the broader pattern of old/new effects seen in standard tests of declarative memory retrieval. © 2004 Published by Elsevier B.V.

Keywords: Recency memory; Prefrontal cortex; Medial temporal lobe; Declarative memory; Event-related potentials; Old/new effect; Recollection; Familiarity

1. Introduction

1.1. Declarative memory: a neuropsychological account

The kind of memory one ordinarily means when using the term 'memory' is declarative memory, involved in the retrieval of past events and facts (Cohen and Squire, 1980;

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^{0301-0511/\$} – see front matter © 2004 Published by Elsevier B.V. doi:10.1016/j.biopsycho.2003.10.009

Tulving, 1983). Neuropsychological assessments of amnesic patients with circumscribed lesions have firmly linked declarative memory to the medial temporal lobe (MTL) (Squire et al., 1993; Zola-Morgan and Squire, 1993). In contrast, patients with lesions to the prefrontal cortex (PFC) are not amnesic (Shimamura et al., 1990). They nevertheless exhibit impairments in certain declarative memory tasks, notably free recall or source memory, where study items have to be associated with their appropriate context (for review see Stuss et al., 1994). These findings have led to the proposal that, in addition to the declarative memory retrieval mediated by the MTL, the PFC is especially involved in the recollection of contextual information (Stuss et al., 1994).

1.2. Electrophysiological evidence for dissociable processes

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Neuropsychological evidence identifies the likely neuroanatomical structures underlying declarative memory. By contrast, electrophysiological methods like event-related potentials (ERP) provide insight into the timing of the processes involved (Rugg and Coles, 1995), suggesting dissociable processes that map onto the neuropsychological dissociations described above. In a variety of investigations, ERPs have been found to differ according to the study status of words presented during tests of recognition memory (Allan et al., 1998). The principal finding is that ERPs to items judged correctly to be old are more positive than those to items judged correctly to be new. Based on experiments designed to elicit variable engagement of the processes involved in declarative memory retrieval, this 'old/new effect' has been dissociated into a number of 'components processes' (for review see Donaldson et al., 2002). Here we describe evidence for three functionally distinct old/new effects, each of which is associated with an identifiable time course and scalp distribution.

1.2.1. The left temporo-parietal old/new effect

The first old/new effect identified during tests of recognition memory onsets approximately 400 ms post-stimulus, typically lasts around 400-600 ms, and is largest in amplitude over left temporo-parietal scalp electrodes. The left temporo-parietal old/new effect has been firmly linked to recollection, primarily on the basis of studies that have varied the likelihood of recollection, either during source memory tasks (Allan et al., 1998 for review; Wilding and Rugg, 1996, 1997) or using associative recall (Donaldson and Rugg, 1998, 1999; Tendolkar et al., 1997). These studies suggest that the left temporo-parietal old/new effect indexes recollection in a graded fashion; its magnitude is modulated by the amount of information available for recollection (Wilding, 2002). Localization of the neural generators of the effect is difficult due to the spatial resolution of EEG data. However, there are several findings supporting the idea that the left temporo-parietal old/new effect is modulated by MTL activity at least indirectly. Firstly, this proposal receives support from intracranial recordings from within the MTL (Elger et al., 1995; Guillem et al., 1995; Smith et al., 1986) as well as from scalp ERP studies in patients with temporal lobe lesions including the hippocampus (Rugg et al., 1991; Smith and Halgren, 1989). Secondly, an MEG study (Tendolkar et al., 2000) of episodic memory retrieval found a magnetoencephalographic correlate of the temporo-parietal old/new effect and was able to localize its neural generators to the hippocampal region and the temporo-parietal cortex. It seems therefore likely that the MTL modulates activity in a different region which in turn elicits the ERP signal. In short, the left temporo-parietal effect appears to provide an ERP correlate of recollection, most likely reflecting an indirect index of the contribution of the MTL to declarative memory retrieval.

1.2.2. The late right frontal old/new effect

Consistent with neuropsychological accounts of declarative memory, additional frontally distributed old/new effects typically accompany the left temporo-parietal effect. A frontal old/new effect onsets with a bilateral distribution at a similar latency as the left temporoparietal effect (discussed below), and from 800 ms onwards shows a sustained maximum over right frontal scalp electrodes (henceforth this effect will be referred to as right frontal old/new effect). At present, a consensus on the functional role of this right frontal old/new effect is, however, missing. Early studies where recollection was tested as the ability to retrieve and make use of contextual (source) information, suggest that the right frontal old/new effect is largest for ERPs associated with correct source judgments (Wilding and Rugg, 1996, 1997). These authors also suggest, largely on the basis of its time course, that the right frontal old/new effect is hypothesized to reflect post-retrieval operations, which are engaged by tasks requiring contextual discrimination, such as monitoring processes (Moscovitch, 1992) that operate upon retrieved information. Although there is evidence that the magnitude of the right frontal old/new effect increases with the amount of information recollected (Allan et al., 1998; Donaldson and Rugg, 1998, 1999; Wilding and Rugg, 1996, 1997), this finding is not seen in all studies (Düzel et al., 1997; van Petten et al., 2000; Senkfor and van Petten, 1998). In fact, in another study, the right frontal old/new effect was even larger when source retrieval was unsuccessful (Trott et al., 1999). Moreover, the right frontal effect was seen in tests of mere recognition memory (Ranganath and Paller, 1999) and there even elicited by false alarms (new items judged as old, Trott et al., 1999). In sum, these findings suggest that the right frontal effect is rather an inconsistently observed correlate of recognition memory with only an epiphenomenal relationship with source monitoring.

