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Event-related potential correlates of declarative and non-declarative sequence knowledge

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ABSTRACT

The goal of the present study was to demonstrate that declarative and non-declarative knowledge acquired in an incidental sequence learning task contributes differentially to memory retrieval and leads to dissociable ERP signatures in a recognition memory task. For this purpose, participants performed a sequence learning task and were classified as verbalizers, partial verbalizers, or nonverbalizers according to their ability to verbally report the systematic response sequence. Thereafter, ERPs were recorded in a recognition memory task time-locked to sequence triplets that were either part of the previously learned sequence or not. Although all three groups executed old sequence triplets faster than new triplets in the recognition memory task, qualitatively distinct ERP patterns were found for participants with and without reportable knowledge. Verbalizers and, to a lesser extent, partial verbalizers showed an ERP correlate of recollection for parts of the incidentally learned sequence. In contrast, nonverbalizers showed a different ERP effect with a reverse polarity that might reflect priming. This indicates that an ensemble of qualitatively different processes is at work when declarative and non-declarative sequence knowledge is retrieved. By this, our findings favor a multiple-systems view postulating that explicit and implicit learning are supported by different and functionally independent systems.

1. Introduction

It is often assumed that incidental sequence learning can result in different kinds of knowledge. A frequently used distinction is that between declarative sequence knowledge that individuals can report verbally, and non-declarative knowledge that is primarily expressed in terms of reaction time savings to sequentially structured material. Typically, only a subset of participants in a sequence learning experiment, subsequently referred to as verbalizers, are able to verbally describe the sequential regularity of the training phase that is responsible for the observed reaction time savings (cf. Frensch & Rünger, 2003). How many participants become verbalizers during an incidental learning phase depends on the exact experimental conditions as, for example, the amount of training, the type of training, and the type of sequence all influence whether people are able to report the regularity (Frensch, Lin, & Buchner, 1998).

There are two classes of theories regarding the generation of explicit sequence knowledge in incidental learning situations. Single-system accounts assume that all indices of learning provide different expressions of the same underlying memory representations. Learning increases the quality of representations, which, in turn, leads to improved performance in all available measures of learning (e.g., Perruchet & Amorim, 1992; Perruchet, Bigand, & Benoit-Gonin, 1997). In contrast, multiple-systems accounts propose that explicit and implicit learning are supported by different memory systems that are functionally independent and reliant on different brain areas (e.g., Reber & Squire, 1994, 1998).

A theory about how explicit knowledge can develop in an incidental learning situation and that concurs with the core assumption of the multiple-systems view is the unexpected-event hypothesis (Frensch et al., 2003). This theory assumes that performing a sequentially structured task automatically triggers learning in a non-declarative memory system (cf. Cleeremans, 2006, 2008). In contrast, reportable sequence knowledge is generated by an explicit reasoning system: some individuals attain the ability to verbally describe an experienced regularity because they actively and intentionally search for an explanation to an observed unexpected event. Such an event could be a feeling of familiarity during the incidental learning phase or a rapid anticipatory motor response that occurs before the next stimulus is even shown. Empirical support for this view comes from a study by Rünger and Frensch (2008). The authors conducted an incidental sequence learning experiment with a modified serial reaction time task

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(SRTT; Nissen & Bullemer, 1987). Unexpected events were induced by repeatedly inserting a systematic transfer sequence during learning of the training sequence. After the training phase, the availability of reportable knowledge about the training sequence was found to be increased compared to a control condition in which sequence learning proceeded without disruption by a transfer sequence. The unexpected-event hypothesis thus provides a theoretical ground for the identification of distinctive neuronal signatures of non-declarative and declarative learning.

Although recent research has begun to tackle the mechanisms that are involved in the acquisition of reportable knowledge, much remains unclear about the exact nature of these processes. With the current experiment, we intended to provide novel electrophysiological evidence for the multiple-systems view of sequence learning. Specifically, we focused on the products of learning and examined differences in the retrieval of memories that were acquired during incidental sequence learning. To this end we recorded event-related potentials (ERPs) for participants with and without reportable sequence knowledge in a recognition memory task with test sequences that had either been presented in a previous incidental learning phase or that were new to participants.

Usually, recognition memory tasks follow an explicit learning phase and items correctly classified as old are compared with items correctly classified as new. When explicit memory performance is examined like this, dual-process models of recognition memory assume that recognition can be based on two distinct processes, namely familiarity and recollection (for reviews see Aggleton & Brown, 2006; Mecklinger & Jäger, 2009; Yonelinas, 2002). Familiarity is assumed to be a fast and automatic retrieval process through which the global strength of a memory trace is assessed without the retrieval of qualitative details. Recollection-based recognition, on the other hand, is assumed to be a process through which additional qualitative information associated with the episodic context in which an event was encountered can be retrieved. While recollection is assumed to rely on the hippocampal formation, the surrounding parahippocampal region, especially the perirhinal cortex, seems to be one of the neural generators of the familiarity signal (Aggleton & Brown, 2001, 2006; Meyer, Mecklinger, & Friederici, 2010).

Aside from employing methods that rely on performance measures like the process-dissociation procedure (Jacoby, 1991) or the remember/know procedure (Tulving, 1995), the contribution of familiarity and recollection to recognition judgments can be estimated by dissociable ERP correlates. Familiarity is reflected in more positive-going ERPs for old as compared to new items. This effect is most pronounced over frontal brain areas approximately between 300 and 500 ms post-stimulus and hence has been termed the FN400 or the mid-frontal old/new effect. Recollection, in contrast, is associated with a parietal old/new effect, characterized by more positive-going waveforms for old as compared to new items between 400 and 800 ms post-stimulus over parietal electrodes (for reviews see Friedman & Johnson, 2000; Mecklinger, 2000, 2006; Rugg & Curran, 2007; Wilding & Herron, 2006). In an illustrative study by Curran and Cleary (2003) participants studied line drawings and had to discriminate between studied pictures, mirror-reversals and new pictures in a subsequent recognition task. They found that at frontal electrodes in an early time window, voltages were more positive-going for studied pictures and mirror-reversals as compared to new pictures, presumably reflecting a familiarity signal. Additionally, for subjects with good behavioral discrimination between studied items and mirror-reversals a parietal old/new effect was found, i.e., ERPs were more positive-going for studied items at parietal electrode sites. Similarly, Woodruff and colleagues employed a recognition memory task including studied words and new words. For each test item, subjects had to judge whether (1) the word was old and they were able to recollect something specific about the study episode (remember response), (2) they were confident or (3) unconfident that the word was old in the absence of a recollective detail, (4) they were unconfident or (5) confident that the word was new (Woodruff, Hayama, & Rugg, 2006). They found that items confidently judged old demonstrated a frontally distributed deflection that was more positive-going than the waveforms for confident new items, reflecting familiarity. Additionally, a later positive component was enhanced in ERPs elicited by recollected relative to highly familiar items, reflecting recollection. Both studies are consistent with the claim that the mid-frontal old/new effect is related to familiarity and the parietal old/new effect is related to recollection (see also Jäger, Mecklinger, & Kipp, 2006).

When, after an incidental learning phase, sequence knowledge is probed in a recognition memory task that requires participants to first execute a test sequence and then to decide whether it was old or new, several outcomes are possible. The first possibility concerns participants that have acquired reportable knowledge about the training sequence. For these participants, we expected to find RT priming—faster RTs to learned test sequences than to novel sequences—and superior recognition performance. Upon presentation of a test sequence, these verbalizers should be able to retrieve the sought-for sequence information and to consciously compare the test sequences with the recollected training sequence. These forms of explicit memory retrieval should be reflected in the ERP correlates of familiarity and recollection.

