Monetary rewards influence retrieval orientations

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Published online: 1 May 2012 © Psychonomic Society, Inc. 2012

Abstract Reward anticipation during learning is known to support memory formation, but its role in retrieval processes is so far unclear. Retrieval orientations, as a reflection of controlled retrieval processing, are one aspect of retrieval that might be modulated by reward. These processes can be measured using the event-related potentials (ERPs) elicited by retrieval cues from tasks with different retrieval requirements, such as via changes in the class of targeted memory information. To determine whether retrieval orientations of this kind are modulated by reward during learning, we investigated the effects of high and low reward expectancy on the ERP correlates of retrieval orientation in two separate experiments. The reward manipulation at study in Experiment 1 was associated with later memory performance, whereas in Experiment 2, reward was directly linked to accuracy in the study task. In both studies, the participants encoded mixed lists of pictures and words preceded by highor low-reward cues. After 24 h, they performed a recognition memory exclusion task, with words as the test items. In addition to a previously reported material-specific effect of retrieval orientation, a frontally distributed, reward-associated retrieval orientation effect was found in both experiments. These findings suggest that reward motivation during learning leads to the adoption of a reward-associated retrieval orientation to support the retrieval of highly motivational

information. Thus, ERP retrieval orientation effects not only reflect retrieval processes related to the sought-for materials, but also relate to the reward conditions with which items were combined during encoding.

Keywords Event-related potentials · Reward-motivated learning · Retrieval orientation · Episodic memory

Humans are unique among animals in that they are able to acquire new knowledge both via the influence of direct reward and via the anticipation of remote reward. Changes in neuronal activation patterns that are driven by these processes of reward-motivated learning can take place even before new knowledge has been encountered (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006), and such changes are an important determinant of whether an event will be recovered at a later time (Sanguist, Rohrbaugh, Syndulko, & Lindsley, 1980). Previous brainimaging studies (Adcock et al., 2006; Wittmann et al., 2005) have indicated that two neural systems play a crucial role during reward-motivated learning: the mesolimbic system and the medial temporal lobes (MTL). Activation of the first system has been shown not only to redirect attention, but also to interact with hippocampal memory processes in the second system, mainly by activating dopaminergic pathways in the ventral tegmental area (VTA) and projections to the nucleus accumbens (NAcc) in the ventral striatum.

In one brain-imaging study, Wittmann et al. (2005) presented pictures that either cued possible monetary reward or were neutral. On reward trials, participants earned money for a correct and fast response in a subsequent reaction time task, whereas they lost money for an incorrect or slow response. After 3 weeks, an unexpected recognition memory test followed in which pictures that had previously been

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presented had to be discriminated from new, unstudied pictures. Reward anticipation during the reaction time task was found to activate brain regions associated with the dopaminergic system (mainly substantia nigra and striatum), which in turn coactivated the hippocampus (in MTL) and led to enhanced recognition memory performance. In a related fMRI study (Adcock et al., 2006), reward cues were incorporated into an intentional memory paradigm. The participants' task was to study pictures that were preceded by either a high- or a low-reward cue and to perform a visual-motor task on each trial. The cues indicated the amount of money that would be received for each correctly recognized study picture during a recognition test the next day. Memory performance was better for pictures studied with a high- than with a low-reward cue, an effect linked to enhanced brain activation in areas related to the dopaminergic system (VTA and NAcc) and of the hippocampus during learning. This enhanced activity in the high-reward condition during learning predicted later memory of the picture, even though it occurred before the stimulus had been presented.

These findings support the view that reward or anticipation of reward during learning modulates memory formation via direct neuronal connections between the mesolimbic reward system and the MTL memory system. An important and yet unexplored issue is the role of reward during retrieval. Common to the principles of transfer-appropriate processing and the cortical reinstatement hypothesis (Morris, Bransford, & Franks, 1977; Rugg, Johnson, Park, & Uncapher, 2008; Tulving & Thomson, 1973) is the notion that the reactivation of processes that were engaged at encoding is beneficial for memory retrieval during test. In order to optimally retrieve information, therefore, an incentive to memorize an item should influence not only encoding but also retrieval processes. It is conceivable that the anticipation of reward could influence a number of retrieval processes, such as the extent to which the reward-related processes from encoding are reimplemented during retrieval, the amount of effort that is engaged during retrieval attempts, and the overall likelihood of retrieval success.

One way of measuring the processes related to the recovery of previously studied information is by examining retrieval orientations, a class of retrieval processes related to the concept of retrieval mode (Mecklinger, 2010; Rugg & Wilding, 2000). Whereas retrieval mode refers to a cognitive state that has to be adopted in order to ensure that environmental stimuli are treated as episodic retrieval cues (Lepage, Ghaffar, Nyberg, & Tulving, 2000; Tulving, 1983; Wheeler, Stuss, & Tulving, 1997), retrieval orientations are assumed to provide a more constrained and task-specific form of retrieval processing that supports the recovery of specific kinds of studied information (Rugg & Wilding, 2000). Processes of this kind have been investigated in recognition memory tests in which the neural activity elicited by correctly rejected new items has been compared between test conditions that differ with respect to the type of information encoded at study or the type of study task (Dzulkifli & Wilding, 2005; Herron & Rugg, 2003; Hornberger, Morcom, & Rugg, 2004; Hornberger, Rugg, & Henson, 2006a; Robb & Rugg, 2002). Across studies of this kind, event-related potential (ERP) analyses have been limited to new items, because this ensures that any differences in the contrasts can be attributed to changes in retrieval cue processing, while confounding changes in retrieval success are removed (Donaldson, Wilding, & Allan, 2003).