1.2.3. The early bilateral frontal old/new effect

The right frontal old/new effect has also been dissociated from an earlier bilateral frontal old/new effect (noted above), which is present between 400 and 800 ms post-stimulus (Wilding and Rugg, 1997). Studies of associative recognition (Donaldson and Rugg, 1998, 1999) suggest that the magnitude of the bilateral frontal old/new effect is not sensitive to a variation in the amount of recollection. Consistent with this finding, a number of studies investigating dual process models of recognition memory (Curran, 1999, 2000; Mecklinger, 2000; Rugg et al., 1998; Tendolkar et al., 1999), have interpreted the bilateral frontal effect as reflecting a familiarity process (supporting a contextual retrieval). For example, the bilateral frontal effect was not influenced by variables held to influence recollection, but is elicited by unstudied items misclassified as old on the basis of familiarity (Curran, 2000). Recently, however, the notion that the bilateral frontal effect is a direct reflection of familiarity-driven recognition memory has been called into question. Tsivillis et al. (2001) examined the bilateral frontal effect associated with multi-component stimuli (digitized pictures composed of an object superimposed in a background context). Critically, the bilateral frontal effect was not present for recognized stimuli composed of a studied object in an unstudied context (and vice versa). Tsivillis argued that this finding is difficult to reconcile with a familiarity

account and that the effect is actually sensitive to novelty (which is inversely correlated with familiarity, unless multi-component stimuli are employed).

As noted above, conclusions about the neural substrates of the aforementioned frontal old/new effects are tentative. Regardless, taken together, the findings from a large number of studies suggest that the bilateral frontal ERP old/new effect reflects operations supporting familiarity (at least indirectly), while the right frontal old/new effect is involved in post-retrieval processes associated with contextual retrieval.

1.3. Recency memory: a frontopolar old/new effect

The right frontal old/new effect is, however, not the only ERP correlate associated with contextual retrieval. Tendolkar and Rugg (1998) investigated the neural activity related to retrieval of temporal context information by employing an experimental design derived from Milner and coworkers (Milner, 1971; Milner et al., 1991). ERPs were recorded while subjects were presented with pairs of previously studied words and required to judge which word had been presented most recently. Test pairs were composed of two old words drawn from each of two study lists ('Old + Old' pairs), one old and one new word ('Old + New' pairs), or two new words ('New + New' pairs). A second experiment used the same experimental design, but a recognition rather than recency judgment had to be performed. In both experiments, ERPs to pairs containing at least one previously studied item elicited a left temporo-parietal old/new effect between 300 and 1200 ms. However, only for 'Old + Old' pairs associated with correct *recency* judgments, a frontopolar old/new effect was evident from around 300 ms onwards.

The frontopolar old/new effect is dissociable from the two frontal old/new effects described earlier, based on both location and time course. This finding led the authors to conclude that it may be specific to the retrieval of temporal context and/or reflects different working memory operations than the right frontal old/new effect. Moreover, they rejected the hypothesis that the frontopolar effect merely reflected the requirement to retrieve more information, as it was only observed when a recency rather than recognition judgment was required.

1.4. Open questions: aims of the present experiment

In their study Tendolkar and Rugg did not ensure that recency judgments could only be performed on the basis of contextual information. Hence, it remains unclear whether the frontopolar old/new effect is specifically sensitive to contextual retrieval. This question is the focus of the current experiment. Here we compare ERPs to correct recency judgments of Old + Old pairs derived either from the same (henceforth called 'Old + Old same') or different study list ('Old + Old different'). By this experimental manipulation, both 'Old + Old' categories should share the same item characteristics, and discrimination between them cannot be based on a simple assessment of familiarity. Instead, recency judgments to 'Old + Old same' pairs demand the retrieval of additional contextual information as compared to 'Old + Old different' pairs (where assigning the items to the correct study list would be sufficient to solve the task). To allow a comparison with the findings of previous studies, we have included a baseline condition of 'New + New' pairs.

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We anticipate the following outcomes: if the magnitude of the frontopolar old/new effect to correct recency judgments of 'Old + Old same' pairs is greater than that to 'Old + Old different' pairs, this would suggest that the effect is sensitive to differences in contextual retrieval. An absence of a difference between ERPs to both correctly judged 'Old + Old' pairs over frontopolar electrode sites, on the other hand, could be interpreted as supporting the null hypothesis, e.g. both conditions require an equal amount of contextual retrieval. However, the previous study by Tendolkar and Rugg (1998) might serve as a pilot study to ensure that co-occurrence of frontopolar and temporo-parietal old/new effect, which has been observed in this previous study, can be taken to answer this question: while the frontopolar old/new effect appeared only when recency judgments were made to word pairs where both members were old (thereby at least sensitive to some kind of contextual retrieval), the temporo-parietal old/new effect was elicited by ERPs to 'Old + Old' and 'Old + New' pairs (being larger when both members of a pairs were old as more information had to be retrieved). Hence, a similar old/new effect to both 'Old + Old' pairs over frontopolar sites in the presence of a difference in the old/new effects over temporo-parietal sites (with a larger effect to 'Old + Old' different pairs) could be taken as evidence that the frontopolar old/new effect more likely reflects processes that are insensitive to contextual retrieval, such as familiarity-based retrieval, or more general working memory operations related to retrieval support processes required for temporal judgments. No difference in the old/new effects over both frontopolar and temporo-parietal sites, finally, could be related to the fact that both 'Old + Old' pairs require an equal amount of contextual retrieval.

2. Methods

2.1. Subjects

Twenty healthy, right-handed young adults served as subjects. The data from four of these subjects were rejected because excessive artifact led to ERPs from one or more of the critical experimental conditions to be formed from fewer than 16 trials (see below). Of the 16 remaining subjects (mean age: 24.35 ± 2.18 years) contributing data to the study, seven were female.