When reportable sequence knowledge is largely absent, however, recollection-based recognition is unavailable and no parietal old/new effect should be discernible in the ERP analysis. In contrast, we should still be able to observe RT priming given the assumption that implicit sequence learning is a mandatory consequence of performing a sequentially structured task (cf. Cleeremans, 2006, 2008; Frensch et al., 2003). If sufficiently large, differences in perceptual-motor fluency for old and new test sequences might provide a differential familiarity signal that allows participants to discriminate between old and new sequences in their recognition judgments (cf. Buchner, Steffens, Erdfelder, & Rothkegel, 1997; Rünger, Nagy, & Frensch, 2009; Whittlesea & Williams, 1998, 2000). This familiarity signal should be reflected in a mid-frontal ERP old/new effect. Alternatively, RT priming effects might be too small to yield a reliable fluency-based familiarity signal. In this case, recognition should not exceed chance level and no mid-frontal old/new effect should be discernible. What ERP effects can be expected in that case?

The electrophysiological correlates of priming are highly divergent across studies (for reviews see Paller, Voss, & Westerberg, 2009; Rugg & Allen, 2000; Voss & Paller, 2008). For example, Rugg et al. (1998) found that during a recognition memory task studied words led to a more positive-going ERP effect between 300 and 500 ms post-stimulus at parietal electrode sites as compared to new ones irrespective of whether the word was consciously recognized. They concluded that this ERP effect reflects memory in the absence of awareness. Similarly, Nessler, Mecklinger, and Penney (2005) found more positive-going ERP waveforms at centro-parietal electrodes between 300 and 450 ms for repeated faces in an implicit memory task (for similar results see Groh-Bordin, Zimmer, & Mecklinger, 2005). In contrast, Paller and colleagues used face stimuli that were encoded only to a minimal extent as to promote priming while recognition performance was at chance level. Using this procedure, they found a negative potential at anterior recording sites between 200 and 400 ms after stimulus presentation, presumably representing perceptual priming for face stimuli (Paller, Hutson, Miller, & Boehm, 2003). All in all, the results regarding the ERP correlates of implicit memory are heterogeneous and different findings have been obtained depending, for instance, on the kind of stimulus material and task characteristics. It is therefore

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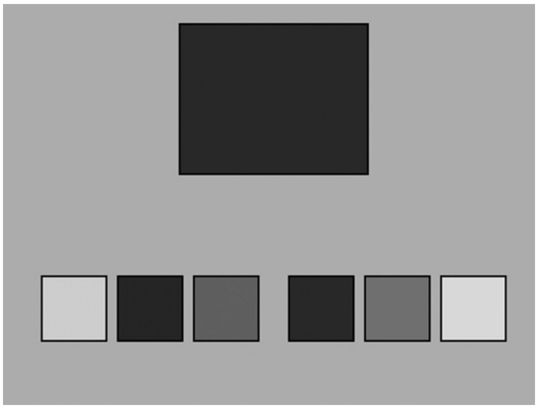

Fig. 1. Example of a stimulus display used in the color-matching SRTT (training and recognition phase).

difficult to derive a precise prediction of ERP effects for participants that show RT priming in the absence of explicit sequence knowledge. However, the absence of an ERP old/new effect in combination with a qualitatively different ERP effect of priming would corroborate the distinction between declarative and non-declarative sequence knowledge.

To summarize, the goal of the present study was to demonstrate that declarative and non-declarative knowledge that was acquired in an incidental sequence learning phase contribute differentially to performance in a recognition memory task with old and new sequence parts and lead to dissociable ERP signatures in this task. In more detail, we expected to find qualitatively distinct ERP patterns for participants with and without reportable sequence knowledge that reflect the differential contributions of familiarity, recollection, and priming. In order to assess the relative contributions of these processes to recognition judgments, we recorded ERPs during a sequence recognition task that was administered after a training phase with a color-matching version of the serial reaction time task (SRTT). Test items consisting of sequence fragments that were either part of the training sequence or part of a completely new sequence were used as retrieval cues.

2. Materials and methods

2.1. Participants

28 volunteers (13 female/15 male, aged 19–26 years, mean age 21.8 years) participated in the experiment which was approved by the local ethic committee and was in accordance with the ethical guidelines of the Declaration of Helsinki. All subjects were right-handed and had normal or corrected-to-normal vision. All signed informed consent before the experiment and were paid 8€ per hour.

2.2. Stimuli and procedure

A large colored rectangle (visual angle $3.5^\circ \times 4.3^\circ$) and six small colored target rectangles (visual angle $1.5^\circ \times 1.6^\circ$, respectively) were displayed simultaneously on a light-gray background (see Fig. 1). Each target rectangle was mapped to a spatially compatible response key on the computer keyboard (X, C, V, B, N, M). The response keys were labeled “1” to “6” from left to right. On each trial, participants had to determine which of the six target rectangles at the bottom of the screen matched the color of the large rectangle on top and to press the response key that was assigned to that target rectangle. They responded to target rectangles 1, 2, and 3 with the ring, middle, and index fingers of their left hand, and to target rectangles 4, 5, and 6 with the index, middle, and ring fingers of their right hand, respectively.

The same six colors (green, red, cyan, dark-gray, magenta, and blue) were used in every trial, but each rectangle changed its color pseudo-randomly from one trial to the next. On any given trial, the top rectangle and the six target rectangles were displayed simultaneously for 1000 ms, followed by a light-gray blank screen for 200 ms. Participants were required to respond within 1000 ms after stimulus onset. If no response was made during that time, the visual feedback “zu langsam” (too slow) was shown for 800 ms. In case of an erroneous response, the visual feedback read “falsche Taste” (wrong key).

Response locations during the training phase with the color-matching version of the SRTT were governed by a repeating 6-element first-order conditional sequence (FOC; Reed & Johnson, 1994). Each of the six possible response locations occurred once in the sequence (e.g., 1–5–2–6–4–3). Consequently, the response location on any given trial was predictive of the response location on the next trial. The SRTT contained no further sequential regularities other than the repeating sequence of response locations. Each participant was randomly assigned to a different 6-element sequence from a pool of 24 sequences. The sequences were permutations of the six response locations that satisfy the following conditions: First, ‘runs’ of three or more adjacent response locations (e.g., 1–2–3, 2–3–4–5, 6–5–4) were not permitted. Second, adjacent response locations (e.g., 1–2, 3–4, 6–5) occurred exactly once in a sequence. The first target location in each trial block was determined randomly with the constraint that the response location had to differ from the response location on the final trial of the previous block. Thereafter, response locations were chosen according to the sequential regularity.

Participants were told that they were taking part in an experiment designed to examine how practice affects the ability to discriminate colors. They were not informed about the fact that correct response locations during the training phase followed a repeating pattern. Learning of the sequential regularity was thus incidental. Before the experiment started, the SRTT was practiced with 40 warm-up trials during which response locations were determined randomly. The warm-up trials were repeated if a participant produced errors or time-outs in more than 20% of the trials. The training phase comprised 8 blocks of trials during which participants performed the 6-choice color-matching version of the SRTT. Each block consisted of 120 trials, for a total of 960 trials, i.e., 160 sequence repetitions.