In some reports, the adoption of specific retrieval orientations has been found to relate to memory performance (Bridger, Herron, Elward, & Wilding, 2009; Herron & Rugg, 2003; Herron & Wilding, 2004). For example, in one recent report, Rosburg, Mecklinger, and Johansson (2011) presented words at study that were followed either by a picture depicting the object of the word (perceived condition) or by a white rectangle, which meant that participants had to create a mental image of the object word themselves (imagined condition). In subsequent test blocks, these old items were represented intermixed with new items. In one test, participants were asked to respond on one key to previously imagined items (targets) and on a second key to seen items (nontargets) as well as to new words. The designation of items to "target" and "nontarget/new" responses in this way is typical of the retrieval demands employed during recognition memory exclusion tasks (Jacoby, 1991). To enable a comparison of the ERPs to new items that were exposed to different retrieval demands (a change in retrieval orientation), the target/nontarget designation was switched in a second retrieval block. ERP deflections for new words were more positive when items from the imagined condition were targets than when the perceived items were targets. Memory performance was lower in the imagined target condition, and frontal ERP retrieval orientation effects were larger for those participants who showed a greater memory performance difference between the imagined and perceived target conditions. This pattern comprises an important link between the adoption of specific retrieval orientations and recognition memory performance (see Bridger et al., 2009, for a comparable relationship) and highlights the influential role of the engagement of certain retrieval orientations on memory performance. Influential processes of this kind may also be sensitive to reward manipulations, and may thus provide one locus by which reward modulates memory performance. Retrieval orientations, as a sensitive and influential index of retrieval processes, therefore provide a suitable starting point for assessing the impact of rewardmotivated learning on episodic memory retrieval.

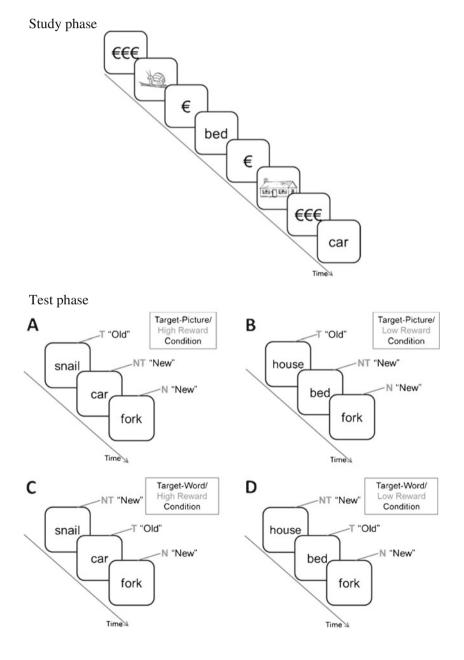
The main goal of the present study was to examine whether and, if so, how the ERP correlates of retrieval orientations are modulated by reward expectancy. At study, the participants encoded a mixed list of pictures and words that were preceded by high- or low-monetary-reward cues. The participants' memory for these items was tested 1 day



after study, via a series of recognition memory tests with exclusion task response requirements (Jacoby, 1991). At test, the participants were presented with words that either were new, had previously been presented as words, or had previously been presented as pictures, and which of the classes of old information was designated as the target class was manipulated across test phases. A correct target response was rewarded with the amount of money indicated in the study phase. The class of targeted material (pictures/words) and reward conditions (high/low incentive; cf. Fig. 1) were orthogonally manipulated across these tests. In line with the logic of retrieval orientation contrasts (Rugg & Wilding, 2000), all of the retrieval cues were words, in order to keep the retrieval cues physically constant and to vary only the type of memory representation that was sought for.

Fig. 1 Schematic illustration of sample items per condition in the study (upper panel) and test (lower panel) phases. In the study phase, reward cues (high and low) and items (pictures and words) were randomly intermixed with each other. In the test phase, four test blocks (A, B, C, and D) were used, and reward conditions were nested within target conditions. One of the blocks in each target-picture or target-word condition contained items that had been accompanied by high-reward cues in the study phase, while the other block contained items that had been accompanied by low-reward cues. In the targetpicture condition, a response with one key was required for words that had formerly been studied as pictures, and a response with a second key was required for words that had been studied as words, as well as for new words. In the targetword condition, a response with one key was required for words that had been studied as words, and a response with a second key was required for words that had formerly been studied as pictures, as well as for new words. In the lower panel, T, NT, and N correspond to targets, nontargets, and new items, respectively, and words in quotes indicate the correct responses

Herron and Rugg (2003) have previously reported the outcomes of contrasts between new-item ERPs from a comparable task. ERPs elicited by new words were more negative-going in blocks in which studied pictures served as the targets, as compared to blocks in which studied words were the targets. This effect was most pronounced between 300 and 1,000 ms poststimulus and was broadly distributed over the scalp. This effect is thought to reflect retrieval cue processes that maximize the likelihood of retrieving targeted memory representations in each test phase, in line with the notion that participants can, in principle, perform the exclusion task on the basis of recovering target items alone (Bridger et al., 2009; Herron & Rugg, 2003). Support for this conjecture comes from experiments that have reported characteristically similar retrieval orientation effects in item





recognition tests in which all old items in a test phase either did or did not match their studied formats (Hornberger et al., 2004; Hornberger, Rugg, & Henson, 2006a). The ERP correlates of retrieval orientations in these paradigms are thus assumed to reflect strategic retrieval processes that optimize the resemblance between a cue and a memory representation in order to facilitate the retrieval of targeted information.

In line with this idea, we predicted that the ERPs elicited by new words would differ between the target-word and targetpicture conditions, in a manner similar to that reported in experiments with comparable contrasts (e.g., Herron & Rugg, 2003; Hornberger et al., 2004) in which ERPs elicited by new items were more negative-going when the sought-for material was dissimilar to the retrieval cues. The sensitivity of these effects to the sought-for material leads us to refer to these as material-specific retrieval orientation effects. Moreover, in light of the fact that both reward and the adoption of a specific retrieval orientation have separately been shown to influence later memory performance, we considered the possibility that reward might affect retrieval processing via retrieval orientation. We expected either that reward would enhance the material-specific orientation effect (by eliciting a larger material-specific ERP effect for pictures and words encoded with high than with low reward expectancy) or that reward would elicit a reward-associated retrieval orientation effect (an ERP difference between high- and low-reward trials, irrespective of the target materials). On the behavioral level, we also expected higher memory accuracy for stimuli that were preceded by high-reward cues, as compared to those preceded by low-reward cues.