2.2. Overview of experimental design

The experiment consisted of four study-test blocks. Subjects first studied two consecutively presented word lists. They were instructed to try to remember each word in the study lists, using different tasks for each list (either linking each word to an image, or embedding the words in a sentence). The order of the study tasks was counterbalanced across subjects. At test, participants were presented with word pairs, and required to indicate which of the two words had been presented most recently. Three different types of word pair were presented. In the 'Old + Old same' condition, both members of a pair had been previously studied in the same list. In the 'Old + Old different' condition, both members of a pair had been previously studied, one in each list. In the 'New + New' condition, neither word had been studied. Subjects were not informed that the test blocks contained previously unstudied words but told that in the case of uncertainty they should guess which word had been studied most recently. By this token, ERPs to 'New + New' pairs could serve as a baseline with the possibility to control whether there would be any preference for the word position in the judgment of top or bottom 'New' items. Although participants need not inspect both items of a 'New + New' pair to solve the task, the critical comparison between 'Old + Old same' and 'Old + Old different' pairs does not suffer this confound.

2.3. Stimuli

The stimulus lists were selected from a pool of 448 German words (Celex data base (Baayen et al., 1993), mean word frequency 5.37 ± 1.9 per million, length 5.8 ± 1.2 letters). These items were randomly allocated to one of four study-test blocks. Each block comprised two study lists, each of 40 words, and a test list of 55 word pairs. Twenty test pairs were 'Old + Old same' (10 pairs from the first and 10 pairs from the second list with a minimum distance of 25 words between both items in the study list), 20 were 'Old+Old different', and 15 were 'New + New'. Different versions of each study-test block were created, such that across versions, items rotated across the different experimental conditions. Each version of the lists from each of the four blocks employed a different, randomly determined ordering of items and conditions. The different versions of each block were rotated across subjects.

For the study tasks, each word was displayed for 500 ms on a computer monitor as white characters on a dark background in central vision (subtending vertical and horizontal visual angles of approximately 0.5° and 2.0° , respectively). The inter-stimulus interval was 3 s during which subjects performed the study task. At test, each trial began with the presentation of the two members of each word pair which were presented left justified for 400 ms above and below fixation, separated by a visual angle of 0.7° . The pairs subtended a maximum horizontal visual angle of 2.0° , and a vertical visual angle of 2.1° . The screen remained blank for 3 s post-stimulus offset while subjects gave their response. Extremely long responses above 3.5 s were taken as misses.

2.4. Procedure

Following application of the recording electrodes, subjects were seated in a testing chamber in front of the display monitor. The study and test task was explained to them as described above. The interval between the end of the first study list and the administration of the second list was approximately 8 min, which was spent in conversation with the experimenter. The aim of this conversation was to distract subjects from the previous study phase by talking about things that were not related to the experimental situation. A similar interval separated the end of the second study list from the beginning of the test task. For the test task, subjects were instructed to determine whether the top or the bottom word of each pair had been presented most recently, and to press one of two response buttons accordingly. Speed and accuracy were given equal emphasis. The mapping of keys to word position was counterbalanced across subjects. Subjects were further instructed to remain relaxed throughout the test phase, to maintain fixation on the center when the screen was blanked, and to restrict eye-movements to the period after they made their button press.

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2.5. ERP recordings

Scalp EEG was recorded from 31 tin electrodes embedded in an elasticated cap. Recording locations were based on the international 10–20 System, and consisted of 5 midline sites (Nz, Fz, Cz, Pz, Inz), and 13 sites over each hemisphere: FP1/FP2, F9/F10, F7/F8, F3/F4, FT7/FT8 (50% of the distance from F7/F8 to T3/T4), FC3/FC4 (50% of the distance from F3/F4 to C3/C4), T3/T4, C3/C4, TP7/TP8 (50% of the distance from T3/T4 to T5/T6), T5/T6, P3/P4, P9/P10 and O1/O2. Electrooculogram (EOG) was recorded bipolarly from F9/F10 and from FP2/right infraorbital electrode. All channels were referenced to Cz. EEG data were sampled on-line in DC-mode (SYNAMPSR, Neuroscan) at a rate of 2 ms per point for a duration of 1600 ms, commencing 100 ms before stimulus presentation. Offline, data were algebraically adjusted to a common average reference and bandpass-filtered (0.01–70 Hz).

ERPs were formed for a variety of different response categories, as described below. EEG was corrected for intrusion of EOG artifact (Gratton et al., 1983). Trials in which base-to-peak EEG amplitude exceeded 70 μ V or on which A/D saturation occurred were rejected. In order to maintain an acceptable signal-to-noise ratio, and in keeping with previous studies (Rugg et al., 1998; Tendolkar et al., 1997; Tendolkar and Rugg, 1998), only ERPs formed from 16 or more artifact free trials for any given response category were accepted for analysis.

2.6. ERP data analysis

The ERPs of most relevance to the aims of this study are those associated with accurate responses to 'Old+Old same' and 'Old+Old different' pairs, relative to a baseline provided by 'New + New' pairs. On the basis of exploratory 100 ms analyses and visual inspection of the data, ERP waveforms were quantified by measurement of the mean amplitudes (with respect to the mean of the pre-stimulus baseline) over three latency regions. These three epochs (400–700, 700–1000 and 1000–1500 ms post-stimulus) were chosen to capture the different sub-components of the old/new effects. In keeping with the previous study by Tendolkar and Rugg (1998), an initial ANOVA (in this and all subsequent analyses *P*-values were corrected using the Greenhouse–Geisser procedure as described by Winer, 1971) was performed on the data from all response categories and sites, in order to confirm that the data set as a whole was sensitive to the experimental variables of interest. In the event of a reliable effect involving the factor of response category, subsidiary ANOVAs were performed to characterize the different patterns of effect at frontal (FP1/FP2, F3/F4, F7/F8) and lateral parietal electrodes (P3/P4, P7/P8, TP7, TP8). Final *t*-tests, corrected for multiple comparisons, were performed to elucidate possible interactions. To investigate amplitude differences between the old/new effects to 'Old + Old same' and 'New + New' as well as 'Old + Old different' and 'New + New', simple ANOVAs were conducted on the difference waveforms over those electrode sites, where the prior analysis had shown a reliable difference.