Participants received feedback about their mean reaction times, error rates, and percentage of responses that were too slow after blocks 1–7. If error rate or time-outs exceeded ten percent for the first time, participants were prompted to make fewer mistakes. After a second block with more than ten percent errors or time-outs, participants were warned that the experiment would not be continued if they did not lower their error rates.

Upon completion of the final block of trials, participants’ reportable knowledge about the training sequence was assessed in a free recall. The experimenter presented a cue card with six boxes labeled “1” to “6” and told the participant that the boxes represent the six response keys that correspond to the six target rectangles. The experimenter then declared that responses in the training phase followed a regular pattern and asked the participant to verbally describe the serial order of response locations by referring to the labels on the cue card. In order to prevent any spontaneous typing activity, participants had to cross their arms in front of their upper body and hold a pencil in each hand while attempting to report the sequence.

After recall, subjects completed a recognition memory task for sequence parts. The general format of the recognition task closely matched that used by Shanks, Wilkinson, and Channon (2003). Participants performed three consecutive trials with the color-matching SRTT. They were then asked to judge whether they had executed the same sequence of key presses during the training phase. Ratings were made in two steps: first, subjects had to decide whether the sequence had been (a) old, and they remembered a certain reason why it had to be old (old-reason), (b) old, but their decision had been based on a feeling of familiarity rather than remembering a certain reason (old-feeling), or (c) new (new). Next, they had to give a confidence judgment (rather sure vs. rather unsure). Participants expressed their confidence by pressing a corresponding response key. The sides for the old/new and sure/unsure responses were counterbalanced across subjects.

During the recognition memory task, twelve different three-trial test sequences were presented as retrieval cues. Six of these sequence triplets were constructed by starting at each position in a participant’s training sequence. The other six triplets were derived in the same way from a new sequence that differed in all pairwise transitions from the training sequence and that contained one reversal of adjacent elements in the training sequence. One participant’s new sequence was used as another participant’s training sequence and vice versa. In order to maximize the number of trials available for ERP analysis, we presented each of the twelve test triplets six times. The colors, however, in which the rectangles appeared, were different for each presentation.[1] The order of test sequence presentation was determined

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[1] Colors were chosen for each old test sequence according to the following procedure: We pseudo-randomly generated six permutations of the color list (green, red, cyan, dark gray, magenta, blue) with the constraint that each color had to appear at each position in the list. The resulting lists determined the colors of the six target rectangles on the first trial of each of the six presentations of an old test sequence. Consequently, for each presentation, the top rectangle on the first trial appeared in a different color. The colors on the second and third trial were then chosen randomly with the constraints that no rectangle appeared in the same color on consecutive trials within a test sequence and that across repetitions of an individual test sequence, there was a different sequence of colors for the top rectangle. Each new test sequence was yoked to the old test sequence with the same response location on the first trial such that the colors of all rectangles were identical on the first trial. Put differently, for each old test sequence there was a new test sequence with an identical first trial. For the second and third trial of the new test sequence, the colors of the top rectangle and the colors of the six target rectangles were determined randomly in accordance with the predetermined response sequence and the requirement that each rectangle had to change its color on consecutive trials.

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Table 1
Group assignments based on performance in free recall.

Subject	Correctly recalled				Group
	Pairs	Triplets	Quadruples	Quintuples	
1	6	6	6	6	Verbalizer
3	6	6	6	6	Verbalizer
4	6	6	6	6	Verbalizer
6	6	6	6	6	Verbalizer
8	6	6	6	6	Verbalizer
22	6	6	6	6	Verbalizer
23	6	6	6	6	Verbalizer
24	6	6	6	6	Verbalizer
2	3	2	1	0	Partial verbalizer
10	1	0	0	0	Partial verbalizer
11	3	2	1	0	Partial verbalizer
12	1	0	0	0	Partial verbalizer
17	1	0	0	0	Partial verbalizer
19	1	0	0	0	Partial verbalizer
25	2	0	0	0	Partial verbalizer
27	1	0	0	0	Partial verbalizer
5	0	0	0	0	Nonverbalizer
7	0	0	0	0	Nonverbalizer
13	0	0	0	0	Nonverbalizer
14	0	0	0	0	Nonverbalizer
15	0	0	0	0	Nonverbalizer
16	0	0	0	0	Nonverbalizer
18	0	0	0	0	Nonverbalizer
20	0	0	0	0	Nonverbalizer
21	0	0	0	0	Nonverbalizer
26	0	0	0	0	Nonverbalizer
28	0	0	0	0	Nonverbalizer

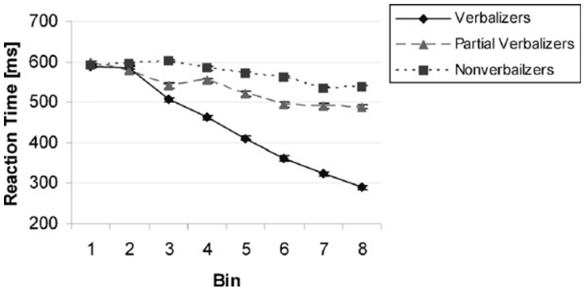

Fig. 2. Reaction times during training phase. Bars depict standard errors of the mean.

pseudo-randomly for each participant in the following way: we created six sets of sequences, each of which contained the six new and six old test sequences. The sets differed with respect to the order of test sequences and the color arrangement for individual items. The ordering of test sequences was random except for the fact that no more than three old items could be presented in a row. Because of the relatively small number of test sequences used in the recognition task, we implemented the following procedure to prevent data loss due to inadmissible responses: a recognition test triplet was repeated at the end of the recognition task phase if one of the three SRTT trials contained an error or a time-out. Item repetitions occurred in the order of the original presentation until each test triplet was responded to in an admissible way.

2.3. EEG recording

Subjects were seated in a dimly lit, electrically shielded, and sound-attenuated chamber. While performing the experiment, the electroencephalogram (EEG) was recorded from 59 Ag/AgCl electrodes embedded in an elastic cap and amplified from DC to 100 Hz at a sampling rate of 500 Hz. The left mastoid served as reference. To control for vertical and horizontal eye-movements, the electrooculogram (EOG) was recorded from the outer ocular canthi and the right sub- and supraorbital ridges. Impedances for all electrodes were kept below 10 kΩ. Further off-line data processing included a digital band-pass filter from 0.5 to 30 Hz in case of low-frequency signal drifts or high-frequency noise in the EEG channels. Recording epochs including eye-movements were corrected by using a linear regression approach (Gratton, Coles, & Donchin, 1983), and epochs with other recording artifacts were rejected before averaging whenever the standard deviation in a 200 ms time interval exceeded 30 μV in any EOG channel.

2.4. Data analyses

Data from free recall were used to divide subjects into three different groups. If the correct training sequence was recalled, a participant was assigned to the group of verbalizers. If parts of the training sequence were recalled correctly, the participant was assigned to the group of partial verbalizers, and if no sequence parts were recalled correctly, the participant was allotted to the group of nonverbalizers.

