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Research Report

Feature binding in perceptual priming and in episodic object recognition: Evidence from event-related brain potentials

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Abstract

It is argued that explicit remembering is based on so-called episodic tokens binding together all perceptual features of a visual object. In episodic recognition, these features are collectively reactivated. In support of this view, it has been shown that changing sensory features of a stimulus from study to test decreases subject's performance in an episodic recognition task, even though the changed features are irrelevant for the recognition judgment. On the other hand, repetition priming is unaffected by such manipulations of perceptual specificity. Implicit memory performance is therefore thought to depend on structural representations, so-called types, comprising only invariant perceptual features, but no exemplar-specific details. Event-related potentials (ERPs) in our study revealed electrophysiological evidence for the differential involvement of these perceptual memory traces in explicit and implicit memory tasks. Participants attended either a living–nonliving task or an episodic recognition task with visually presented objects. During test both groups of participants processed new objects and old objects, which were repeated either identically or in a mirror-reversed version. In the implicit task ERPs showed an occipitoparietal repetition effect, which was the same for identically repeated items and mirror reversals. In contrast, in the explicit task an early mid-frontal old/new effect for identical but not for mirror-reversed old objects was observed indicating involuntary access to perceptual information during episodic retrieval. A later portion of the old/new effect solely differentiated both types of old items from new ones.

Theme: Neural basis of behavior
Topic: Cognition, Learning and memory—humans

Keywords: Event-related potential; ERP; Repetition priming; Episodic recognition; Familiarity; Recollection; Perceptual specificity

1. Introduction

One of the most attended topics in memory research is the distinction between implicit and explicit memory. Implicit memory refers to a processing advantage for repeatedly presented stimuli, so-called repetition priming [52]. It is normally quantified by improvements of accuracy or reductions in reaction time in conceptual or perceptual tasks (e.g., stem completion or identification tasks). Importantly, priming effects emerge independently of conscious remembering of the stimulus' prior occurrence. In contrast, explicit memory implies that intentional reference to a prior incidence of the stimulus is made (like in free recall or episodic recognition tasks; cf. [51]).

Although subjects' performance in (explicit and implicit) memory tests can be traced back to explicit and implicit memory processes to variable degrees, these processes probably rely on different memory traces. Thus, explicit and implicit memories are thought to rely on different memory systems or at least different components. Early support for this assumption was provided by the observation that amnesic patients showed only rudimental accuracy in episodic memory tests, but nearly unaffected priming effects [53]. Experimental work with healthy participants additionally supported the independence of implicit and explicit memory measures. For instance, some of the factors

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differentially affecting both types of test are the following: levels of processing [44], attention [9], aging [21], and modality changes between study and test [11] (reviews can be found in [22,31,43]).

Critical to our study is that priming effects[1] have been shown to diminish or even disappear when presentation modality is changed from study to test [54]. No such effects have been observed for explicit memory performance [5]. Similarly, the alteration of visual object form (for example, by presenting two different exemplars) can in fact attenuate priming effects (for an overview, see [32]). In contrast, a change of incidental perceptual stimulus features within the visual modality (e.g., color, size, luminance, orientation) from study to test has been shown not to affect repetition priming, whereas the same manipulation usually interferes with recognition memory [4,59,61]. These latter effects occurred although the change of perceptual features was – as in the implicit test – irrelevant for the old–new decision (i.e., changes of sensory information should be ignored).

On the basis of these findings, Schacter [41,42] has assigned implicit effects to perceptual representation systems and conscious recollection to an explicit memory system. Srinivas [47] has assumed that implicit memory processes operate on pre-semantic abstract representations of the visual object form. Analogous to Marr's [17] object-centered descriptions, these representations should be independent of changes to accidental sensory stimulus attributes. Explicit processes, on the other hand, are thought to be based on representations including any kind of spatial, temporal, semantic, or structural information about the object. For this reason, they should be sensitive to the modification of metric attributes, although these are superfluous for object recognition (similar ideas can be found in [4,18,58]).

Following Treisman's distinction between 'types' and 'tokens' [48,49], we assume that implicit memory effects are based on memory-efficient alterations of types, whereas explicit memory relies on tokens. Types code for the invariant, nonaccidental features of objects that are used for identification and for the sake of 'understanding' a stimulus. It is also a modality-specific representation, meaning that in a visual type only visual information is included. Tokens are representations that code for the specific features of particular objects encountered. The negative effects of perceptual manipulations on episodic object recognition prove that information used in these tasks is not purely conceptual but includes sensory information about (ideally) all perceived attributes of the specific object. The fact that these effects are generally not present in perceptual implicit memory tasks speaks strongly in favor of two different memory structures. In sum, there is behavioral evidence that explicit and implicit memory performances rely on different kinds of memory representations, which differ in the information represented (for a detailed description of our model, see [10]).

The main goal of the present study was to examine whether event-related potentials (ERPs) provide evidence that different memory processes are engaged during the access to perceptual information in an implicit vs. an explicit memory task. As processes are usually interpreted as acting on cognitive representations, the study should additionally provide information on the properties of the memory representations underlying implicit and explicit memory.

Beyond the behavioral evidence mentioned above, electrophysiological measures have already shed further light on implicit and explicit memory processes. ERPs of perceptual priming are typically associated with more positive deflections for repeated stimuli [34]. Nevertheless, divergent findings have been obtained depending on the kind of stimulus material used. For words, positive-going deflections for repeated vs. new items have typically been found at parietooccipital recording sites, beginning at 250–300 ms after stimulus onset [25,36,40]. In a recent study by Paller and colleagues [28], priming of faces was associated with a frontal negativity from 250 to 400 ms after stimulus onset. Conversely, Nessler, Mecklinger, and Penney [24] found positive-going ERP waveforms between 300 and 500 ms for repeated faces. For visual objects, the results have been similarly divergent with respect to topography, polarity, and the temporal properties of the observed repetition effects. Besides more positive deflections for repeated items over parietooccipital recording sites in a time range from 500 to 700 ms [29], frontally distributed repetition effects along with reduced amplitudes at posterior sites have also been observed [30,38].