Topographic analyses were employed to investigate whether the scalp distribution of the old/new effects to 'Old + Old same' and 'Old + Old different' differed across time (using normalized difference scores, see McCarthy and Wood, 1985). In keeping with previous

studies (Tendolkar et al., 1997; Tendolkar and Rugg, 1998), ANOVAs were first conducted over frontal and temporo-parietal sites of interest, employing the factors of time epoch (400–700, 700–1000 and 1000–1500 ms), normalized difference category ('Old+Old same' minus 'New + New', and 'Old + Old different' minus 'New + New'), anterior/posterior (frontal electrodes versus temporo-parietal sites) and electrode site (FP1/FP2, F3/F4, P3/P4, TP7/TP8). The principle logic behind the division of the electrodes into the factors anterior/posterior and electrode site, similar to the factors of hemisphere and electrode site used in the analyses of the raw data (see also Tendolkar and Rugg, 1998), was that the factor "anterior/posterior" would allow to divide the electrodes into two sets dissociating the old/new effects according to their frontal and parietal topography. This should also help to elucidate a change of the topography of the old/new effects over time. In the case of a significant difference in topography (either between the critical response categories over time, or for either of the critical response categories over time), comparisons between the normalized difference data were again made over the different time epochs separately for the frontal and temporo-parietal sites of interest.

Finally, the onset latencies of the old/new effects were estimated using point-by-point *t*-tests conducted on subtraction waveforms. Following previous practice (Tendolkar et al., 1997; Tendolkar and Rugg, 1998; Wilding and Rugg, 1996), onset latency was defined as the time point at which a *t*-value indicated a significant difference from zero at P < 0.05 or better, and which was followed by at least 15 consecutive significant values. All statistical analyses were computed with SPSS for Windows 95[®] (Version 7.5) (Table 1).

3. Results

3.1. Behavioral performance

Subjects made correct judgments to a mean of 62% (S.D.: $\pm 6.2\%$) of 'Old + Old same', and 69% ($\pm 8.4\%$) of 'Old+Old different' pairs. These scores were both significantly greater than chance (t(1, 15) = 5.39 and 7.85, respectively, both P < 0.001), and differed from one another (t(1, 15) = 3.23, P < 0.01). There was no difference between performance to 'Old+Old same' pairs from the first or second list, nor any consistent preference for the word judged as most recent on 'New+New' trials (48% (\pm 4.1%) bottom position). Mean reaction times (RTs) were 2015 ms (± 37.8 ms), 2011 ms (± 38.2 ms) and 1088 ms (± 29.1 ms) for correct judgments to 'Old+Old same', 'Old+Old different' and judgments to 'New+New', respectively. An overall ANOVA on these RTs showed a significant main effect of response category (F(2, 30) = 9.55, P < 0.01). After a one-sample Kolmogornov–Smirnov test revealed a Gaussian distribution of the data ('Old + Old same': z = 0.57, P > 0.5; 'Old + Old different': z = 0.36, P > 0.5; 'New + New': z = 0.54, P > 0.5), paired *t*-tests were performed, corrected for multiple comparisons. While there was no difference between the RTs to 'Old + Old same' and 'Old + Old different' pairs (t(1, 15) = 1.38, P > 0.1), the comparison between 'Old+Old same' and 'New+New' pairs (t(1, 15) = 4.19, P < 0.001) and between 'Old + Old different' and 'New + New' pairs (t(1, 15) = 2.99, P < 0.01)revealed that RT to 'New + New' was reliably shorter than the RTs to both 'Old + Old' pairs.

	400–700 ms	700–1000 ms	1000–1500 ms
Fp1_New	1.33	1.55	1.20
Fp2_New	1.52	2.75	1.67
F3_New	-0.77	-0.64	-1.12
F4_New	-1.08	-0.75	-1.19
P3_New	0.83	0.75	0.95
P4_New	0.43	0.18	0.51
TP7_New	-0.02	-0.45	0.13
TP8_New	-0.72	-0.95	-0.23
Fp1_Old_same	1.00	2.01	3.50
Fp2_Old_same	1.41	2.27	3.71
F3_Old_same	-0.32	-0.49	0.56
F4_Old_same	-0.62	-0.77	0.55
P3_Old_same	1.21	1.04	0.25
P4_Old_same	0.82	-0.06	-1.21
TP7_Old_same	0.22	0.73	0.32
TP8_Old_same	-0.55	-1.23	-1.15
Fp1_Old_different	0.85	1.69	2.85
Fp2_Old_different	1.23	2.41	3.17
F3_Old_different	-0.56	-0.27	-0.65
F4_Old_different	-0.46	-0.77	-0.48
P3_Old_different	1.43	1.13	0.11
P4_Old_different	1.02	0.25	-0.82
TP7_Old_different	-0.20	0.15	0.13
TP8_Old_different	-0.65	-1.06	-0.47

Summary of the mean amplitudes (μV) for the critical electrode sites and time windows subjected to statistical analyses

3.2. ERPs

Table 1

Figs. 1 and 2 show the waveforms for 'Old + Old same' and 'Old + Old different' pairs, alongside the ERPs to 'New + New' pairs, and Fig. 3 compares the ERPs for all three response categories over the sites chosen for statistical analyses. The mean numbers of trials forming the ERPs for these categories were 45 ('Old + Old same'), 51 ('Old + Old different'), and 54 ('New + New'), and the mean numbers of trials rejected were 4, 5, and 6, respectively.