Experiment 1

Method

Participants

A group of 24 students (12 men, 12 women) were recruited from Saarland University, Saarbrücken, Germany. All of the participants were right-handed (as assessed by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected-to-normal vision. Participants were excluded if they reported sleeping less than 5 h, taking psychoactive drugs, or drinking more than four cups of tea/coffee/energy drinks or two glasses of alcohol the day before the experiment started. All of the participants gave written informed consent before participating in the study (which was approved by the institutional ethics committee) and were paid between €25 and €45 (including the earned reward). Five of the participants' data were discarded as a result of excessive eye movement artifacts (two participants), fewer than 16 artifact-free trials in one of the critical conditions (one participant), or below-chance-level

behavioral test performance (two participants). The data from 19 participants (10 men, 9 women; mean age = 24 years, range: 18–31 years) are reported and analyzed.

Stimuli and procedure

A set of 480 black-and-white line drawings of common, nameable objects and the corresponding words were used in this experiment. All of the stimuli were taken with permission from the database of the International Picture Naming Project (Szekely et al., 2004). In both experimental sessions, the stimuli were presented in the center of a white background on a computer monitor. The pictures had a mean name agreement of 89 % (min. > 30 %) and relatively low visual complexity, and they were shown with maximum vertical and horizontal visual angles of 4.5 ° each. The words were of low mean frequency usage (M = two per)million in the CELEX corpus; Szekely et al., 2004), word length did not exceed 16 characters (M = 7), and the words were displayed in black letters and subtended a vertical visual angle of 0.4 ° and a maximum horizontal angle of 4.5°.

Two 170-item study lists were formed for each participant by randomly intermixing 85 pictures and 85 (noncorresponding) words. The test list consisted of 480 items and was divided into four blocks of 120 items each. Each test block was composed of 50 target words, 35 nontarget words, and 35 new words. In two of these blocks, the participants were to respond "old" to words that had formerly been studied as pictures (targets) and to respond "new" either to words that had formerly been studied as words (nontargets) or to completely new words. In the other two blocks, the target/nontarget designation changed such that targets were the studied words and nontargets were words that had formerly been studied as pictures. The participants used the index finger of each hand to respond using the buttons "C" and "M" on a standard German keyboard. The assignment of response keys to old/new status at test was balanced across participants. Four test blocks allowed target material (pictures/words) and reward material (high/ low incentive) to be manipulated orthogonally: One targetpicture block contained only old items that had been accompanied by high-reward cues in the study phase, while the second target-picture block contained old items that had been accompanied by low-reward cues. Items associated with high and low reward were similarly allocated across the two target-word blocks. The participants were not informed about the blocked nature of the reward condition, in order to ensure that the possible influences of reward at retrieval were driven by reward processes during encoding and not by additional reward instructions at test.

Items were rotated across the study and test lists such that they were equally often presented as studied pictures,



studied words, and new items across reward conditions. The test blocks were administered to participants in a counterbalanced fashion to ensure that blocks started equally often with target pictures or target words that had been studied with a high- or low-reward cue. Additionally, two consecutive blocks always consisted of the same target materials, in order to make sure that all of the participants needed to switch retrieval task only once.

The participants took part in two sessions, a study phase on the first day and a test phase on the following day (range: 23–25 h after study). Before each phase of the experiment, the participants were fitted with an electrode cap (see the EEG Recording and Data Analysis sections). Prior to the study and test phases, each participant completed a short practice run to become familiar with the experimental task. Items presented in the practice run were not used during the experimental sessions.

Study trials consisted of the presentation of a fixation character ("+") for 500 ms, which was followed by either a low-reward (" \in " = \in 0.05) or a high-reward (" \in \in \in " = \in 0.50) cue for 300 ms. The remaining cue interval was filled with a fixation character for 500 ms. Then, either a picture or a word appeared on the screen for 1,000 ms, followed by a fixation character ("+") for 500 ms. After that, the word "size?" was presented for 2,000 ms, during which time interval the participant responded. Next, the screen was blanked for 500 ms before the next trial began. Whenever the question "size?" appeared on the screen, the participants had to decide whether the real-life size of the shown object (depicted as a picture or a word) would be larger or smaller than the size of the monitor and to press one of the two response keys as quickly as possible without sacrificing accuracy. This task was used to minimize the use of mnemonic strategies. The participants were told that the reward cue preceding an item indicated the money that they would gain in the case of correctly recognizing the item in the later memory test. Therefore, they were additionally instructed to pay attention to both the reward cues (in order to be aware of the reward status) and the pictures/words. The high- and low-reward cues were equiprobable and followed a pseudorandomized order to prevent more than three consecutive pictures or words being preceded by the same reward cue. Between presentation of the two study lists, the Edinburgh Handedness Inventory (Oldfield, 1971) and a questionnaire on demographic information was filled in, and the participants were given a short rest (the total time of the delay was between 5 and 10 min).

Test trials began with the presentation of a fixation character ("+") for 500 ms, after which a test word was presented for 400 ms. This interval was followed by the presentation of a fixation character ("+") for 1,200 ms, and the trial ended with a feedback cue presented for 300 ms (a red, frowning "smiley" for an incorrect or too-slow response, or a green, smiling "smiley" for a correct response). The participants'

task was to respond with one key to words from the respective target material condition (targets) and to press another key to new, unstudied words as well as to those words that had been studied in the other material condition (nontargets). The instructions were to respond as quickly as possible without sacrificing accuracy. The participants were informed about the target designation (studied pictures or studied words) prior to each test block. They were also told that they would be rewarded for each correct recognition of a target (€0.50 or €0.05) and penalized for false alarms. A penalty of –€0.275 for false alarms was included in order to prevent participants from providing "old" responses for all items. After each of the four test blocks, a participant's general performance (as a percentage) was shown, and a brief rest interval was provided (the total delay was approximately 5 min). At the end of the test, the cumulative total of the amount of money gained was presented on the screen (in euros).