Addressing the issue of perceptual specificity, Paller and colleagues [26,27] conducted some studies in which the perceptual match of visual word form between study and test was manipulated. They reported a more pronounced positivity (i.e., a larger repetition priming effect) at occipitoparietal electrodes during test if words were repeated identically (i.e., presented forward/as a whole in both study and test) relative to when presented in a different manner (i.e., backward vs. forward/rapid serial presentation of letters vs. word as a whole). Similarly, changing the presentation modality of words (visual–visual vs. auditory–visual) led to an attenuation of the repetition positivity (at widespread recording sites) [35]. Presenting visual objects from either canonical or unusual views, Schendan and Kutas [45] revealed a similar repetition-related positivity at occipitoparietal recording sites that was also sensitive to perceptual study-test congruency. These findings are in line with the view of form-specific priming in extrastriate and temporal cortices that is diminished when the specific attributes being essential for identification are changed from study to test.

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[1] Note that, for the purpose of the present experiment, we focus on perceptual priming, leaving conceptual priming aside.

However, as behavioral data suggest, the abstract structural object-form representation (type) used in perceptual priming tasks should be independent of changes to sensory stimulus attributes not relevant for identification (cf. [55]). Accordingly, we designed an implicit memory test manipulating an irrelevant stimulus feature (orientation in the picture plane) to further explore the properties of the visual representations underlying implicit memory performance. Thus, being presented with visual objects, one group of subjects in our experiment had to accomplish a living–nonliving task during which some stimuli were repeated in an identical way and others were repeated as mirror reversals. Along the above argumentation, we expected similar repetition priming effects in reaction times for both kinds of repeated items. ERP repetition effects should emerge as positive deflections for repeated objects mainly over posterior electrodes starting at approximately 300 ms after stimulus onset, whereby waveforms for both types of repeated stimuli should not differ from each other.

In order to dissociate implicit and explicit memory processes, it is necessary to show that both forms of memory are associated with qualitatively different ERP components. In ERPs, recognition memory usually appears as more positive-going waveforms for correctly identified old items compared to new ones (e.g., [34]). Moreover, distinct spatiotemporal aspects of these old/new effects have been linked to different subcomponents of recognition memory [1,20,39]. Recently, explicit retrieval of detailed perceptual information has also been investigated by means of ERP recordings. Curran and colleagues [6,7] reported a frontal positivity for old compared to new items at around 400 ms after stimulus onset, which was shown to be independent of manipulations of some rather superficial stimulus attributes (words presented in singular or plural; objects presented identically or mirror reversed). This mid-frontal old/new effect has also been demonstrated to be elicited by semantically similar words [23] and therefore assumingly reflects familiarity-based recognition. In the former two studies by Curran and colleagues [6,7], a parietal positivity at around 600 ms (reflecting recollection) was sensitive to changes of perceptual features. Perceptually identical items provoked more positive-going waveforms than perceptually changed and new items. In these studies, subjects were explicitly asked to encode the orientation of the stimuli during study, as they were to reject similar lures at test. Hence, the modulation of the parietal old–new effect by the sensory mismatch might have been expected. However, the aforementioned behavioral data (e.g., [4,59,61]) suggest that recognition memory is affected by such feature manipulations even if they are irrelevant for the decision. Thus, the involuntary influence of changed perceptual features on episodic object recognition suggests that participants access an integrated token binding all features independently of whether or not they are relevant for the decision. This is the effect we are interested in.

An open issue is whether differential ERP old/new effects are also obtained if one manipulates perceptual features of a retrieval cue that are incidentally encoded and irrelevant for the memory task to be performed. In order to test this, another group of subjects in our experiment was asked to perform an episodic recognition task on new, identical old and mirror-reversed old items. Both types of old items were to be accepted. According to previous behavioral results, we expected differences in the processing time of old congruent and incongruent items (i.e., faster reaction times for congruent stimuli). We were further interested in whether ERPs reflected the indirect impact of our perceptual manipulation. On the basis of the Curran et al. studies we expected a modulation of the (left) parietal old/new effect, i.e., identical old items should elicit more positive deflections than mirrored ones. Moreover, the mid-frontal old/new effect should not be affected by our perceptual manipulation, i.e., old congruent and incongruent items should elicit similar positive deflections compared to new stimuli.

2. Materials and methods

2.1. Participants

Subjects were 55 right-handed students of Saarland University, which were paid for their participation. All subjects had normal or corrected-to-normal vision. 22 subjects were assigned to the implicit task, 33 subjects participated in the explicit task. The higher number of subjects in the explicit group was caused by the fact that subjects with low recognition accuracy were replaced in order to arrive at a sufficient number of trials per condition. The cutoff was a Pr-score of 0.40 (proportion of hits minus proportion of false alarms). After this selection 17 subjects remained in the explicit group. Additionally, the data of participants with insufficient numbers of artifact-free trials were rejected (a minimum of 14 trials per condition was considered necessary). We ended with 18 subjects (mean age 25 years, range 21–32, 7 female) in the implicit test condition, and 14 subjects in the explicit test condition (mean age 27 years, range 21–38, 7 female).

2.2. Stimuli, design, and procedure

Stimuli were 120 common objects designed to resemble the plates of “Ishihara’s Tests for Colour Blindness”. The red outlines of 60 living and 60 nonliving objects were copied into a green circle which itself contained a number of small disks in different shades of green, resulting in the fractional superimposition of red outline and green circles. This kind of stimulus was chosen to maximize the demands on perceptual processing. Items were presented in the center of a 17-in. Multiscan Color Monitor with a resolution of 800 × 600 dpi against a black background. Stimuli had a size of 130 × 124 pixel, resulting in an angle of vision of 3°, approximately. In order to manipulate the perceptual features of objects, the items were mirror-reversed horizontally. Assignment of stimuli to experimental phases and item status (i.e., congruent/incongruent) was counterbalanced across subjects. In all experimental phases, half of the stimuli depicted living objects and half nonliving objects, respectively.