3.2.1. Analyses of ERP raw data

• 400–700 ms: A global ANOVA over all electrode sites gave rise to a main effect of response category (F(2, 30) = 7.15, P < 0.01) and an interaction between the factors of response category and electrode site (F(48, 720) = 3.36, P < 0.001). Subsidiary ANOVAs over anterior sites showed an interaction between the factors of response category and site for ERPs to 'Old + Old same' and 'New + New' (F(2, 30) = 7.28, P < 0.01). Simple comparisons over each electrode revealed that this interaction reflected the old/new effect between ERPs to 'Old + Old same' and 'New + New' over the lateral frontal site F3 (t(1, 15) = 3.23, P < 0.01) and F4 (t(1, 15) = 3.41, P < 0.01). For ERPs



Fig. 1. Grand average ERPs, shown for all scalp sites (see text), elicited by 'New+New' (gray line), and 'Old+Old same' (solid black line) pairs attracting correct judgments. Positive voltage in this and the following figures is up, and waveforms are depicted over the full recording epoch (until 1500 ms post-stimulus) using 200 ms ticks on the x-axis.

to 'Old + Old different' versus 'New + New', a reliable interaction between the factors of response category and site (F(2, 30) = 7.53, P < 0.01) occurred during this latency range. The *t*-tests showed, that this interaction could be related to a significant difference between ERPs to 'Old + Old different' and 'New + New' over lateral frontal sites F3 (t(1, 15) = 3.93, P = 0.004) and F4 (t(1, 15) = 3.87, P = 0.005). Final ANOVAs between difference scores over electrode sites F3 and F4, which had shown a reliable old/new effect for both response categories, were not significant (F3: (F(1, 15) = 0.11, P > 0.05; F4: F(1, 15) = 1.8, P > 0.05).

A subsidiary ANOVA over parietal sites, showed a reliable main effect of response category between ERPs to 'Old+Old same' and 'New+New' F(1, 15) = 5.21, P < 0.05) reflecting the positive-going old/new effect over these sites. For the ERPs to 'Old + Old different' and 'New + New', a significant interaction between the factors of response category and site occurred (F(2, 30) = 4.92, P < 0.05). Final *t*-tests indicated, that this difference occurred due to a more positive-going waveform for ERPs to 'Old + Old different' over P3 (t(1, 15) = 3.19, P < 0.01) and P4 (t(1, 15) = 2.91, P < 0.05). However, over inferior temporal sites TP7, the significant difference between the two response categories (t(1, 15) = 3.87, P < 0.01) occurred due to a more negative-going waveform for ERPs to 'Old + Old different'. Analysis of the difference data revealed



Fig. 2. Grand average ERPs, shown as in Fig. 1, elicited by 'New + New' (gray line), and 'Old + Old different' (solid black line) pairs attracting correct judgments.

no reliable effects over P3 (F(1, 15) = 0.14, P > 0.5), but over TP7 (F(1, 15) = 5.12, P < 0.05) because ERPs to 'Old + Old same' show a significant positive-going old/new effect compared to 'Old + Old different'.

• 700–1000 ms: As for the previous latency region, the overall ANOVA again revealed a reliable interaction between the factors of response category and site (F(48, 720) =2.92, P < 0.001). Contrary to the results for the previous latency region, however, the subsidiary ANOVA did not reveal any significant differences over frontal electrode sites, neither for the comparison between 'Old + Old same' and 'New + New' (highest F(1, 15) = 0.94, P > 0.5) nor for the comparison between 'Old + Old different' and 'New + New' (highest F(1, 15) = 2.53, P > 0.5).

Over parietal sites, ANOVAs on the data to 'Old + Old same' and 'New + New' as well as 'Old + Old different' and 'New + New' items showed an interaction between response category, hemisphere and site (F(2, 30) = 5.35, P < 0.05, and F(2, 30) = 3.29, P < 0.05, respectively). As is evident from Fig. 3, these results reflect the fact that the old/new effect is lateralized to the left hemisphere. This was also supported by the final *t*-tests which showed a reliable old/new effect between 'Old + Old same'/'New + New' over electrode sites P7 (t(1, 15) = 3.51, P < 0.01) and TP7 (t(1, 15) = 3.93, P < 0.01) and between 'Old + Old different'/'New + New' over electrode P7 (t(1, 15) = 3.34, P < 0.01). A comparison between difference scores revealed a trend over TP7 (F(1, 15) = 3.88, P < 0.07), as there is only an old/new effect for 'Old + Old same'.



Fig. 3. Grand average ERPs to 'Old + Old same' (solid black line), 'Old + Old different' (dashed black line) and 'New + New' (gray line) pairs. Waveforms are shown as in Fig. 1, but only the scalp sites selected for analysis are shown.

• 1000–1500 ms: Again, the global ANOVA gave rise to a significant interaction between the factors of response category and site (F(48, 720) = 3.65, P < 0.001). Unlike in the first two latency regions, subsidiary ANOVAs over frontal sites on the data to 'Old + Old same' and 'New + New' as well as 'Old + Old different' and 'New + New' showed a main effect of response category during this final epoch (F(1, 15) = 17.2, P < 0.001, and F(1, 15) = 8.84, P < 0.01, respectively) reflecting the more positive-going waveform of ERPs to 'Old + Old' pairs compared to 'New + New' items. There were, however, no significant effects in the analyses of the difference data (highest F(1, 15) = 2.92, P > 0.1).

Over parietal sites, there was a significant interaction between the factors of response category and site for the comparison between 'Old + Old same' and 'New + New': F(2, 30) = 5.74, P < 0.01). Subsequent *t*-tests revealed that this interaction reflected the fact that there was a significant difference between the two response categories over electrode P3 (t(1, 159 = 4.04, P < 0.01) and P4 (t(1, 15) = 3.57, P < 0.01). As is evident from Figs. 1 and 3, however, this effect reflects a negative shift in the ERPs to 'Old + Old same' compared to 'New + New' over the central parietal electrodes. Statistical comparison between response category and site (F(2, 30) = 7.5, P < 0.01). Final *t*-tests showed, that this interaction occurred also due to a negative shift for ERPs to 'Old + Old different' compared to 'New + New' over electrode P3 (t(1, 15) = 2.9, P < 0.01). Once again, analysis on difference data did not reveal any significant effect over electrode P3 (F(1, 15) = 2.21, P > 0.1).