EEG recording

During both tasks, the electroencephalogram (EEG) was recorded by Brain Vision Recorder V1.02 (Brain Products) from 58 Ag/AgCl electrodes embedded in an elastic cap. The recording locations were based on the extended International 10-20 System (Jasper, 1958). The EEG from all sites was recorded with a reference at the left mastoid electrode and re-referenced offline to the average of the left and right mastoids. Electro-ocular activity (EOG) was recorded from above and below the right eye (vertical EOG) and from the outer canthi of both eyes (horizontal EOG). The electrode impedance was kept below 5 k Ω . The EEG and EOG were recorded continuously, analog-todigital converted with 16-bit resolution and with a bandpass from direct current to 70 Hz, with a sampling rate of 500 Hz. Offline data processing was performed with EEProbe (ANT Software). The data were band-pass filtered offline (0.03– 30 Hz, 3-dB points). Prior to averaging, trials containing large EOG or muscle artifacts and trials containing analog/ digital saturation were rejected from further analysis using a preset criterion (threshold within a sliding window of 200 ms: standard deviation $[SD] > 30 \mu V$ for any EOG channel, and $SD > 20 \mu V$ for electrode Cz, representative of artifacts at more posterior locations). EOG blink artifacts were corrected using a modified linear regression technique (Gratton, Coles, & Donchin, 1983). Furthermore, all channels were scanned manually for additional disturbances.

Data analysis

The mean amplitudes of the ERPs recorded in the test phase were computed separately for all electrodes, conditions, and participants. For the ERP analysis, the selection of time windows was based on visual inspection of the grand-



average waveforms and on previous research. We restricted statistical analyses of the ERP data to scalp electrodes similar to those that have been used in other ERP studies on retrieval orientation (cf. Bridger & Mecklinger, in press; Dzulkifli & Wilding, 2005) and employed electrodes F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4. The particular laterality chains employed were chosen because they best reflected where the effects were largest. In addition to the experimental factors of interest, the topographical factors Location (frontal, central, and parietal electrodes) and Laterality (left, middle, and right electrodes) were included in the analysis. The ERPs were computed time-locked to the test words, with epochs of 1,600-ms duration and a 100-ms prestimulus baseline.

The data were analyzed using repeated measures analyses of variance (ANOVAs) with a significance level set to .05. A Greenhouse–Geisser correction for nonsphericity (Keselman & Rogan, 1980) was applied when necessary, and epsilon-corrected p values are reported, together with uncorrected degrees of freedom and Greenhouse–Geisser epsilon values. The p values for the follow-up analyses were adjusted by applying Holm's sequential Bonferroni correction (Holm, 1979). All analyses were limited to correct responses, and the follow-up analyses were restricted to target material and reward conditions. Main effects and interactions are reported only if they include the factors of interest.

Results

Behavioral data

Study phase The mean likelihood of correct responses in the size judgment task was .87 ($SD = \pm .05$), and the mean latency of responding was 505 ms ($SD = \pm 156$ ms). An ANOVA with the factors Material (picture vs. word) and Reward (high vs. low) revealed no main effects or interactions.

Test phase Table 1 shows the mean reaction times and probabilities of correct responses to targets, new (unstudied) words, and nontargets in the four test blocks. Performance on the memory exclusion task was operationalized with the discrimination index Pr (p[target hit] - p[nontarget false]alarm]; derived from Snodgrass & Corwin, 1988). The Pr values were .25 (pictures-high reward), .15 (pictures-low reward), .19 (words-high reward), and .21 (words-low reward). An ANOVA with the factors Target Material (picture vs. word) and Reward (high vs. low) gave rise to a marginally significant interaction between target material and reward, F(1, 18) = 4.05, p = .06. Pairwise t tests revealed that in the target-picture blocks, Pr values were higher for pictures studied with high than with low reward [t(18) = 2.72, p< .05, two-tailed]. No reward-related differences were found for the Pr values in target-word blocks (p = .68). This reward

Table 1 Mean proportions of correct responses [p(correct)] and reaction times (RTs, in milliseconds) to targets, nontargets, and new items, separated according to target material and reward condition (n=19) in Experiment 1

| | | Item Type | | |
|----------------------|------------|-----------|-----------|-----------|
| Test Block | Target | Nontarget | New | |
| Pictures-High Reward | P(correct) | .56 (.12) | .69 (.14) | .75 (.13) |
| | RT | 928 (115) | 950 (116) | 932 (124) |
| Pictures-Low Reward | P(correct) | .54 (.12) | .60 (.12) | .76 (.10) |
| | RT | 962 (117) | 964 (131) | 967 (124) |
| Words-High Reward | P(correct) | .58 (.11) | .61 (.11) | .71 (.15) |
| | RT | 923 (157) | 942 (157) | 932 (152) |
| Words–Low Reward | P(correct) | .59 (.12) | .62 (.14) | .69 (.13) |
| | RT | 932 (160) | 936 (159) | 910 (155) |

Standard deviations are in parentheses.

effect in the target-picture blocks was primarily due to a lower false alarm rate for nontargets in the high-reward condition (.31) than for nontargets in the low-reward condition (.40) in these blocks [t(18) = 2.94, p < .05, two-tailed]. This reward-related difference between false alarms of the nontargets was not found in the target-word blocks (p = .67).