In the study phase (phase 1), subjects of both groups incidentally learned 60 objects by performing a living-nonliving task, indicating their decision by a "shift-left" or "shift-right" key press (assignment of keys to response class was counterbalanced across subjects). In order to have comparable study conditions, and in order to avoid that intentional retrieval contaminates the implicit test, both groups had incidental study conditions. At the beginning of each trial, a fixation cross was presented for 250 ms followed by the stimulus (500 ms). Trials ended with the subject's response or when the time limit of 2500 ms was reached. The inter-stimulus interval was 2500 ms.

In the test phase (phase 2) both groups were presented with 120 objects, 60 of which had been previously seen in phase 1 and 60 that were new. Half of the repeated items were presented identically and half as mirror reversals. Subjects from the implicit group again had to perform the living-nonliving task, whereas subjects from the explicit group were given an unexpected recognition memory test. In the latter condition, old objects presented in the same orientation (congruent) as well as mirror-reversed objects (incongruent) had to be accepted as old, while new items had to be rejected.

In order to have comparable conditions in the analyses of both experimental groups, statistical analysis of behavioral and ERP measures was restricted to data from the test phase (phase 2). Additionally, only trials with correct answers were included in the analysis. The reason for rejecting incorrect trials in the implicit group, as well, was the high perceptual demand of the task, owing to which quite a number of items may not have been identified at all, thus not making contact to their memory entry. On this note, correct identification can be considered a prerequisite for priming. For comparable reasons, in the explicit test the analysis of merely correct trials seems to be the only possible way to examine explicit memory retrieval. False recognition judgments are usually not based on successfully retrieved memory entries. It can thus be assumed that only remembered items show perceptual congruency effects.[2]

2.3. EEG/ERP methods

The experiment was run in a sound- and electromagnetically shielded chamber. EEG signals were recorded continuously from 64 Ag/AgCl electrodes mounted in a preconfigured cap (Electro-Cap International, Inc., Eaton, Ohio), arranged according to the international 10–20 system [2]. Recording was sampled at a rate of 250 Hz (with a 50-Hz notch filter) by an AC-coupled amplifier (time constant 10 s; Brain Amp MR, Brain Products, Munich) and referenced on-line to the left mastoid electrode. For further analysis, electrodes were re-referenced off-line to an average of the left and right mastoids. Impedances for all electrodes were kept below 10 kΩ. Two electrodes located medially to the right eye, one above and one below, were used to monitor vertical eye movements. Electrodes placed at the outer canthi of the eyes measured horizontal eye movements. EOG artifacts were corrected off-line [13].

ERPs were obtained by averaging EEG recordings time locked to stimulus presentation from 200 prior to 1000 ms after stimulus onset. Data were baseline corrected with respect to the 200-ms pre-stimulus interval and digitally bandpass filtered at 0.2–20 Hz. Trials containing artifacts (maximum amplitude in the recording epoch ± 200 μV; maximum difference between two sampling points 50 μV; maximum difference of two values in the interval 200 μV; lowest allowed activity between minimum and maximum 0.5 μV in successive intervals of 100 ms) were rejected. Furthermore, averages were collapsed across living and nonliving categories.

ERPs were computed for three different conditions in each experimental group. In the implicit group, ERPs were averaged for first presentation items (a mean number of 46 trials was included), second congruent (23), and second incongruent (25). ERPs in the explicit group were averaged for old congruent (mean number of 22 trials), old incongruent (22), and new items (47).

Statistical analysis was performed by means of an ANOVA on mean voltages for each condition in each experimental group in two time windows: 250–450 ms and 500–800 ms (the choice of the exact position and expansion of the time windows was based upon visual inspection). Mean amplitudes were computed for each of the following nine regions of interest[3] (ROIs): left-frontal: F7, F5; left-central: T7, TP7, CP5; left-parietal: P7, P5, PO7; mid-frontal: F3, Fz, F4; mid-central: C3, Cz, C4; mid-occipito-parietal: P3, Pz, P4, O1, O2; and the right counterparts of left-sided electrode regions. This procedure resulted in a 3

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[2] Given that accuracy is determined by different factors for the two tasks and that items are therefore excluded for different reasons in the two groups, we tried to deal with this factor possibly affecting the implicit/explicit comparison by additionally analyzing the data according to the objective old/new status. The analysis including all trials yielded qualitatively similar results as the analysis using correct trials only. There were just minor quantitative differences due to higher variance levels through inclusion of (partially small numbers of) errors.

[3] We tried to define functionally sensible and coherent ROIs with respect to the underlying brain regions [15]. To control for differential signal to noise ratios in several ROIs due to different numbers of recording sites we conducted parallel analyses with one representative electrode from each ROI (F7, T7, P7, Fz, Cz, Pz, F8, T8, P8), respectively. ANOVAs revealed similar results to those reported in the following result section, thereby confirming the validity of our results based on the ROIs chosen.

(anterior/posterior) × 3 (laterality) electrode arrangement. For statistical analysis of ERP data, the Greenhouse–Geisser [14] correction for nonsphericity was used; original degrees of freedom, the correction coefficient ε, and corrected P values (significant at $\alpha = 0.05$) are reported in the following. When performing multiple planned comparisons, significance levels were adjusted according to the Bonferroni procedure (and all P values that are given in the corresponding result paragraphs are significant with respect to adjusted α levels). Topographic analyses were conducted after normalization according to the vector scaling procedure proposed by McCarthy and Wood [19].

3. Results

3.1. Behavioral data

Mean accuracy and reaction times of subjects from the implicit task from both experimental phases are shown in Table 1, data from the explicit task are shown in Table 2.