"Old+Old same" minus "New+ New"



Fig. 4. Topographic maps with isovoltage lines each $0.3 \,\mu$ V apart showing the scalp distribution of the ERP old/new effects for the early, middle and late time range. The distribution was interpolated from the difference between 'Old + Old same' minus 'New + New' pairs and 'Old + Old different', minus 'New + New' items. The number of lines indicates the actual voltage over the scalp region.

3.2.2. Analyses of normalized difference data

Normalized difference categories were analyzed as indicated in Section 2. The analysis comparing the two critical response categories did not reveal any reliable differences in topography over time. For each response category, there was, however, an interaction between the factors of time epoch, anterior/posterior and site (F(6, 90) = 2.65, P < 0.05), reflecting the fact that the distribution of effects changes over time. Therefore, subsequent analyses for each of the normalized difference categories were conducted, first for anterior and then posterior sites across all time latencies. Over anterior sites, there was a main effect of time ('Old + Old same' minus 'New + New' F(2, 30) = 4.92, P < 0.05; 'Old + Old different' minus 'New + New' F(2, 30) = 4.86, P < 0.05) and site ('Old + Old same' minus 'New + New' F(3, 45) = 15.64, P < 0.001; 'Old + Old different' minus 'New + New' F(3, 45) = 12.66, P < 0.001) for both normalized difference categories, but no interaction between these factors that would indicate a topographic shift over time (Fig. 4). However, over posterior sites, there was a significant interaction between the factors of time epoch and site for 'Old + Old same' minus 'New + New' (F(6, 90) = 3.52, P < 0.05) and a trend for an interaction for 'Old + Old different' minus 'New + New' (F(6, 90) = 2.05, P < 0.07). Subsequent analyses for each of the posterior sites over time indicated that for both normalized difference categories, this interaction arose because there was a main effect of time epoch only over electrode TP7 ('Old + Old same' minus 'New + New'

F(2, 30) = 3.52, P < 0.05; 'Old + Old different' minus 'New + New' F(2, 30) = 3.9, P < 0.05) but no other of the posterior sites. This effect reflects the fact that the difference between 'Old + Old same' and 'New + New' items disappears from 1000 ms onwards and for 'Old + Old different' items changes already from 700 ms onwards.

3.2.3. Analyses of onset latency

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Over frontal sites, serial *t*-tests indicated that the old/new effects onset much earlier over lateral than frontopolar electrodes. For 'Old + Old same', the effects onset around 884 and 898 ms over frontopolar electrodes (FP1 and FP2 respectively), but compared to 400 and 424 ms over lateral frontal electrodes (electrodes F3 and F4, respectively). A similar pattern is evident for the old/new effect for 'Old + Old different', with onset times around 914 and 896 ms (electrodes FP1 and FP2, respectively) and 416 and 408 ms (electrodes F3 and F4, respectively).

In addition, the old/new effects onset somewhat later over temporo-parietal sites than at lateral frontal sites. At lateral parietal electrodes (P3 and P4, respectively), the effect for 'Old + Old same' onsets at 478 and 486 ms, and similarly for 'Old + Old different' the effects onset at 442 and 484 ms. Finally, over inferior temporal electrodes, the onset latency for the old/new effect for 'Old + Old same' is 496 ms at site TP7. As prior analysis did not show any significant old/new effects for 'Old + Old different' at electrode TP7, and for neither of the 'Old + Old' pairs over TP8, no onset times were calculated in these cases.

3.2.4. Summary

Relative to the waveforms to 'New + New' items, both types of old pairs exhibited statistically significant positive-going shifts over frontopolar, lateral frontal, parietal and inferior temporal electrode sites. Topographic analyses revealed that the old/new effects associated with 'Old+Old same' and 'Old+Old different' items did not exhibit significantly different distributions. Nonetheless, the time course and magnitude analyses did reveal two clear dissociations.

First, the onset latency analysis revealed that, under the task conditions employed here, processes reflected by the ERP old/new effects onset first over lateral frontal sites, followed by slightly later onsetting effects over central parietal and inferior temporal sites, and by a very late onsetting sustained old/new effect over frontopolar sites from around 1000 ms onwards to the end of the recording epoch. This late onsetting frontopolar old/new effect contrasts sharply with the effect over lateral frontal electrodes; the later effect was presented between 400 and 700 ms and again from 1000 ms until the end of the recording epoch. This pattern of findings which suggests a temporal dissociation between two distinct frontally distributed old/new effects present over lateral and frontopolar electrodes. As is evident from Fig. 3, no old/new effects were present over frontal sites between 700 and 1000 ms, most likely due to a confound of a positive-going shift of ERPs to 'New + New' pairs. Secondly, the pattern of old/new effects over posterior sites suggests a functional dissociation. Over central parietal electrodes, an old/new effect was presented between 400 and 1000 ms. Though the effect was lateralized to the left between 700 and 1000 ms, it did not differ in magnitude for 'Old + Old same' and 'Old + Old different'. By contrast, however, during the same latency period, there was an old/new effect over inferior temporal sites that was only present for 'Old + Old same' whereas the ERPs to 'New + New' pairs were more positive-going than those to 'Old + Old different'. Although the distribution of effects were equivalent, the significant difference in magnitude over inferior temporal electrodes suggest a differential engagement of the generators of this effect by the 'Old + Old same' and 'Old + Old different' conditions.

4. Discussion

The focus of the present experiment was to investigate whether a frontopolar old/new effect found in a previous study of recency memory by Tendolkar and Rugg (1998) is sensitive to variation in the contextual retrieval necessary to solve a recency task. To address this issue, we compared the old/new effects between a response category which demanded the retrieval of additional contextual information ('Old + Old same') as compared to a response category ('Old + Old different') where assigning the items to the correct study list would be sufficient to solve the task. In this context, we identified distinct old/new effects overlying frontopolar, lateral frontal, parietal and inferior temporal electrodes, of which only the inferior temporal effect differed in magnitude between the 'Old + Old' response categories.