Statistical analyses of behavioral data include measures of reaction times in the training phase and reaction times to sequence triplets in the recognition memory task. To examine the temporal development of the reaction times in the training phase, mean reaction times were calculated for each of the eight blocks. For analyzing performance in the recognition memory task, we used the Pr measure (hit rate minus false alarm rate) as described by Snodgrass and Corwin (1998) and the percentage of correct old-reason and old-feeling judgments. With the latter analysis, we intended to provide additional support for the distinction between recollection-based and familiarity-based recognition judgments. Analyses of EEG data include ERPs locked to the presentation of the second and third stimulus in the recognition memory task for old and new sequence triplets, respectively. ERPs were not analyzed for the first stimulus of the sequence triplet, since old and new triplets cannot be distinguished at that point. Selection of the time windows for ERP analyses was based on previous studies and on visual inspection of the waveforms. Old/new effects in the recognition memory task were measured as the difference in mean voltage between old and new sequence parts, independently of classification accuracy, in a time window from 300 to 500 ms after presentation of the second and third stimulus. Since we used a motor sequence, ERP effects might have been more closely tied to the responses that to the visual stimuli, so we additionally conducted an analysis locked to subjects' responses to the third stimulus. Time windows between 200 and 100 ms prior to the response and between 100 ms prior to 100 ms after the response to the third stimulus were chosen. A 100 ms pre-stimulus baseline was used for all ERP averages.

Behavioral and ERP data were analyzed using *t*-tests or repeated measures analyses of variance (ANOVAs) with an alpha level of .05. The Greenhouse-Geisser correction for non-sphericity was used whenever appropriate and epsilon-corrected *p*-values are reported together with uncorrected degrees of freedom and Greenhouse-Geisser epsilon values. Statistical analyses of the ERP data were calculated at electrodes C5, C6, CP5, CP6 for the CNV and F3, Fz, F4, C3, Cz, C4, P3, Pz, P4 for all other ERP components, using the factors laterality (left, middle, and right electrodes) and Anterior-Posterior (frontal, central, parietal electrodes). For reasons of clarity, only main effects or interactions including the factors of interest are reported. Post hoc testing was conducted using Tukey HSD. One subject had to be excluded from the analyses due to technical problems during EEG recording. Consequently, all analyses were based on the data of 27 subjects.

3. Results

3.1. Free recall

Free recall was used to divide subjects into three different groups. Using the criteria specified above (see Section 2.4), we obtained 8 verbalizers, 8 partial verbalizers, and 11 nonverbalizers (see Table 1). All analyses reported below were conducted with these group assignments.

3.2. Reaction times during training phase

All groups showed decreasing reaction times to correct responses during the training phase (see Fig. 2). An ANOVA with the between-subjects factor Group (verbalizers, partial verbalizers, nonverbalizers) and the within-subject factor Block (block 1, block 8) showed main effects for Group ($F(2,24) = 11.10$, $p < .01$) and Block ($F(1,24) = 79.09$, $p < .01$), as well as an interaction ($F(2,24) = 18.15$, $p < .01$). This means that all groups started with similar reaction times in block 1 ($p = .89$) but differed in block 8 ($F(2,24) = 17.06$, $p < .01$). Post hoc testing (Tukey HSD) revealed that in block 8, verbalizers (mean = 291 ms) responded faster than partial (mean = 493 ms) and nonverbalizers (mean = 537 ms; all *p*-values < .05). Partial and nonverbalizers did not differ ($p = .53$). However, all groups showed faster reaction times in block 8 as compared to block 1 (verbalizers: $F(1,7) = 60.23$, $p < .01$, partial verbalizers: $F(1,7) = 6.55$, $p = .03$, nonverbalizers: $F(1,10) = 38.24$, $p < .01$). Consistent with this, a Tukey HSD test showed that the reaction time differences between block 1 and 8 were larger for verbalizers (mean = 298 ms) than for partial verbalizers (107 ms) and

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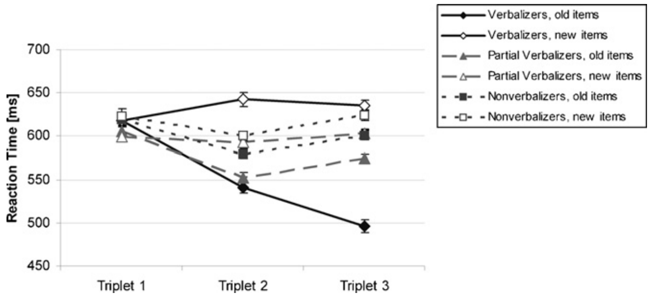

Fig. 3. Reaction times to old and new sequence triplets during recognition memory test. Bars depict standard errors of the mean.

nonverbalizers (56 ms; all *p*-values < .01), while partial and nonverbalizers did not differ (*p* = .45).

3.3. Recognition memory task

An ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Triplet (first, second, third stimulus of sequence triplet), and Item Status (old, new sequence triplet) revealed that reaction times during the recognition memory task showed learning-related differences (see Fig. 3). There were main effects for Triplet ($F(2,48) = 8.16$, $p < .01$, $\varepsilon = .79$) and Item Status ($F(1,24) = 57.37$, $p < .01$), and interactions between Item Status and Group ($F(2,24) = 17.45$, $p < .01$), Triplet and Item Status ($F(2,48) = 55.42$, $p < .01$, $\varepsilon = .86$), and Triplet, Item Status and Group ($F(4,48) = 13.05$, $p < .01$, $\varepsilon = .86$). In this analysis, sequence learning is reflected in the significant main effect of Item Status and the Item Status × Triplet interaction, given that old and new sequences are indistinguishable on the first trial in a triplet. The latter, i.e., no difference between old and new items in reaction times to the first stimulus of a triplet, was confirmed in an ANOVA on first-trial RTs with Group as a between-subjects variable and Item Status as a within-subject variable. The significant three-way interaction indicates group differences in the amount of sequence learning. To further quantify these differences, we computed RT priming values (i.e., the difference in mean RT between old and new sequences collapsed across the second and third trial of a triplet) for verbalizers (120 ms), partial verbalizers (39 ms), and nonverbalizers (20 ms). A Tukey HSD test showed that RT priming was greater for verbalizers than for partial verbalizers and nonverbalizers ($p < .01$, respectively) while the latter two groups exhibited similar amounts of priming.

As a measure of performance in the recognition memory task, Pr was calculated and compared between groups (see Fig. 4). The ANOVA with factor group (verbalizers, partial verbalizers, nonverbalizers) showed a main effect ($F(2,24) = 41.34$, $p < .01$) and Tukey HSD revealed that verbalizers' Pr was larger than that of partial and nonverbalizers (all *p*-values < .05). One-sample *t*-tests revealed that verbalizers showed above-chance Pr ($t(7) = 11.02$, $p < .01$), whereas partial and nonverbalizers did not ($p = .15$ and $p = .79$, respectively).

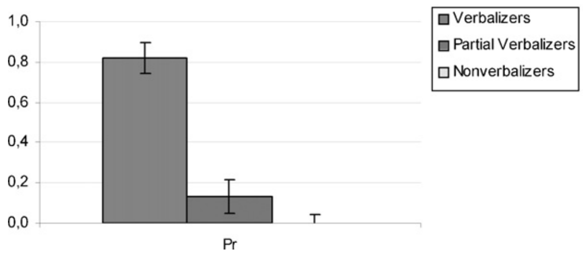

Fig. 4. Pr measure during recognition memory test. Bars depict standard errors of the mean.

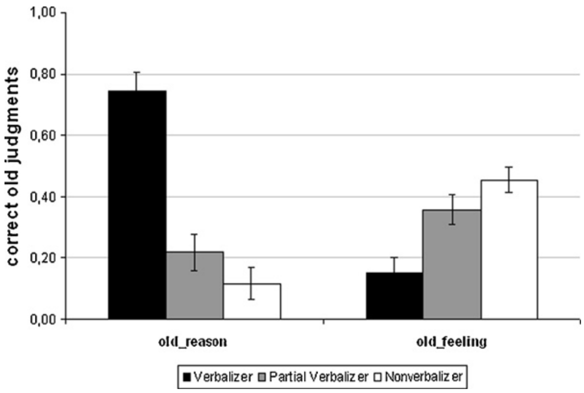

Fig. 5. Relative frequencies of correct old judgments for each group during recognition test. Bars depict standard errors of the mean.