During study, subjects from both groups had similar accuracy levels in the living–nonliving task ($F(1,30) < 1$), despite a slight tendency for faster reaction times in the explicit group ($F(1,30) = 3.91$, $P = 0.06$). In the implicit test, subjects' accuracy for second congruent items was significantly worse than for first presentations ($F(1,17) = 11.45$, $P < 0.01$) and for second incongruent items ($F(1,17) = 6.29$, $P < 0.05$). Responses to reversed items did not differ from those to first presentation stimuli ($F(1,17) < 1$). In this test, the absence of any perceptual interference was predicted. However, if the manipulation of congruency operated in a way similar to the explicit test, we would expect a data pattern pointing in the opposite direction than the one found here, so it will not be further pursued. In the explicit test, recognition accuracy (Pr discrimination score, measured as proportion of hits minus proportion of false alarms) was equivalent for both kinds of old items (Pr = 0.53 for identical stimuli, Pr = 0.52 for reversed stimuli; $F(1,13) < 1$). Both conditions differed significantly from chance-level performance ($t(13) = 15.61$ for old congruent and $t(13) = 19.45$ for old incongruent items, $P < 0.001$, respectively).

Reaction time data were analyzed in a between-subjects design to directly compare possible effects of perceptual congruency over experimental groups. This led to a 2 (group; between-subjects factor) × 3 (condition) design. ANOVA revealed a main effect of condition ($F(2,60) = 17.69$, $P < 0.001$) but only a marginally significant interaction of group × condition ($F(2,60) = 2.29$, $P = 0.11$). Nevertheless, a direct test of our hypotheses by planned comparisons revealed a clearly differential impact of our perceptual manipulation on both types of test. In the implicit task (see Table 1), reaction times to second presentation stimuli were shorter than to first presentations ($F(1,30) = 6.73$, $P = 0.015$). No differences between second congruent and second incongruent could be observed ($F < 1$). In the explicit group (see Table 2), hits were made faster than correct rejections ($F(1,30) = 14.19$, $P < 0.001$). Additionally, subjects were faster in judging old congruent items than old incongruent ones ($F(1,30) = 10.47$, $P < 0.01$).

3.2. ERP data

Fig. 1 shows grand average ERPs for correct responses in the implicit test (living/nonliving decision). There was a larger positive deflection for repeated stimuli relative to first presentations between 500 and 800 ms after stimulus onset. This ERP repetition effect was most prominent at midline centro-parietal recording sites. Additionally, this positive deflection was very similar for congruent and incongruent items.

Fig. 2 depicts grand average waveforms in the explicit object recognition task for hits to old_congruent and old_incongruent items, as well as for correct rejections. ERPs in the earlier time interval (250–450 ms) showed that waveforms for hits to congruent old items were less negative than those to new ones, mainly at frontocentral electrodes. In contrast, old incongruent items elicited waveforms similar to those of new stimuli. In the later time interval (500–800 ms), there was a more positive deflection for both congruent and incongruent old items with respect to new ones.

In order to examine the different effects of perceptual congruency on the ERPs in both experimental tasks, a repeated measures ANOVA comprising a 2 (group; between-subjects factor) × 3 (anterior/posterior) × 3 (laterality) × 3 (condition) design was conducted for each time window. In the early time interval, a main effect of condition was observed ($F(2,60) = 3.87$, $P < 0.05$, $\varepsilon = 0.94$), as well as a

Table 1
Mean reaction times and accuracy in the implicit test (living–nonliving task) as a function of item status (first presentation, second congruent, second incongruent) and experimental phase

Implicit test	Phase 1	Phase 2		
	Item status	Study–test relation		
	First presentation	Second congruent	Second incongruent	First presentation
Reaction times (ms)	1018 (274)	890 (180)	886 (182)	958 (230)
Accuracy (% correct)	77 (09)	76 (08)	81 (11)	83 (06)

Values in parentheses display standard deviations.

Table 2
Mean reaction times and accuracy in the explicit test (episodic recognition) as a function of item status (new, old congruent, old incongruent) and experimental phase

Explicit test	Phase 1	Phase 2		
	Item status	Study–test relation		
	New	Old congruent	Old incongruent	New
Reaction Times (ms)	834 (242)	802 (244)	858 (254)	946 (308)
Accuracy (% correct)	77 (09)	71 (11)	70 (08)	76 (13)

Values in parentheses display standard deviations.

significant interaction of group × condition ($F(2,60) = 3.17$, $P \leq 0.05$, $\varepsilon = 0.94$). The analysis in the later time interval revealed a significant main effect of condition ($F(2,60) = 5.09$, $P < 0.01$, $\varepsilon = 0.99$) along with a significant interaction of group × anterior/posterior × condition ($F(4,120) = 2.90$, $P \leq 0.05$, $\varepsilon = 0.59$), suggesting specific condition effects at different electrode sites for the two groups. To further explore this pattern of results, we performed 3 (anterior/posterior) × 3