The behavioral findings indicate that subjects were able to perform judgments of recency at levels well above chance for both classes of 'Old + Old' pairs. As expected, judgments to 'Old + Old same' items were less accurate than those to 'Old + Old different' items, most likely because of the different retrieval demands that are required to make a correct recency judgment to 'Old + Old same' items. There was, however, no difference in RTs to 'Old + Old same' and 'different' items, although both response categories were significantly slower than 'New + New' items. These findings suggest that differences between the Old + Old response categories are unlikely to reflect a mere difference in the preparation of a motor response.

4.1. The frontal old/new effects

Consistent with our previous ERP study on recency memory (Tendolkar and Rugg, 1998), a bilateral frontopolar old/new effect was evident here. In the study by Tendolkar and Rugg, this frontopolar effect was only evident for correct recency judgments to 'Old + Old' and not 'Old + New' pairs, therefore probably reflecting a recency specific activity sensitive to the fact that the information was studied before. The present study extends this view; the effect was presented for both classes of 'Old + Old' pair, both of which required the retrieval of recency information. However, the magnitude of the frontopolar old/new effect did not differ between the two classes of 'Old + Old' pair, suggesting that the generators of the effect are not sensitive to manipulation of retrieval demands employed here. Thus, at face value, the frontopolar effect appears to be insensitive to the amount of information that must be retrieved during a recency task (although see further discussion of this issue below).

The frontopolar effect seen here onset much later than the effect found in the study by Tendolkar and Rugg (1998). As can be seen from the waveforms, at least between 700 and 1000 ms, this delayed onset can be attributed to the relative positivity of ERPs to 'New + New' words, which disrupts the effect. The positivity to 'New + New' pairs over frontal sites was not evident in the earlier recency study by Tendolkar and Rugg (1998). It

is possible that the presence of this effect is due to the fact that the likelihood of a word being 'New' was lower in the present experiment compared to the study by Tendolkar and Rugg.

Along with the frontopolar effect, a bilaterally distributed lateral frontal effect was also observed. This effect could be dissociated into an earlier part between 400 and 700 ms and a later part from 1000 ms onwards, again disrupted by the relative positivity of ERPs to 'New+New' pairs. The early onset and topography of the initial part of the lateral frontal old/new effect is similar to that of an early bilateral frontal effect found in studies investigating familiarity-related retrieval process (Curran, 1999, 2000; Mecklinger, 2000; Rugg et al., 1998; Tendolkar et al., 1999). For example, ERP experiments using the plurality recognition procedure (Curran, 1999) suggest that an early frontal effect may be more associated with familiarity-related retrieval operations as it does not vary with depth of processing (Rugg et al., 1998) and occurs faster than recollection (Hintzman, 1988; Hintzman and Curran, 1994).

The bilateral appearance of both frontal old/new effects is consistent with the proposal of Friedman and Johnson that both right and left frontal old/new effects are evident in retrieval tasks where complex retrieval judgments need to be made (Friedman and Johnson, 2000). It remains to be elucidated in further studies whether this bilateral activation represents the co-occurrence of left and right prefrontal sub-components mediating different aspects of declarative memory retrieval processes. Alternatively, the observed bilateral maximum reflects activity of those regions that are dependent on the nature of the task rather than the material being used (Petrides, 1995). Though localizing the generators of the old/new effect over frontal electrode sites to the prefrontal cortex is supported by findings from functional neuroimaging studies of memory for temporal information (Nyberg et al., 1996; Zorilla et al., 1996), the brain regions responsible for the frontal old/new effects found in this study are unclear. Recent studies with non-human primates suggest that neuronal repetition effects (which have been proposed as a substrate of familiarity-driven recognition memory) could be recorded from the anterior temporal cortex (Brown and Xiang, 1998). Given that these repetition-sensitive neurons directly project to orbito and lateral prefrontal cortex (Rempel-Clower and Barbas, 2000), one may, especially in the case of the lateral frontal old/new effect, postulate an anterior temporal rather than prefrontal origin. This issue, therefore, needs to be validated by future neuroimaging studies.

With respect to their relation to the previously reported late right frontal old/new effect, the frontal effects found in the present study provide evidence for a functional dissociation. As in some studies (Allan et al., 1998 for review; Donaldson and Rugg, 1998, 1999; Wilding and Rugg, 1996, 1997; but see also Düzel et al., 1997; Ranganath and Paller, 1999; Trott et al., 1999; Senkfor and van Petten, 1998; van Petten et al., 2000) the right frontal effect has been shown to be sensitive to the different amount of information. By contrast, the frontal old/new effects related to familiarity-driven recognition directly or indirectly, because they are not sensitive to the amount of information which is retrieved. One reason for this insensitivity may be that recency judgments could be made by comparing the relative memory strengths of the previously studied words. Moreover, the fact that there were no 'Old + New' pairs may have led the subjects to use a metacognitive strategy: knowing that they are more likely to forget older information, they would by process of elimination, pick the forgotten

word as the older item. Finally, given that the recency task also demands other aspects of declarative memory retrieval, it may well be the case that other aspects of working memory-related processes are reflected in the frontal old/new effects found in the present study. Therefore, one aim of future studies should be to investigate whether these effects reflect more non-specific working memory operations related to contextual retrieval (rather than task-specific processes).

4.2. The temporo-parietal old/new effects

In contrast to previous studies investigating the recollection of contextual information (Wilding and Rugg, 1996, 1997; Wilding, 2002), we did not find a single left lateralized temporo-parietal old/new effect. Instead we identified two distinct old/new effects over posterior sites, overlying central parietal and left inferior temporal electrodes. These two effects were dissociated by the manipulation of retrieval that was employed here; only the inferior temporal effect was sensitive to the different demands imposed by making recency judgments for 'Old+Old same' versus 'Old+Old different' pairs. This differential sensitivity to the processing of 'Old + Old same' and 'Old + Old different' pairs suggests a functional dissociation between the parietal and left inferior temporal old/new effects.