We additionally compared correct old-reason and correct old-feeling judgments from the recognition memory task (see Fig. 5). The ANOVA with factors group (verbalizers, partial verbalizers, nonverbalizers) and judgment (old-reason, old-feeling) showed a main effect for group ($F(2,24) = 21.1$, $p < .01$) and an interaction between group and judgment ($F(2,24) = 26.24$, $p < .01$). Separate ANOVAs for each group revealed that verbalizers used the old-reason judgment more often than the old-feeling judgment to correctly classify old triplets as being old ($F(1,7) = 24.8$, $p < .01$) while the opposite, i.e., more old-feeling than old-reason judgments, was the case for partial and nonverbalizers ($F(1,7) = 7.31$, $p = .03$ and $F(1,10) = 12.69$, $p < .01$, respectively).

3.4. ERP data

3.4.1. Stimulus-locked analyses

Figs. 6 and 7 show the stimulus-locked ERPs for old and new items in the recognition memory test for the second and third stimulus of the triplet, respectively. Visual inspection suggests that there is a parietal old/new effect for verbalizers and, to a lesser extend, for partial verbalizers. Additionally, there appears to be a contingent negative variation (CNV) over central and centro-parietal areas stimulus-locked to the second triplet stimulus and a frontal N100 to the third stimulus, for verbalizers only. In the following, the analyses of these components are reported in order of their chronological occurrence.

For the parietal old/new effect, an ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Laterality (left, middle, right electrodes), Anterior-Posterior (frontal, central, parietal electrodes), and Item Status (old, new sequence triplet) was calculated in a 300–500 ms time window after the second stimulus of the sequence triplet. Since it revealed an interaction between Group, Item Status, and Anterior-Posterior ($F(4,48) = 3.36$, $p = .04$, $\varepsilon = .57$), separate ANOVAs with factors Laterality, Anterior-Posterior, and Item Status were calculated for each group. Verbalizers showed an interaction between Anterior-Posterior and Item Status ($F(2,14) = 11.83$, $p < .01$, $\varepsilon = .52$) which was due to old items eliciting more positive-going ERP waveforms than new ones at posterior electrode sites ($F(1,7) = 15.39$, $p < .01$). There was no main effect or interaction involving the factor Item Status for partial and nonverbalizers, In a time window from 900 to 1100 ms after the second stimulus of the sequence triplet, a CNV was found for verbalizers only. It was measured at central and centro-parietal, lateral electrodes where largest CNV amplitudes were obtained. An ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Laterality (left (C5/CP5), right (C6/CP6)), and Item Status (old, new sequence triplet) revealed a marginally significant interaction between Group and Item Status ($F(2,24) = 3.23$, $p = .06$). Separate ANOVAs with factors Laterality and Item Status were cal-

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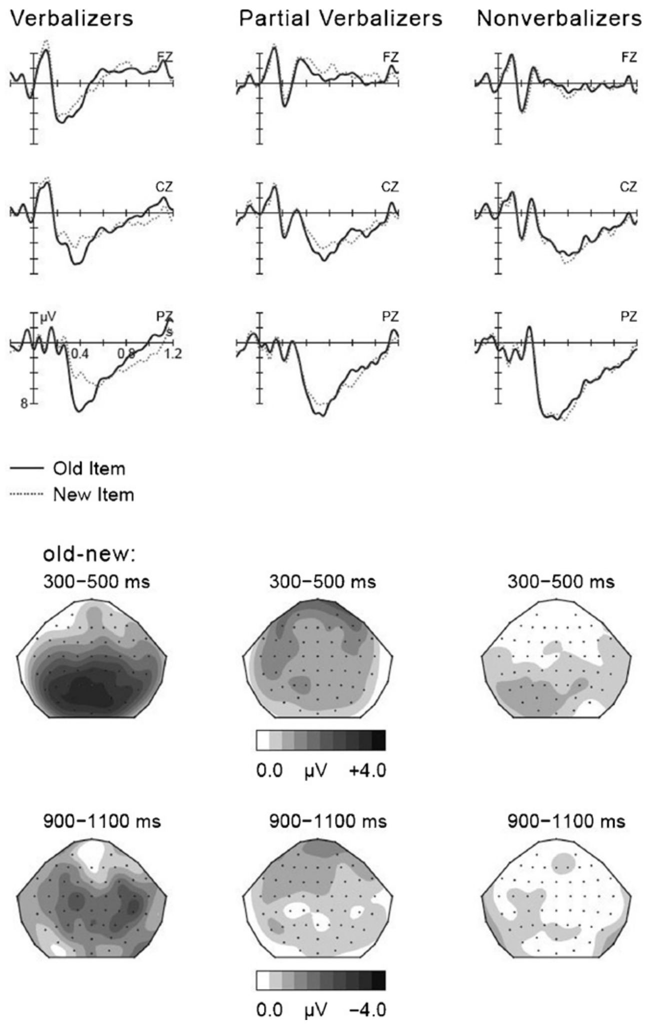

Fig. 6. ERPs for old and new items during recognition memory test locked to the second stimulus of the sequence triplet.

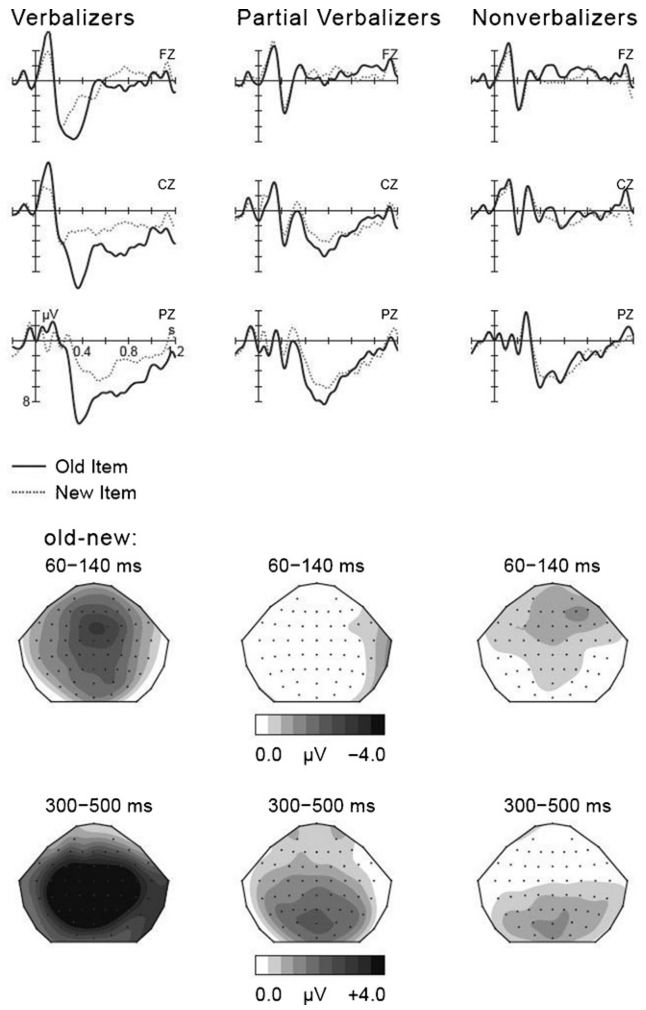

Fig. 7. ERPs for old and new items during recognition memory test locked to the third stimulus of the sequence triplet.

culated for each group. Verbalizers' mean amplitudes for old items were more negative going than those for new ones ($F(1,7) = 9.18$, $p = .02$), while there was no main effect or interaction containing the factor Item Status for nonverbalizers and partial verbalizers.