An ANOVA for the accuracy data with the factors Target Material (picture vs. word), Item Type (target vs. nontarget vs. new), and Reward Condition (high vs. low) revealed only a significant effect for item type, F(2, 36) = 15.99, p < .001. Follow-up t tests revealed that accuracy was higher for new words than for either nontargets [t(18) = 5.25, p < .001, two-tailed] or targets [t(18) = 4.78, p < .001, two-tailed]. An ANOVA of the RT data with the factors Target Material (picture vs. word), Item Type (target vs. nontarget vs. new), and Reward Condition (high vs. low) did not reveal any significant differences (all p values > .12).

In sum, the behavioral results from the test phase indicated that the high-versus-low reward manipulation during study had an effect at retrieval when pictures, but not words, were the targets. In addition, performance was better for new items than for nontargets or targets, but it did not differ as a function of the target material.

ERP data

Grand-average waveforms elicited by correct rejections of new test words in the two material conditions, separated for the high- and low-reward conditions, are illustrated in Fig. 2a. The ERPs in both reward conditions are relatively more negative-going in the target-picture condition than in the target-word condition. These effects start at around 400 ms,



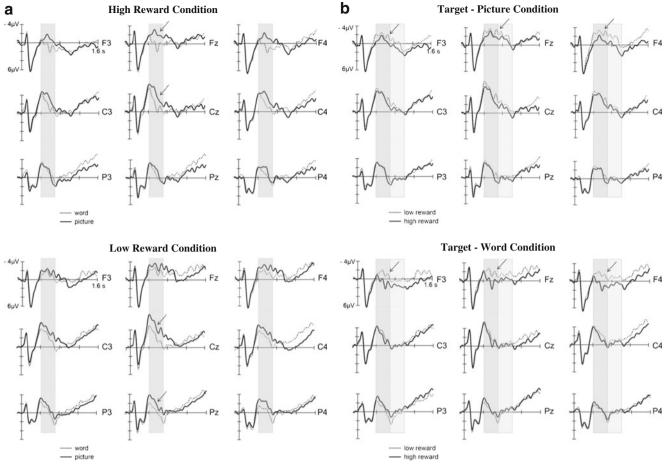


Fig. 2 a Upper panel: Grand-average ERPs elicited by correct rejections in the target-word and target-picture blocks for the high-reward condition of Experiment 1. Lower panel: Grand-average ERPs elicited by correct rejections in the target-word and target-picture blocks for the low-reward condition of that experiment. In both panels, data are shown for nine electrodes over frontal (F3, Fz, and F4), central (C3, Cz, and C4), and parietal (P3, Pz, and P4) scalp sites. Arrows mark the electrodes at which the effects were maximal. For this visual presentation, all waveforms depicted in the figures were low-pass filtered at

12 Hz. Negative values are plotted upward. **b** Upper panel: Grandaverage ERPs elicited by correct rejections in the two reward conditions for the target-picture condition of Experiment 1. Lower panel: Grand-average ERPs elicited by correct rejections in the two reward conditions for the target-word condition of that experiment. In both panels, data are shown for nine electrodes over frontal (F3, Fz, and F4), central (C3, Cz, and C4), and parietal (P3, Pz, and P4) scalp sites

extend for about 300 ms, and show a broad topographical distribution, which is more anteriorly distributed in the high-reward condition. Figure 2b shows the grand-average waveforms elicited by correctly rejected new words in the two reward conditions, separated for the target-picture and target-word material conditions. (For topographic maps, see Fig. 3.) In both target material conditions, ERPs elicited by high-reward items show a relative positivity over frontal sites from approximately 400 ms. Although this effect appears to remain until the end of the recording epoch for the target-word condition, the effect in both target material conditions is most robust between 400 and 1,000 ms poststimulus, and thus this is the time window over which the principal analyses were focused.

The observations outlined above suggest a difference in timing between the two contrasts in the critical 400–1,000 ms

epoch: a shorter-lived ERP difference related to material type from 400 to 700 ms, and a more temporally protracted ERP effect associated with level of reward. To test this, and in line with the statistical analyses of ERP data used in the study of Herron and Rugg (2003), ANOVAs were conducted on the data from the 400- to 700-ms and 700- to 1,000-ms latency ranges.

Early time window (400–700 ms) In line with previous studies (e.g., Hornberger et al., 2004), the analysis revealed a main effect of target material in the early time window [F(1, 18) = 5.49, p < .05]. There were also interactions between reward and location [F(2, 36) = 12.33, p < .01, $\varepsilon = .61$] and between target material, reward, and location [F(2, 36) = 6.92, p < .05, $\varepsilon = .66$]. The three-way interaction was deconstructed by examining reward effects at each level of the Target



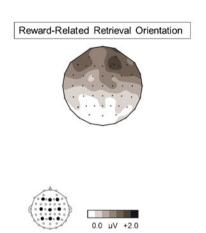
Correct Rejections Early Time Window (400 – 700ms) Material-Specific Retrieval Orientation High Reward Condition Low Reward Condition Condition Reward-Related Retrieval Orientation Target – Picture Condition Target – Orientation Target – Orientation

Fig. 3 Upper left panel: Topographic maps showing the scalp distributions of the differences between neural activity elicited by new test words in the target-word and target-picture blocks, separated for the high- and low-reward conditions in the early time window from 400 to 700 ms (material-specific retrieval orientation). Lower left panel: Topographic difference maps showing the scalp distributions of the differences between neural activity elicited by new test words in the high-

Material and Location factors. The ANOVAs for the target-picture condition revealed a main effect of reward [F(1, 18) = 4.37, p < .05], whereas for the target-word condition there was a significant interaction between reward and location $[F(2, 36) = 15.95, p < .001, \varepsilon = .66]$, indicating reliable effects of reward at frontal [F(1, 18) = 10.39, p < .01] and central [F(1, 18) = 9.72, p < .01] sites, but not at parietal sites (p = .27). These effects confirm that, in both material conditions, high-reward items elicited more positive-going ERP waveforms than did low-reward ones in this time window, although the effect was more frontally distributed in the target-word condition.