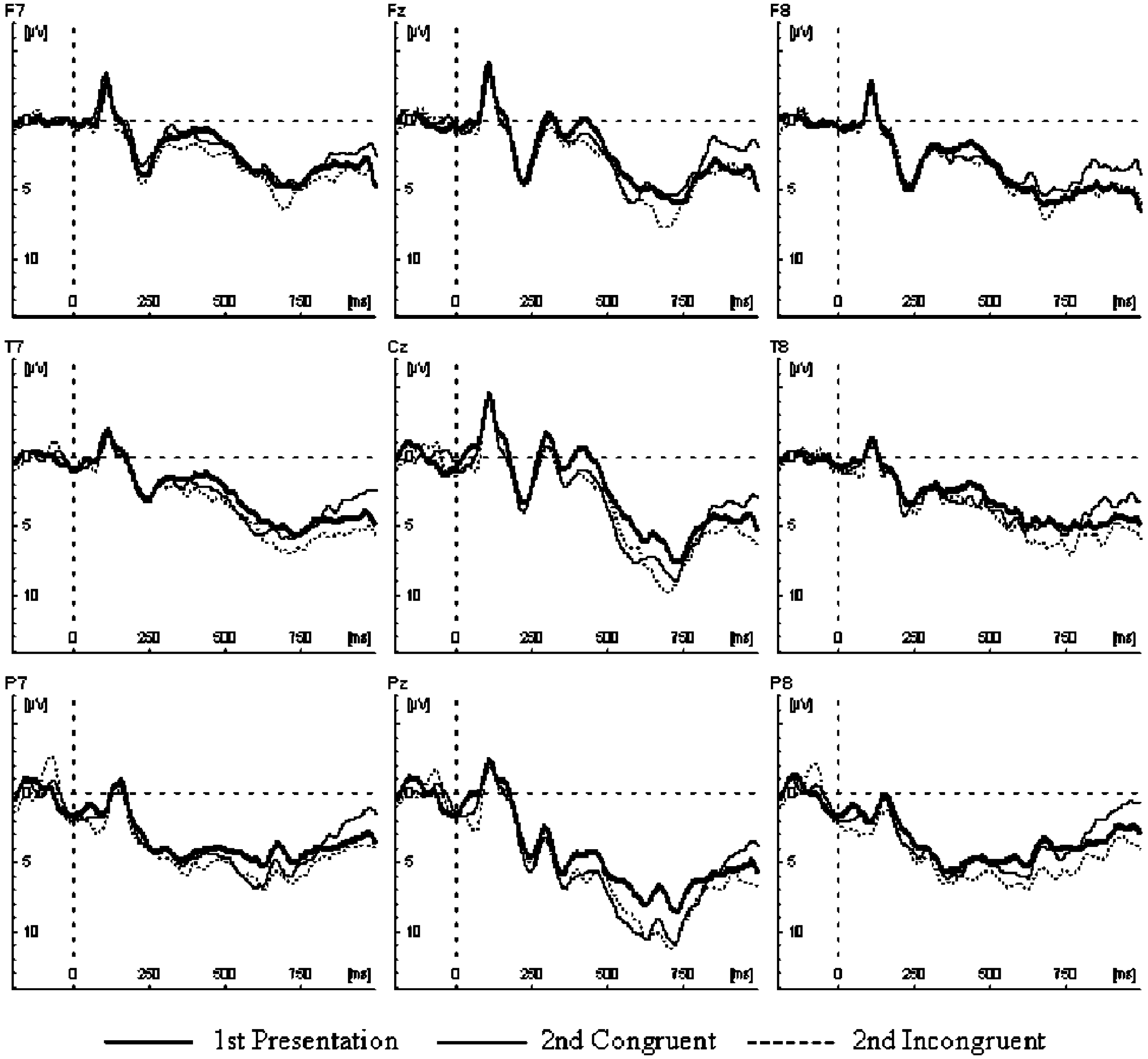

Fig. 1. Grand average waveforms (linked mastoids referenced) in the implicit test as a function of item status (first presentation, second congruent, second incongruent); time scaling ranges from −200 to 1000 ms after stimulus onset; stimulus offset is at 500 ms; positive deflections are displayed downward.