In addition, an N100 component was visible for verbalizers between 60 and 140 ms stimulus-locked to the third stimulus of the sequence triplet. An ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Laterality (left, middle, right), Anterior-Posterior (frontal, central, parietal), and Item Status (old, new sequence triplet) revealed a marginally significant interaction between Group and Item Status ($F(2,24) = 2.69$, $p = .08$). Separate ANOVAs for each group showed that old items were marginally more negative than new ones ($F(1,7) = 5.00$, $p = .06$) for verbalizers only.

Similarly to the parietal old/new effect to the second triplet stimulus, an ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Laterality (left, middle, right electrodes), Anterior-Posterior (frontal, central, parietal electrodes), and Item Status (old, new sequence triplet) was conducted in a 300–500 ms time window after the third stimulus of the sequence triplet. It revealed an interaction between Group and Item Status ($F(2,24) = 8.34$, $p < .01$) and ANOVAs were calculated for each group. For verbalizers, old items were more positive-going than new ones ($F(1,7) = 13.54$, $p < .01$) and additionally, the interaction between Anterior-Posterior and Item Status was significant ($F(2,14) = 7.27$, $p = .02$, $\varepsilon = .62$). Post hoc testing revealed a significant old/new effect at frontal, central, and posterior electrodes ($F(1,7) = 9.54$, $p < .01$, $F(1,7) = 14.27$, $p < .01$, and $F(1,7) = 12.09$, $p = .01$, respectively). However, as indexed by the effect size, this effect for verbalizers was larger at central ($\omega^2 = .45$) and parietal ($\omega^2 = .41$) electrode locations than at frontal ones ($\omega^2 = .35$). For partial verbalizers, there was a marginally significant interaction between Anterior-Posterior and Item Status ($F(2,14) = 4.47$, $p = .06$, $\varepsilon = .56$) which was due to old items being more positive than new ones at parietal electrode locations only ($F(1,7) = 5.87$, $p = .04$). For nonverbalizers, an interaction between Anterior-Posterior and Item Status ($F(2,20) = 9.41$, $p < .01$, $\varepsilon = .61$) was obtained. Further analyses showed that the interaction was not due to an old/new effect at frontal, central, or parietal electrodes (all p-values > .19,) but rather to the theoretically less relevant fact that old items show a stronger Anterior-Posterior gradient than new ones.

In sum, for the second stimulus of the sequence triplet, an old/new effect emerged for verbalizers only. Consistent with the parietal old/new effect that has been reported in studies of item recognition before, this effect showed a parietal distribution and can be taken to reflect recollection (e.g., Curran, 2000; Mecklinger, 2000; Rugg & Curran, 2007). After the third stimulus of the triplet, the old/new effect was more broadly distributed for verbalizers and was also present for partial verbalizers. In addition to the parietal old/new effects, there were a CNV to the second stimulus and a tendency for an N100 to the third stimulus of the sequence triplet for verbalizers only.

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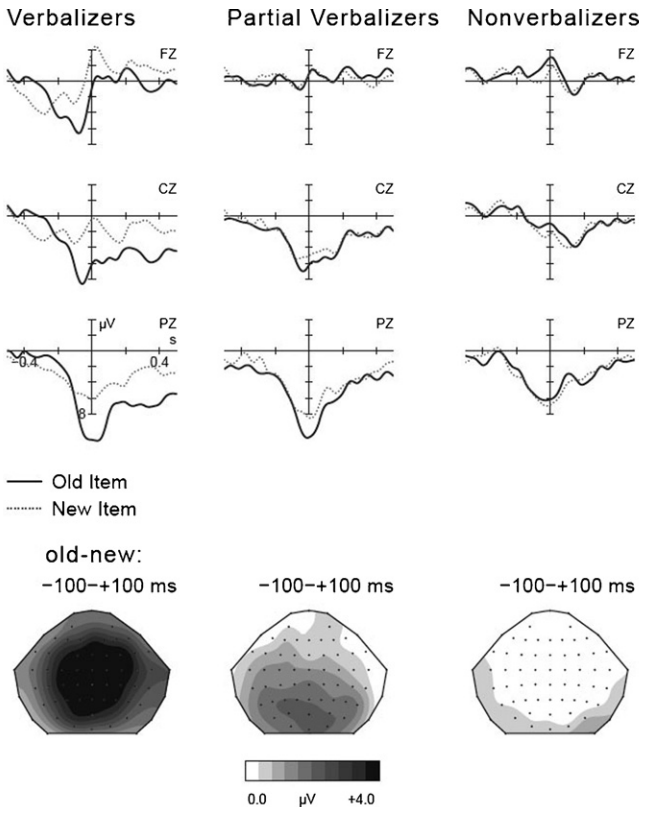

Fig. 8. ERPs for old and new items during recognition memory test locked to the third response to the sequence triplet.

3.4.2. Response-locked analyses

Surprisingly, there was no hint of an early frontal old/new effect in any group. But as the training sequence was a motor sequence, it is conceivable that the old/new effects were more closely tied to the motor response than to the stimulus and, due to variability in response speed, might be better visible in a response-locked ERP analysis. We therefore analyzed the ERP data in the recognition memory task time-locked to the response to the third stimulus of the triplet. As the stimulus-locked old/new effect was most pronounced after the third stimulus of the test triplet, the response-locked analysis was conducted for the third response only. After visual inspection of the response-locked ERP averages (see Fig. 8), we found an old/new effect between 100 ms prior and 100 ms past the response with a parietal distribution for verbalizers and partial verbalizers. Based on its resemblance to the stimulus-locked parietal old/new effect, we will further refer to this effect as the response-locked parietal old/new effect. Interestingly, for nonverbalizers, there seemed to be a polarity-reversed effect in the same time window. After having established the time window for the response-locked parietal old/new effect, between 100 ms preceding and following participants' responses, we searched for a frontal old/new effect in a time window prior to that because the early frontal old/new effect usually precedes the parietal old/new effect. The analyses of both components are reported in order of their chronological occurrence.

An ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Laterality (left, middle, right), Anterior-Posterior (frontal, central, parietal electrodes), and Item Status (old, new sequence triplet) from 200 to 100 ms prior to the response revealed an interaction between Anterior-Posterior, Group, and Item Status ($F(4,48) = 5.09$, $p = .01$, $\varepsilon = .58$). For verbalizers there was an interaction between Anterior-Posterior and Item Status ($F(2,14) = 5.11$, $p = .05$, $\varepsilon = .57$). Contrasts showed, however, that the interaction was due to a tendency of new items being more positive at parietal than at frontal and central electrodes ($F(1,7) = 4.47$, $p = .07$) rather than differences between old and new items (all p-values > .24). For partial and nonverbalizers, there was neither a main effect nor an interaction involving Item Status.