Late time window (700–1,000 ms) In this time window, we found an interaction between reward and location $[F(2, 36) = 8.89, p < .01, \varepsilon = .73]$. No effects involving the Target Material factor were obtained in the late time interval. To deconstruct the two-way interaction between reward and location, reward effects were again examined at each level of the Location factor. The ANOVA yielded a significant effect of reward at frontal sites [F(1, 18) = 6.85, p < .05], but not at central or parietal sites (both p values > .32), indicating that the reward-related ERP effect in this later time window was most pronounced at anterior electrode sites and did not differ between the two material conditions.

Correct Rejections Late Time Window (700 – 1000 ms)



and low-reward conditions, separated for the target-picture and target-word blocks in the early time window from 400 to 700 ms (reward-related retrieval orientation). Right panel: Topographic difference map showing the scalp distribution of the differences between neural activity elicited by new test words in the high- and low-reward conditions in the late time window from 700 to 1,000 ms (reward-related retrieval orientation)

Figure 2b also indicates that ERPs to correctly rejected new words in the high- and low-reward conditions continue to diverge from one another in the 1,000- to 1,600-ms interval. To test this observation, reward effects were examined in two additional time windows (1,000-1,300 ms and 1,300-1,600 ms). A five-way repeated measures ANOVA with the same factors as in the initial analysis, but with the additional factor Time Window (1,000-1,300 ms or 1,300-1,600 ms), revealed a two-way interaction between reward and location $[F(2, 36) = 4.23, p < .05, \varepsilon = .71]$. Deconstruction of the interaction yielded a marginally significant effect of reward at frontal sites [F(1, 18) = 4.2, p = .055] but not at central or parietal sites (all p values > .22). This analysis confirmed that the reward-related ERP effect continued from 1,000 ms onward and that it was most pronounced at frontal electrodes, as had been the case in the preceding time windows. Although these analyses were only marginally significant, they indicate a temporally protracted frontal reward-related effect.

Discussion

The main goal of Experiment 1 was to investigate the influence of reward-motivated learning on retrieval orientations. Relevant to this was whether the incentive to memorize an item would enhance the material-specific orientation effect, or whether it would elicit a separate retrieval



orientation effect. In the latter case, this would presumably reflect the engagement of additional retrieval cue processes engaged as a consequence of the possibility of retrieving items studied with a high incentive.

We assumed that the most efficient retrieval strategy for earning the greatest amount of money would be to prioritize retrieval processes toward the recovery of high-reward items.

On the behavioral level, we found that memory performance was relatively low and that high monetary incentives during learning promoted memory performance after a delay of 24 h, as compared to low incentives, only when pictures served as the targets. However, this study is the first to report performance in a memory exclusion task with a study–test interval of this length, and the possibility has to be considered that the mnemonic demands of this task were so high that the long study–test interval may have masked reward-related benefits in the behavioral data. The electrophysiological measure nonetheless remained sensitive to these differences.

Consistent with previous studies (Herron & Rugg, 2003; Hornberger et al., 2004; Hornberger et al., 2006a; Robb & Rugg, 2002), our findings confirmed the view that different retrieval orientations are adopted as a function of the targeted memory representation. ERPs to correctly rejected new items in the target-picture condition were more negative-going relative to ERPs in the target-word condition. This material-specific retrieval orientation effect was present from 400 to 700 ms poststimulus and was most pronounced at central scalp sites. Notably, while the present effect showed a more anterior distribution in high-reward blocks, neither its magnitude nor its temporal characteristics differed between the two reward conditions, indicating that the requirement to adopt a material-specific retrieval orientation was only minimally influenced by motivation.

While the results replicated the standard material-specific orientation effect reported previously (e.g., Hornberger et al., 2004), they also revealed a distinct reward-related effect. In the high-reward condition of the memory exclusion task, ERPs to correctly rejected new test items were more positive than those in the low-reward condition between 400 and 1,600 ms after presentation of the retrieval cue. This rewardassociated retrieval orientation effect was present in both the target-picture and target-word conditions, although the distribution was less anterior in the target-picture condition in the early time window of 400-700 ms. Beyond 700 ms, the reward effect became most pronounced at anterior electrode sites, irrespective of the target materials. That is, from that point in time, reward generated a spatiotemporally distinct ERP effect (see Fig. 3). This change in retrieval cue processing in the different phases may have come about, in part, because of a tendency to retrieve more information in the high- than in the low-reward condition, as a consequence of the learned association between high-reward cues and items at study. The recovery of information associated with high reward at test might then have led to the reengagement of reward-related processes comparable to those engaged during study, in line with the cortical reinstatement hypothesis (Rugg et al., 2008) and the associated principle of transferappropriate processing (Morris et al., 1977).

An alternative interpretation is that the recovery of information associated with high reward may have led to the engagement of more effortful retrieval operations at test for these items. This possibility is supported by the similarity in scalp distributions between this frontally distributed rewardassociated effect and the prefrontally distributed retrieval effects reported by Ranganath and Paller (1999) and Werkle-Bergner, Mecklinger, Kray, Meyer, and Düzel (2005). In those studies, retrieval tasks that differed in their demands on the maintenance and specification of retrieval cue features were compared. More-positive ERPs were found for responses in the tasks with higher retrieval cue specification demands and greater relative task difficulty. Accounts based on these data assume that the distribution of these effects reflects the greater engagement of prefrontally supported strategic control mechanisms required for retrieval under such circumstances. With these findings in mind, it might be reasonable to assume that the reward manipulation in Experiment 1 led participants to initiate more extensive retrieval cue processing in order to increase the likelihood with which items studied with high incentives were retrieved. This account raises the issue of whether the term "reward-related" is appropriate for this temporally extended frontal effect, or whether it is primarily a reflection of effort or control-related processes that, in this instance, were elicited by the reward manipulation at study. For this reason, we conducted a second experiment designed to explicitly address whether these effects relate generally to reward manipulations at study or to the effortful processing of retrieval cues in test blocks with high-reward items.