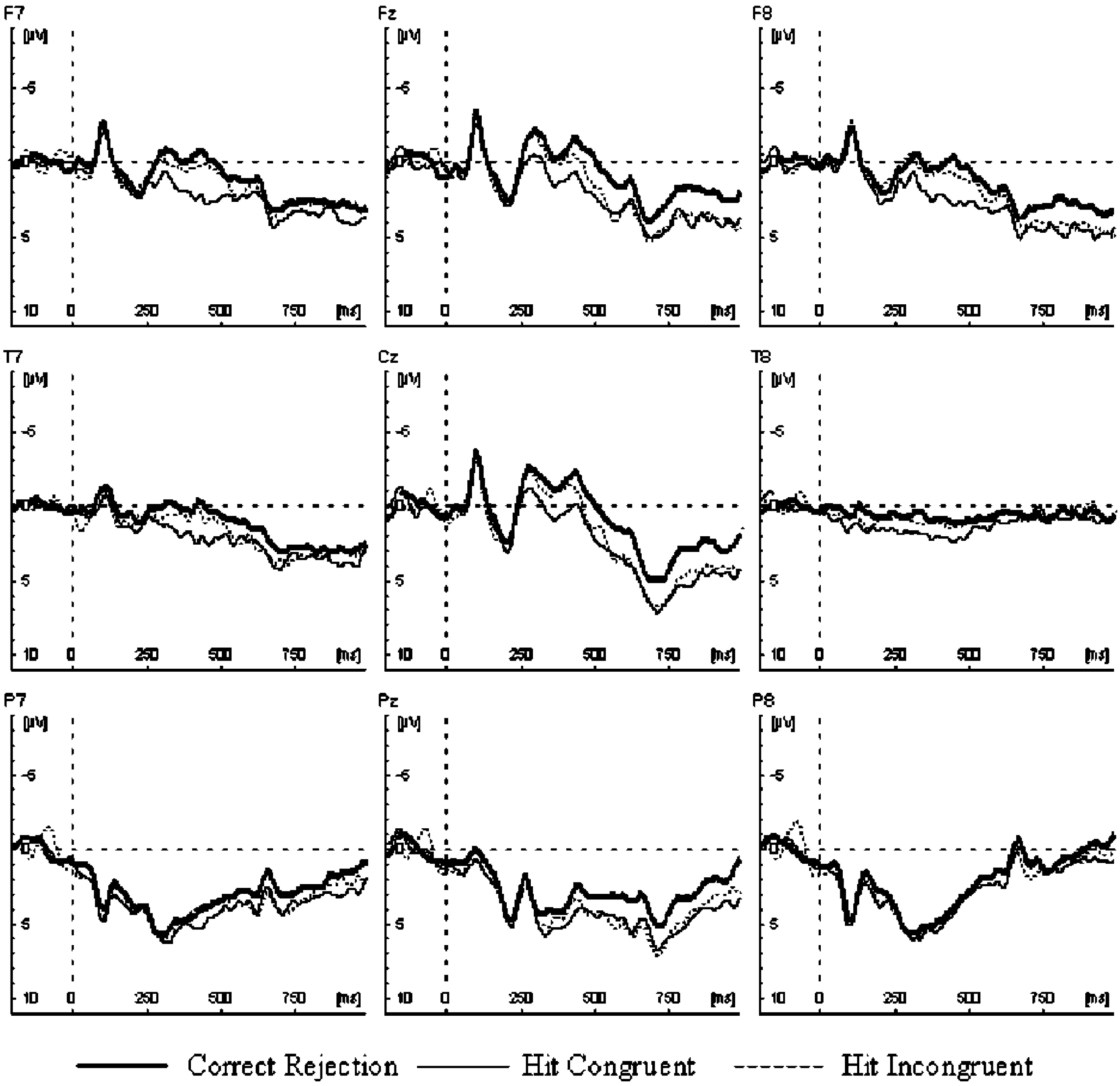

Fig. 2. Grand average waveforms (linked mastoids referenced) in the explicit test as a function of item status (correct rejections, hits congruent, hits incongruent); time scaling ranges from −200 to 1000 ms after stimulus onset; stimulus offset is at 500 ms; positive deflections are displayed downward.

(laterality) × 3 (condition) analyses for each group and time window, separately.

In the 250–450 ms time interval of the implicit test, ANOVA revealed neither a significant main effect of condition, nor interactions of condition with any other factor (P values between 0.21 and 0.77). For the later time interval (500–800 ms), an interaction of anterior/posterior × condition ($F(4,68) = 4.78$, $P < 0.01$, $\varepsilon = 0.63$) was observed, apparently reflecting the more pronounced repetition difference at centro-parietal as compared to frontal ROIs. Accordingly, subsidiary analyses confirmed that the repetition effect for second compared to first presentations was significant at posterior recording sites ($F(1,17) = 4.57$, $P < 0.05$), only marginally significant at central ROIs ($F(1,17) = 3.17$, $P = 0.09$) and not present at frontal regions ($F < 1$). For this analysis, data were collapsed across both types of repetitions, as no difference between second congruent and second incongruent could be found (P values between 0.23 and 0.62 for individual ROIs). A similar procedure of pooling together concurrent conditions for planned comparisons was also applied to the following analyses. Specific contrasts for individual conditions were computed and revealed statistically equivalent results to those reported here.

In the early time window of the explicit task, ANOVA revealed a main effect of condition ($F(2,26) = 6.73$, $P < 0.01$, $\varepsilon = 0.91$) as well as a marginally significant interaction of anterior/posterior × condition ($F(4,52) = 3.18$, $P = 0.07$, $\varepsilon = 0.42$). Planned comparisons yielded similar activation patterns for old incongruent and new items ($F < 1$ at all ROIs). Old congruent items, on the other hand, differed significantly from old incongruent and new ones at anterior ($F(1,13) = 8.75$, $P = 0.011$) and central ($F(1,13) = 11.42$, $P < 0.01$), but only marginally so at posterior ROIs ($F(1,13) = 4.35$, $P = 0.06$). In the later time interval, a main effect of condition ($F(2,26) = 7.50$, $P < 0.01$, $\varepsilon = 0.96$) reflected the more positive-going waveforms for old congruent and old incongruent stimuli at all ROIs. Accordingly, planned comparisons revealed that waveforms for congruent and incongruent items were not statistically different in this time interval ($F(1,13) = 1.36$, $P = 0.26$). Moreover, they indicated a significant old/new effect for both types of old stimuli ($F(1,13) = 14.27$, $P < 0.01$).

In the 500–800 ms period ERP modulations in the two memory tasks were quite similar: in both groups there was a greater positivity for old/second than for new/first presentation items. To elucidate potential topographic differences between the two memory tasks, we conducted an additional ANOVA comparing vector-scaled old/new differences of both tasks over 3 × 3 ROIs. This analysis revealed a significant interaction of memory task × anterior/posterior ($F(2,60) = 3.94$, $P \leq 0.05$, $\varepsilon = 0.55$), suggesting specific topographic modulations of the observed old/new effects according to task. As Fig. 3 points out, the parietooccipital focus of the implicit repetition effect can be clearly discriminated from the more centro-parietal and frontal distribution of the explicit old/new effect. These differences in scalp topography support the assumption that both effects in this time interval index – at least partially – distinct memory processes.

4. Discussion

This study examined electrophysiological correlates of access to detailed perceptual information under implicit and explicit memory demands. For that purpose we manipulated the study-test-congruency of a sensory stimulus feature (orientation). Participants performed either a living/non-living task (implicit group) or an old–new object recognition task (explicit group). The study conditions (incidental study task) and the relevance of perceptual features during test (irrelevant for the decision) were matched for both groups. Nevertheless, we observed a behavioral as well as an electrophysiological dissociation between type of task and perceptual specificity. Reaction times to incongruent items in the explicit test were decelerated relative to congruent ones, whereas both types of items yielded identical repetition priming in the implicit test. Electrophysiological data revealed converging evidence for this dissociation. ERPs in the implicit condition showed similar characteristics for congruent and incongruent stimuli throughout the recording epoch. Waveforms in the explicit condition highlighted the influence of perceptual specificity by differentiating congruent and incongruent items in an early time interval (250–450 ms).