In a time window from 100 ms prior to the response to 100 ms past the response, an ANOVA with factors Group (verbalizers, partial verbalizers, nonverbalizers), Laterality (left, middle, right), Anterior-Posterior (frontal, central, parietal), and Item Status (old, new) provided a main effect for Item Status ($F(1,24) = 10.82$, $p < .01$) and interactions between Item Status and Group ($F(2,14) = 16.42$, $p < .01$) and Item Status and Anterior-Posterior ($F(2,48) = 5.15$, $p = .03$, $\varepsilon = .57$). Separate ANOVAs for each group showed that for verbalizers the ERPs to old items were more positive-going than those to new ones ($F(1,7) = 34.61$, $p < .01$). As in the stimulus-locked analysis, this old/new difference was significant at frontal ($F(1,7) = 23.82$, $p < .01$), central ($F(1,7) = 41.03$, $p < .01$), and parietal ($F(1,7) = 19.59$, $p < .01$) locations. Interestingly, for nonverbalizers an effect with opposite polarity was found. Old items elicited more negative-going ERPs than new ones ($F(1,10) = 5.14$, $p < .05$). Further contrast analyses showed that this effect was significant at frontal ($F(1,10) = 5.97$, $p < .05$) and central ($F(1,10) = 5.03$, $p < .05$) electrode sites. To test whether the aforementioned effect for nonverbalizers is already present for the second response of the triplet, we conducted an additional ANOVA with Anterior-Posterior and Item Status in the time window from 100 ms prior to 100 ms past the second response for the sequence triplet. This analysis did neither yield a main effect for Item Status nor an interaction between Item Status and Anterior-Posterior (all p-values > .53).

Taken together, the response-locked analyses confirmed the stimulus-locked results, as they showed a parietal old/new effect for verbalizers. Moreover, they revealed an additional fronto-central an effect for nonverbalizers which was reversed in polarity. No evidence for a frontal old/new effect was found in the response-locked analysis.

4. Discussion

The present study was designed to examine possible differences between verbalizers and nonverbalizers in access and retrieval of memory representations that were acquired during an incidental sequence learning phase. For this purpose, we recorded ERPs in a recognition memory task time-locked to sequence triplets that were either part of the previously learned sequence or completely new to the subjects. Participants were classified as verbalizers, partial verbalizers, or nonverbalizers according to their ability to verbally report the systematic response sequence of the training phase.

In the recognition memory task, RT savings to old as compared to new sequence triplets showed that there had been learning of the training sequence in all three groups. However, this RT priming effect was most pronounced for verbalizers. In addition, verbalizers discriminated well between old and new test sequences and indicated for the majority of their old responses that they were based on a specific reason (e.g., recall of a specific event from the study episode). Conversely, partial verbalizers and nonverbalizers performed at chance level in the recognition memory task and did not have a specific reason for their old judgments in most cases.

ERP old/new effects were examined after the second and third stimulus of the sequence triplet in the recognition memory task. For the second stimulus, a parietal old/new effect was found for verbalizers only. After the third stimulus of the triplet, this effect was further enhanced for verbalizers and also showed up for partial verbalizers. Usually, the parietal old/new effect is found approximately 500 ms post-stimulus in item recognition experiments (Friedman & Johnson, 2000; Mecklinger, 2000, 2006; Rugg & Curran, 2007;

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Wilding & Herron, 2006). The earlier timing of the present effect (300–500 ms post-stimulus) is most probably due to the specific characteristics of our task where a sequence triplet had to be processed. However, because of its functional characteristics, its polarity and topography, we feel safe to conclude that this effect represents the parietal old/new effect, the ERP correlate of recollective processing, that is typically found in recognition memory studies. The finding that verbalizers stated they had a certain reason for their old judgments in the recognition memory test is also consistent with this view.

Somewhat surprisingly, we found no early frontal old/new effect in any group. Yet, the sequence used in our experiment was a motor sequence, so it is conceivable that the old/new effects were more closely related to the response than to the stimulus and, due to temporal variability of the responses, might be better visible in a response-locked analysis (cf. De Chastelaine, Friedman, & Cycowicz, 2007). Therefore, ERPs in the recognition memory task were additionally analyzed averaged to the response to the third stimulus of the sequence triplet. In this analysis the parietal old/new effect was found between 100 ms prior to and 100 ms after the response, again, for verbalizers only. Also, no hint of a familiarity-related early old/new effect was found, suggesting that familiarity plays a negligible role when recognizing parts of a previously learned sequence and that recollection of the specific serial configuration might be mandatory for correct sequence recognition judgments. This result is at odds with the widely held belief in the sequence learning literature that the perceived fluency of executing a test sequence can result in a feeling of familiarity and thereby serves as the basis for a recognition judgment (e.g., Buchner et al., 1997; Rünger et al., 2009). A possible reason why an ERP correlate of familiarity was not found in the current data could be that individual test sequences were presented repeatedly during the recognition test (each sequence triplet was shown six times to increase the trial number for the ERP analysis). In particular, the repetition of new sequence triplets may have enhanced the familiarity of new items and by this dispersed differences in familiarity between old and new items that may have existed in the beginning of the test phase (see Bader et al., 2010, for similar arguments; see Paller, Voss, & Boehm, 2007, for an alternative view on the mid-frontal old/new effect).

Interestingly, for nonverbalizers the response-locked analysis revealed a significant effect with reversed polarity as compared to the old/new effect found for verbalizers which might reflect priming. This effect is also visible in the stimulus-locked ERP data, but since it occurred slightly later than the parietal old/new effect and thus was not properly captured by the time windows used for the stimulus-locked analyses, it was not significant in the latter analysis. Similar ERP priming effects with negative polarity and anterior topographical distribution have been found when chance-level explicit memory accuracy was used as a criterion for implicit memory (as is the case for nonverbalizers), whereas task-irrelevant repetition of items usually led to positive repetition effects (cf. Groh-Bordin et al., 2005). For example, the perceptual priming effect found by Paller and colleagues (2003) took the form of a negative potential at anterior recording locations about 200–400 ms after stimulus presentation. Face stimuli that were encoded only to a minimal extent evoked more negative-going ERPs than new stimuli. The logic of this design was that contributions from recognition processes would be negligible for these repeated faces and the brain potentials elicited by them would represent implicit memory processes only, i.e., priming (see also Voss & Paller, 2009). Gruber and Müller (2002) presented line drawings either once or repeatedly. They found more positive-going ERPs for repeated stimuli at posterior electrodes and the reversed effect, more negative-going ERPs for repeated stimuli, at anterior sites (see also Gruber, Malinowski, & Müller, 2004). In the current study, priming resulted in more negative-going potentials for old as compared to new sequence triplets at frontal recordings after the third response was given. We further explored whether a similar effect was already present for the nonverbalizers' second response. As no such effect was found at the time of the second response, we assume that, either two sequential responses may have been too weak to trigger implicit knowledge of a six-element sequence or the effect was too small to be detected in the current experiment.

Tulving and Schacter proposed that priming and implicit memory largely reflect changes in a cortically based, presemantic perceptual representation system, composed of several domain-specific subsystems (Schacter, 1992; Tulving & Schacter, 1990). Following that line of thought, the fronto-central topography obtained in the present study might reflect the fact that priming could either be based on perceptual (location of target rectangle on the screen) or motor (button press) representations in the current task. Also, in our study the ERP correlates of implicit and explicit memory are at least partly overlapping in time. This might explain the seeming absence of priming in verbalizers and partial verbalizers: the corresponding ERP effects are of opposite polarity and might have cancelled each other out to some extend. This led to visible ERP priming effects for nonverbalizers, but might also result in underestimating the old/new effects for verbalizers and partial verbalizers in the response-locked analysis.