Experiment 2

The results from Experiment 1 suggest that participants can adopt distinct retrieval orientations as a function of the anticipation of high or low monetary incentives. This temporally extended, frontal retrieval orientation effect may have come about because of the reinstatement of reward-related encoding processes at retrieval, which consequently enabled the greater recovery of learned associations between the high-reward cues and the study items than of the cue—item associations in the low-reward condition. Alternatively, these data can be reconciled with the proposal that the reward-associated retrieval orientation effect mainly reflects differences in retrieval effort or in control-related processes elicited by the reward manipulation at study. One way to test whether this effect reduces to an index of retrieval effort



would be to determine whether it is also present in a comparable task in which the reward manipulation at study is not associated with later memory performance, but is instead linked to the accuracy of the study task. An incidental-reward paradigm of this kind would obviate the need for increasing effort-related resources in retrieval conditions associated with high reward. Thus, the observation of a comparable, frontally based ERP effect in this incidental task would speak against an effort account and in favor of a reward-related retrieval orientation that is elicited in line with the principles of transfer-appropriate processing and of the value of reengaging encoding processes at retrieval.

To test this, we conducted a follow-up experiment that replicated the paradigm employed in Experiment 1 in all respects, except that the reward manipulation during study was directly related to accuracy in the study task rather than to later memory performance. In this manipulation, high and low rewards were present during study and were associated with specific study items, but the participants were not aware that they would be required to perform a later memory test and did not receive rewards for correct target retrieval. If the hypothesis is correct that the reward-related effect found in Experiment 1 reflects the reengagement of reward-dependent encoding processes, a comparable frontally based ERP effect should be obtained under these conditions. If the effect observed in Experiment 1 reflects the differential engagement of retrieval effort, the effect should no longer be present in Experiment 2, in which the reward manipulation at study provided no monetary incentive to increase retrieval effort for items associated with high reward.

Method

Participants

A group of 24 healthy students (11 men, 13 women) from Saarland University, Saarbrücken, Germany, participated and gave written informed consent. The exclusion/inclusion criteria were the same as in Experiment 1. The participants were all right-handed (as assessed by the Edinburgh Handedness Inventory; Oldfield, 1971) and were paid between €34 and €55 (including the earned reward). The data from three participants were discarded because of excessive eye movement artifacts (one participant) or below-chance-level behavioral test performance (two participants). Thus, the data for 21 participants are reported and analyzed (10 men, 11 women; mean age = 25 years, range: 19–36 years).

Stimuli and procedure

The experimental materials and procedure were the same as those employed in Experiment 1, except that a correct size judgment of a study item was rewarded with the amount of money indicated before the study item was presented. As in Experiment 1, correct responses at test were followed by positive feedback, but this time no monetary reward was given for recognition memory performance. To provide participants with sufficient rest breaks during study, four 85-item study lists, instead of two 170-item lists (Exp. 1), were formed. The participants took part in two sessions, an incidental study phase on the first day and an unexpected test phase on the following day (range: 23–26 h after study).

The study trials consisted of the presentation of a fixation character ("+") for 300 ms, followed by a blank screen for 200 ms and either a low-reward (" \in " = \in 0.05) or a highreward (" $\in \in \in$ " = $\in 0.50$) cue for 400 ms. The remaining cue interval was filled with the presentation of another blank screen for 400 ms. Then, either a picture or a word appeared on the screen for 2,000 ms, followed by a blank screen for 200 ms. After that, a feedback cue appeared for 400 ms, notifying participants about the amount of money that they had either gained or not gained ("€" or "€€€" crossed out in red for incorrect low- and high-reward trials, respectively, or these same symbols encircled and presented in green for a correct response). The screen remained blank for 1,400 ms before the next trial began. The participants' task was to decide as quickly and accurately as possible whether the real-life size of the shown object (depicted as a picture or a word) would be larger or smaller than the size of the monitor. These judgments were signaled by pressing one of two response keys with either the left or the right index finger. The response deadline was adjusted individually on the basis of the average reaction time for the preceding 20 trials, in order to ensure that correct-response rates were no higher than 80 %. The participants thus received negative feedback after each incorrect or too-slow response, or were otherwise given positive feedback.

The participants were told that the reward cues preceding each item indicated the money that they would gain if the size judgment was made correctly and within time. They were additionally instructed to pay attention to both the cues (to be aware of the reward status) and the pictures and words, and that they would be penalized for incorrect or too-slow responses, although the exact amount of money subtracted was not announced to the participants (-€1.00). Short breaks were provided between each of the four study lists, and the Edinburgh Handedness Inventory (Oldfield, 1971) and a questionnaire on demographic information were completed halfway through the study phase. At the end of each study list, the amount of money gained was presented on the screen (depicted as a colored bar chart), and at the end of the entire study phase, the cumulative total of the gained amount of money (in euros) was presented on the screen.

The procedures for EEG acquisition and the analyses were the same as in Experiment 1. To equate the analyses of the



behavioral and the ERP data, all study trials (rewarded and nonrewarded) were included in the test phase analyses.

Results

Behavioral data

Study phase The mean likelihood of a correct response in the size judgment task was .79 ($SD = \pm .05$), and the mean latency of responding was 722 ms ($SD = \pm 89$ ms). That is, participants' performance approached 80 % accuracy, showing that the individually adjusted reaction time limits had the intended effect.

Test phase Table 2 shows the mean reaction times and likelihoods of correct responses to targets, nontargets, and new (unstudied) words in the four test blocks. The Pr values were .25 (pictures—high reward), .20 (pictures—low reward), .21 (words—high reward), and .22 (words—low reward). An ANOVA with the factors Target Material (pictures vs. word) and Reward (high vs. low) did not result in any significant differences (all *p* values > .23).