In the implicit memory test, ERPs showed a more pronounced positivity for repeated stimuli relative to new

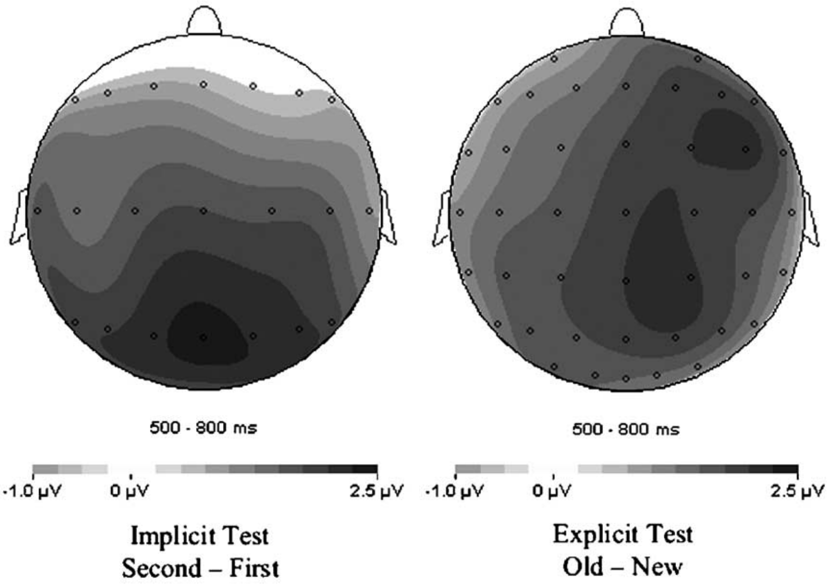

Fig. 3. Spherical-spline interpolated topographical maps of ERP differences in the 500–800 ms interval as a function of memory task: for the implicit test, ERPs to first presentation items were subtracted from second presentations (with second congruent and second incongruent pooled together); for the explicit test, ERPs to new stimuli were subtracted from old items (collapsed over old congruent and old incongruent). The head is depicted from above (with the front facing up, left on left, etc.).

ones in a time interval from 500 to 800 ms, independently of perceptual features. This ERP repetition effect was accentuated at parietooccipital recording sites. Our ERP data are in accordance with other findings for visually presented objects and words [24,29,40], but they deviate from some other studies [30,38,50]. The comparatively late occurrence of the repetition effect in our study was probably due to the specific characteristics of the stimuli, which established the intended difficult perceptual conditions. It takes much more time to identify what is depicted by the dots than to identify an unfragmented picture on a homogeneous background. Another possible factor accounting for the repetition effect in our study (especially for its positive polarity) may be the long-lasting delay between initial and repeated presentation; negative ERP repetition effects have generally been observed with immediate repetitions (cf. [28]), thus probably representing working memory operations (but see [30]). Alternatively, the operationalization of implicit memory may affect the polarity of repetition effects: task-irrelevant repetition of items usually leads to positive repetition effects (e.g., [29]), whereas chance-level explicit memory accuracy as a criterion for implicit memory leads to negative repetition effects (e.g., [28]). A systematic consideration of the potential influences of task manipulations on electrophysiological repetition effects (with electrophysiological measures) would surely help clarify our understanding of implicit memory processes. Correspondingly, Wiggs and Martin [55] suggested 'that the critical brain region(s) mediating perceptual priming may vary as a function of the specific priming task employed' (p. 231).

Important for our argument is the fact that the ERP repetition effect did not differ for identical and reversed repetitions. This finding is in concordance with behavioral data obtained in the present study and also in a series of previous studies (for a review, see [11,32]). However, it is in contrast to earlier studies demonstrating perceptual influences on repetition effects under implicit memory conditions [26,27,45]. In a recent study, Tsivilis and colleagues [50] examined ERPs for repeated visual objects and their backgrounds in an episodic recognition memory paradigm. They reported a more pronounced positivity for old objects at frontopolar electrodes within 100–300 ms after stimulus onset. This effect might reflect repetition priming, as it was observed regardless of whether objects were presented in their original context, were rearranged with familiar backgrounds, or were even presented with new backgrounds. In line with our results, this finding points to the independence of perceptual priming from manipulations of incidental stimulus features. However, the functional significance of the frontopolar repetition effect is unclear. Apart from the priming account, Tsivilis et al. [50] also gave an alternative interpretation of this effect, namely that it represents 'the emergence of information about prior occurrence' (p. 502), thus contributing to recognition memory. According to the latter interpretation a striking difference to our study is that electrophysiological correlates of implicit memory were observed during an explicit memory task. A crucial difference between explicit and implicit memory tasks concerning the effects of perceptual specificity might be the adoption of a retrieval mode (cf. [37]; see below). Our result provides further evidence for the independence of perceptual priming from variations of accidental sensory features under implicit memory conditions. It is conceivable that only those changes to a stimulus that affect its identification reduce the repetition effect [3,46,59]. This assumption might also explain why the previously mentioned ERP studies demonstrated influences of perceptual changes on ERPs, because in these studies, features were varied that are relevant for the identification process (e.g., words spelled forwards or backwards [26]). Following the task appropriate processing approach [33], a simple explanation would be that the perceptual attributes are stored in memory but are not used as long as they are not necessary to solve the task. We then have to explain, however, why the same features influence episodic object recognition despite being task-irrelevant as well.

ERPs in the explicit condition showed a positive deflection for identically repeated stimuli but not for reversed ones. This effect resembles the previously described mid-frontal old/new effect or FN400 (cf. [12,20]) both in its spatial and temporal characteristics. The later portion of the old/new effect, on the other hand, differentiated between old and new items, but it did not dissociate identical repetitions and reversals. Apparently, recollection processes (reflected in the late parietal effect) concerning the two types of old stimuli were not dissociable, while familiarity (reflected in the early mid-frontal effect) depended on the perceptual match between study and test. These findings – though in accordance with behavioral data obtained in the present and previous studies (e.g., [59,60]) – are in contrast to already reported ERP results [6,7]. In these studies, the mid-frontal effect was unaffected by perceptual manipulations, whereas the parietal old/new effect reflected retrieval of such perceptual details. The discrepancy concerning the parietal old/new effect can be resolved by taking into account the different task demands in the Curran et al. studies and the present study. Participants in the former studies intentionally learned not only the presented stimuli but also the relevant features. Moreover, they performed an exclusion task (i.e., they had to reject perceptually modified old objects), thereby enhancing conscious recollection processes. Our participants had incidental learning conditions and performed an inclusion task during test (as they had to accept all previously seen objects, also incongruent ones, as old). Consequently, this design did not require the access to perceptual details for correct recognition judgments, and this may have attenuated the parietal effect for old identical items. A similar pattern of results in an inclusion task has been observed in the Tsivilis et al. study [50] mentioned above, where the left parietal effect showed no context-sensitivity either: all stimuli containing old objects elicited more positive-going waveforms than new objects—regardless of their backgrounds.