An alternative explanation of the seeming absence of priming in the ERP data of verbalizers and partial verbalizers could be derived from a competition between memory systems. That is, the system supporting explicit memory might have inhibited the system responsible for implicit memory. Consistent with this view, several neuropsychological studies have identified different networks for explicit and implicit knowledge (e.g., Hazeltine, Grafton, & Ivry, 1997; Jiménez, Vaquero, & Lupiáñez, 2006; Rauch et al., 1995). For instance, Rauch et al. (1995) conducted a sequence learning task under an implicit and an explicit learning condition and found that implicit sequence learning activated a right-sided corticostriatal system that includes the ventral premotor cortex, ventral striatum, thalamus, and bilateral visual association cortex. In contrast, explicit sequence learning activated language and visual areas including left Broca's area, bilateral temporo-parietal cortex, and bilateral primary visual cortex, as well as the bilateral cerebellar vermis. Willingham and colleagues obtained evidence for procedural knowledge in explicit learners, but only in an experimental condition that was designed to prevent the activation of the explicit system (Willingham, Saldis, & Gabrieli, 2002). Together, this could mean that the explicit system does not prevent implicit learning, but might attenuate its effects under specific testing conditions. In the context of the present study, it was the complete absence of explicit sequence knowledge in nonverbalizers that allowed implicit knowledge to take center stage during the recognition test, while the behavior of verbalizers and partial verbalizers (despite low levels of reportable sequence knowledge in the latter group) was largely under the control of the explicit system. As noted above, the partial verbalizers constitute a heterogeneous group that includes subjects with some chunks of explicit sequence knowledge as well as some without valid explicit knowledge (cf. Table 1). Unfortunately, there is no straightforward way to further separate participants in this group (especially to distinguish the subjects with little explicit knowledge from those without explicit knowledge but "good guessing" because guessing probabilities for small parts of the sequence are relatively high). Our criteria for group assignments in the present study were based on earlier studies with similar goals (Ferdinand, Mecklinger, & Kray, 2008; Rünger & Frensch, 2008) and were chosen with the intent to obtain a clear separation between the groups of verbalizers and nonverbalizers.

Taken together, qualitatively distinct ERP signatures in recognition were found for participants with and without reportable sequence knowledge. Verbalizers and, to a lesser extent, partial verbalizers showed recollection for parts of an incidentally learned sequence. For partial verbalizers, this effect is probably due to recollection of sequence chunks. That might also explain the fact that partial verbalizers needed more specific retrieval cues (parietal old/new effect only after third triplet stimulus) than verbalizers (parietal old/new effect after second and third stimulus) to activate the recollection process. Familiarity seems to have played no role in recognizing sequence parts, presumably because the frequent repetition of new sequence triplets rendered old and new items too similar and thus differences in familiarity between both item types too small to be diagnostic for recognition judgments. In contrast to verbalizers and partial verbalizers, nonverbalizers showed a different ERP effect with a reverse polarity that we take to reflect priming. Since two qualitatively different ERP effects were found for verbalizers (partial verbalizers) and nonverbalizers, the obtained ERPs in this study provide strong support in favor of two different processes contributing to sequence recognition. This implies that implicit and explicit knowledge about an event sequence lead to differences in the processes engaged during retrieval and contribute differentially to performance in a recognition memory task that requires participants to discriminate between learned and novel sequences.

In addition to the old/new effects reported above, we also obtained two other ERP components for verbalizers in the recognition memory task, namely a CNV following the second stimulus of the sequence triplet and an N100 after the third stimulus of the triplet. The CNV is a negative potential with a fronto-central distribution that is usually found on trials defined by the succession of two events, the first serving as a cue that a second stimulus will follow at a fixed interval (Rohrbaugh & Gaillard, 1983; Tecce & Cattanach, 1982). It is related to the salience and the signal value of the cue and reflects motor preparation and the anticipation of the second stimulus (e.g., Brunia, 1988; Brunia & Van Boxtel, 2004, Van Boxtel, Van den Boogaart, & Brunia, 1993). Consistent with this, we found a CNV over motor areas after the second stimulus of the triplet which, due to the use of a first-order conditional sequence, is the first stimulus that makes it possible to distinguish old from new triplets. Its occurrence shows that after the response to the second stimulus of the triplet is recollected as belonging to the training sequence, the next stimulus (or at least its visuo-spatial configuration) is expected and the corresponding motor response is prepared.

Following the third stimulus of the sequence triplet an N100 was elicited for verbalizers. The N100 is a negative-going potential associated with selective attention and is taken to reflect orienting of attention towards task-relevant stimuli (Hillyard, Hink, Schwent, & Picton, 1973; Luck, Heinze, Mangun, & Hillyard, 1990). For example, Hillyard et al. (1973) demonstrated that attention to tones presented to one ear enhances auditory N100 amplitude. Similar findings were obtained for the visual domain (Hillyard & Annlo-Vento, 1998). Also, and especially important for the current context, Hopfinger, Woldorff, Fletcher, and Mangun (2001) were able to demonstrate in a combined PET/ERP study, that increasing task difficulty is accompanied by an increase in anterior N100 amplitude and greater activity in the pulvinar and in parietal regions. They interpreted this as reflecting the top-down recruitment or allocation of attentional resources and the increasing need for more effective filtering of unwanted information. In a similar way, the N100 obtained in the current study might reflect higher engagement of attentional processes to the relevant rectangle or screen position and the filtering out of the irrelevant ones. That is, it depicts the top-down allocation of attention when an item has been identified as old in order to facilitate task processing (for similar results see Mulert et al., 2008).

Although the latter two ERP effects were not predicted by our hypotheses and rest on statistically marginal effects, we still think that they can further our understanding of the current data. As mentioned above, it has been proposed that generating reportable knowledge requires a constructive mental act that can be triggered by observed behavioral changes which the participant does not expect (Frensch et al., 2003; Rünger & Frensch, 2008). Tubau, Hommel, and López-Moliner (2007) recently suggested that the generation of explicit knowledge is associated with a shift from perceptual, stimulus-based control to internal, plan-based control. Consistent with that, the ERP components found for verbalizers in the current experiment show that after the second response to the presented sequence triplet is recognized as belonging to the training sequence (parietal old/new effect), the next stimulus is expected and the corresponding response is prepared (CNV). When the third stimulus then appears on the screen more attentional resources are allocated to process it (N100), before this stimulus, too, is recollected (parietal old/new effect). Because none of these processes seems to be at work for nonverbalizers, it appears that only explicit remembering is associated with additional cognitive processes that help to solve the current task and prepare the appropriate motor responses. As such, the CNV and N100 effects for the verbalizers can be taken as reflections of alterations in stimulus and response processing that are due to the emergence of explicit reportable knowledge. By this they nicely underscore the above mentioned shift from perceptual, stimulus-based to internal, plan-based control that accompanies the generation of explicit knowledge.

Interestingly, since our recognition memory task closely resembled the training phase in some crucial aspects, the current results might also shed light on the generation of reportable knowledge. One might speculate, for example, that these same processes are already involved in the training phase when the sequence is acquired and that they emerge after subjects first encounter an unexpected event. To explore this, further studies are required in which ERP effects in the training and recognition test phase are systematically compared.

Our findings show that an ensemble of qualitatively different processes is at work when declarative and non-declarative knowledge is retrieved. By this, they favor the multiple-systems view postulating that explicit and implicit learning are supported by different systems which are functionally independent. Additionally, we were able to show that together with the emergence of declarative sequence knowledge additional cognitive processes, concerning stimulus processing and response control, can be recruited in order to better solve the current task and prepare the appropriate motor responses.

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