The central parietal old/new effect seen in the present study exhibits a similar time course and topography to the previously reported left temporo-parietal old/new effect (associated with recollection, as described in Section 1). As is typically the case in ERP studies of recognition memory, the central parietal old/new effect gave way to a right-sided negative-going shift in the ERPs for 'Old + Old' pairs. The negative-going effect has been reported in other studies of declarative memory retrieval (for example Wilding and Rugg, 1996) and has been interpreted as a contingent negative variation (CNV) reflecting the preparation of a response. Here, we focus on the positive-going portion of the parietal old/new effect. Critically, this effect did not differ in magnitude or time course between the two 'Old + Old' response categories employed here, suggesting that the processes supported by the generators of this effect were engaged equally in both cases. We describe three possible accounts of these findings.

First, the present findings could reflect little more than an averaging artifact that masks a difference in the magnitude of the parietal effect for the two 'Old+Old' response categories. It is possible that the ERPs to 'Old + Old same' pairs were associated with more guesses than those to 'Old+Old different' pairs (because of a difference in task difficulty), resulting in a similar magnitude between ERPs to both 'Old + Old' pairs. Although plausible, we believe that this explanation is unlikely because of the more positive-going waveform over inferior temporal sites. Second, the finding that the parietal effect is equivalent in size for the two 'Old + Old' pairs could be taken as evidence that parietal effect is not in fact related to recollection, and is instead related to a familiarity-driven processes. This conclusion would rest on the assumption that the experimental manipulation used in the present study necessitates a different amount of recollection for each type of 'Old + Old' pair. Again, this interpretation is possible but unlikely given the weight of evidence supporting a link between the parietal effect and recollection (see Allan et al., 1998 for review). Thus, we consider a third possibility; that subjects recollected equally as much information for both 'Old + Old' response categories and therefore, the effect does not differ in magnitude.

According to this account, despite our intention, the task manipulation employed here did not give rise to variation in the amount of contextual information being retrieved. By this view, our manipulation influenced an aspect of retrieval (such as how precise retrieval had to be) that simply does not produce a modulation of the parietal old/new effect. Although post hoc, this interpretation is attractive because it does not challenge the recollection account of the parietal effect, and also explains why the RTs did not differ between the two 'Old + Old' response categories (when a larger amount of recollection for 'Old + Old same' items should be associated with longer RTs). Note however, that this conclusion also raises questions about our interpretation of the frontopolar old/new effects. As such, the missing statistical difference between ERPs to both 'Old + Old' pairs might be interpreted by the null hypothesis that each condition requires equal amounts of contextual retrieval, and leaves open the possibility that this effect may indeed turn out to be sensitive to the amount of information that is retrieved in support of recency judgments. The future aim should be therefore, to conduct an ERP study where the use of context in recency judgments could be further verified (for example by Remember/Know judgments).

Yet, besides the parietal old/new effect, we also identified a left inferior temporal old/new effect, which was only evident for 'Old + Old same' pairs. Following the logic outlined in Section 1 it is tempting to conclude that this effect is sensitive to the amount of information retrieved thereby possibly contradicting the null hypothesis as outlined before. However, as noted above, the findings with respect to the parietal old/new effect suggest that the task manipulation employed here did not elicit different amounts of retrieval. Moreover, the inferior temporal old/new effect has not been seen in previous studies that have varied the amount of retrieval. Future studies, therefore, need to investigate whether this effect is specific to recency tasks. Clearly, however, the left inferior temporal old/new effect was sensitive to the differing retrieval demands for 'Old + Old same' and 'Old + Old different' pairs, a difference that could reflect the fact that retrieval was more difficult in one case than the other, or that more specific/precise information was required for recency judgments to 'Old + Old same' pairs.

It is possible that the use of a common average reference (instead of the more typical linked mastoid) may have had an influence on the differences in the topography of the old/new effects over parietal and left inferior temporal electrodes. However, topographically, the main difference between a common average reference and a linked mastoid reference is the inclusion of anterior and posterior electrode sites into the reference (Bertrand et al., 1985). Hence, a topographical difference of ERP effects within an axis between left and right mastoid as seen here (P3 versus TP7) is unlikely to result from the use of a common average instead of a linked mastoid reference (Cooper et al., 1980). Moreover, other studies investigating the typical left parietal old/new effect have reported comparable results when ERPs were recorded from the mastoids and both reference methods (linked mastoids versus common average) were calculated afterwards (Curran, 1999). Finally, the choice of reference electrode could not account for the different sensitivity of the parietal and the left inferior temporal old/new effects to the task manipulation employed here. Nonetheless, we raise the important caveat that these effects have been identified using a directed analysis strategy. Therefore, the replication or identification of comparable effects in similar studies is an important goal. For this reason, we refrain from drawing conclusions about possible differences in the underlying neural generators of the effects.

In sum, the present data suggest that there are two functionally and neuroanatomically different temporo-parietal old/new effects. While the appearance of the central parietal old/new effect in general did not add information to the functional significance of the previously reported left temporo-parietal old/new effect, the observation of the left inferior temporal effect suggests a new category of temporo-parietal old/new effects being sensitive to differing retrieval demands that needs to be validated in further studies. Temporal information from ERPs can also be used to draw conclusions about the relative timing of memory effects (Allan et al., 1998 for review). Within this context, it is significant to note that the onset of the lateral frontal old/new effect precedes both temporo-parietal old/new effects suggesting the initiation of some non-specific familiarity-based retrieval process followed by specific operations related to the actual restoration or reactivation of information as reflected in the temporo-parietal old/new effects.

Acknowledgements

This research was supported by grants from the Köln Fortune Program/Faculty of Medicine, University of Cologne and the German Research Foundation (Te 321/2-1) to IT. We thank two anonymous for comments on earlier drafts of the manuscript.

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