In line with the argumentation above, ERPs in the earlier time interval (250–450 ms) showed effects of perceptual congruency that speak in favor of an involuntary retrieval of perceptual features from episodic memory. Congruent old items showed an attenuation of the mid-frontal old/new effect which can be interpreted as indexing a higher level of familiarity. As the familiarity component has been found to be insensitive to specific feature manipulations [6,7,23], the question then arises why perceptually incongruent old items elicited no familiarity effect in the present study. A possible explanation may be found in the discrepancy of the stimuli used. Curran's [6,7] items were common exemplars of a specific category which could easily be recognized. Thus, both old and modified items were equally effective memory cues, e.g., 'dog' and 'dogs'. In contrast, the dot patterns we used were unusual and difficult to recognize. Therefore, by changing an item's orientation direct access to its memory entry is hampered, so reversed items elicit no familiarity signal. In the study by Tsivilis and colleagues [50], an attenuation of the mid-frontal component was observed for objects presented in their original context and for objects rearranged with familiar backgrounds. No such difference to completely new items was apparent for old objects on new backgrounds or new objects on familiar backgrounds. Tsivilis et al. argued that the mid-frontal effect may reflect processes sensitive to stimulus novelty, especially the relative novelty of individual elements of a multicomponent stimulus. Correspondingly, the initial processing of one of our modified items may be comparable to the processing of a new item, inasmuch as access to the memory entry is only gained somewhat later, after the object's representation has been generated anew. In accordance with this view, we observed no mid-frontal effect for incongruent items in the early time range, but a positive deflection for both congruent and incongruent stimuli compared to new ones at posterior electrodes, beginning at 500 ms after stimulus' presentation. A difference between the two old item classes and the new ones was also present at central and frontal electrodes. It became apparent at around 650 ms and persisted until the end of the recording epoch, thus maybe indicating incipient strategic processes related to episodic retrieval (cf. [20,56]). For incongruent items the early part of this late frontal old/new effect may additionally reflect the contribution of a delayed familiarity signal overlapping with the mentioned strategic processes. The idea of later onsetting familiarity processes for incongruent items as compared to congruent ones may also be supported by the reaction time differences between those types of item.

A recent study by Curran and Dien [8] differentiated perceptual priming mechanisms from familiarity by manipulating the study modality (visual or auditory) of visual words in a recognition memory paradigm. In this experiment, the mid-frontal old/new effect was not affected by study modality and was therefore thought to be related to an amodal familiarity process. Interestingly, there was a slight but nonsignificant tendency towards a greater mid-frontal old/new effect for congruent than for incongruent items. Curran and Dien [8] presumed that the familiarity process could include 'perceptual attributes as a minor aspect of the overall global matching process, but it is likely that other attributes (e.g., semantics) play a greater role' (p. 985). On this note, it is conceivable that the difficult perceptual conditions in our experiment placed a stronger emphasis on the perceptual attributes of the stimuli, thereby leading to the observed attenuation of the mid-frontal effect for congruent items and the absence of the very effect for incongruent ones.

Furthermore, our results call into question a position recently brought forward by Yovel and Paller [57], namely that mid-frontal old/new effects may not reflect familiarity but verbally mediated conceptual priming. Following this argument one would not expect differences in the mid-frontal effects for congruent and incongruent items: the semantic concept should be processed identically for both types of repeated stimuli—regardless of their orientation. Admittedly, the stimuli we used were also nameable, and the specific nature of this material may have led to a delay in conceptual processing for mirror-reversed repetitions compared to identical ones. But such a difference should also be observable in the implicit test—which was not the case. Our findings give rise to the interpretation that the early effect indeed reflects familiarity-related processes.

The question remains why the early frontal old–new effect for incongruent items in the explicit task is reduced relative to congruent items, while in the implicit task the processing advantage (repetition priming) was the same for both types of repeated stimulus. Additionally, it is an open question why this early effect is not elicited under implicit memory conditions – not even for identically repeated items – although familiarity processes in some models (e.g., [16]) are considered to be automatic. Our assumption is that the emergence of congruency effects (that show up in the familiarity component) is dependent on subjects' retrieval mode (cf. [37]). In our view, familiarity is available for memory judgments only when retrieval mode is adopted—hence the absence of the congruency effect in the implicit task. In other words, we assume that the interaction of retrieval mode and access to a memory entry is a prerequisite for the familiarity component to emerge. We further suggest that the adoption of a retrieval mode in an explicit memory test leads to a different memory representation being accessed than under implicit memory conditions. Our findings support the view that the memory representations implicit memory relies on do not include information about detailed perceptual features, but rather constitute an abstract (nevertheless perceptual) representation of visual object form ('type'). Transient changes to this representation may cause an implicit old–new effect, since these types are automatically accessed during identification. Explicit memory on the other hand is based on 'episodic tokens' binding all stimulus features of an item, independently of their relevance for identification. When people are in a retrieval mode they try to access such episodic tokens, leading to familiarity- or recollection-based recognition judgments. Incongruent features hinder the reactivation during episodic retrieval even when they are irrelevant because they mismatch information represented by the token. The ERP as well as the behavioral data in our study are in good agreement with this suggestion.

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