Additional hypothesis-driven analyses were included on the basis of the outcomes of Experiment 1, in which the Pr values were higher for target pictures studied with high rather than with low reward. Pairwise t tests revealed a marginally significant trend for higher Pr values for target pictures studied with high rather than with low reward in the target-picture blocks [t (20) = 1.53, p = .071, one-tailed], but there was no indication of reward-related differences for these values in target-word blocks (p = .43). As was the case in Experiment 1, this trend toward a reward effect in the target-picture blocks was primarily due to a lower false alarm rate for nontargets in the high-reward (.29) than in the low-reward (.34) condition [t(20) = 2.53, p < .05, two-tailed] (see also Table 2). No reward-related

Table 2 Mean proportions of correct responses [p(correct)] and reaction times (RTs, in milliseconds) to targets, nontargets, and new items, separated according to target material and reward condition (n=21) in Experiment 2

| | | Item Type | | | |
|----------------------|------------|------------|-----------|-----------|--|
| Test Block | Target | Nontarget | New | | |
| Pictures-High Reward | P(correct) | .54 (.12) | .71 (.12) | .77 (.11) | |
| | RT | 942 (.135) | 954 (133) | 939 (141) | |
| Pictures-Low Reward | P(correct) | .54 (.15) | .66 (.14) | .77 (.13) | |
| | RT | 961 (102) | 965 (103) | 945 (99) | |
| Words-High Reward | P(correct) | .56 (.13) | .65 (.12) | .72 (.11) | |
| | RT | 939 (130) | 945 (131) | 942 (122) | |
| Words-Low Reward | P(correct) | .58 (.15) | .64 (.14) | .71 (.9) | |
| | RT | 940 (150) | 940 (150) | 933 (126) | |

Standard deviations are in parentheses.



differences were found for nontarget false alarms in the target-word blocks (p = .63).

An ANOVA on the accuracy data with the factors Target Material (picture vs. word), Reward Condition (high vs. low), and Item Type (target vs. nontarget vs. new) revealed a main effect of item type [F(2,40)=25.72,p<.001] only. Follow-up t tests showed that accuracy was higher to new words than to either nontargets (p<.01) or targets (p<.001), and that accuracy was higher to nontargets than to targets (p<.05). An ANOVA on the reaction time data with the same factors revealed a main effect of item type [F(2,40)=7.52,p<.01] due to shorter reaction times to new items than to either nontargets (p<.01) or targets (p<.01). Reaction times to targets and nontargets did not differ (p=.70).

In sum, the behavioral data correspond well with the pattern of data reported in Experiment 1. First, performance was better for new items than for nontargets or targets, but it did not differ as a function of target material. Second, we found little indication of a global effect of reward across both target conditions, but did find a trend toward a reward effect when pictures were the targets.

ERP data

Grand-average waveforms elicited by correctly rejected new words in the two material conditions are illustrated in Fig. 4a. As in Experiment 1, the ERPs differed markedly according to whether items were studied as words or as pictures. These effects onset around 400 ms poststimulus, extended for about 600 ms, and took the form of a topographically widespread negative-going deflection for the target-picture condition as compared to the target-word condition. Figure 4b shows the grand-average waveforms elicited by correctly rejected new words in the two reward conditions. (For topographic maps, see Fig. 5.) The ERPs elicited by the high-reward items showed a relative positivity from approximately 400 ms, as compared to the ERPs elicited by low-reward items. As was the case in Experiment 1, this topographically widespread effect remained until the end of the recording epoch, but appeared to be most robust between 400 and 1,000 ms poststimulus. Analyses of the ERP data followed those reported in Experiment 1, in order to enable comparisons between the two experiments. These began with initial ANOVAs conducted on data from the 400- to 700-ms and 700- to 1,000-ms latency ranges, when both effects were present, and then a subsequent analysis was conducted on the 1,000- to 1,600-ms time window specific to the reward-related contrasts.

Early time window (400–700 ms) In line with the results of Experiment 1, the analysis revealed a main effect of target material in the early time window [F(1, 20) = 10.32, p < .01], as well as a main effect of reward [F(1, 20) = 5.10, p < .05].

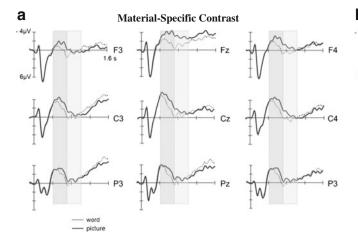


Fig. 4 a Grand-average ERPs elicited by correct rejections in the target-word and target-picture blocks of Experiment 2. The data are shown for nine electrodes over frontal (F3, Fz, and F4), central (C3, Cz, and C4), and parietal (P3, Pz, and P4) scalp sites. **b** Grand-average

Reward-Specific Contrast

4µV

6µV

C3

P2

low reward
high reward

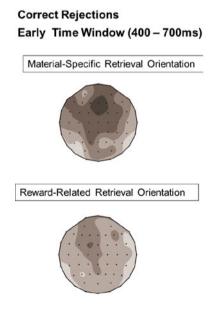
ERPs elicited by correct rejections in the two reward conditions of Experiment 2. Data are shown for nine electrodes over frontal (F3, Fz, and F4), central (C3, Cz, and C4), and parietal (P3, Pz, and P4) scalp sites

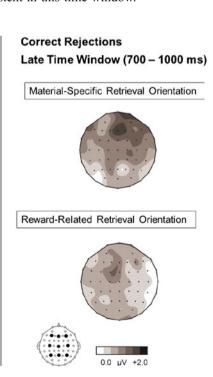
No interaction between target material and reward was found (p > .47). These effects confirm that, in both material conditions, high-reward items elicited more positive-going ERP waveforms than did low-reward ones in this time window.

Late time window (700–1,000 ms) In this time window, the analysis revealed a marginally significant main effect of target material [F(1, 20) = 3.20, p = .089] and a marginally significant main effect of reward [F(1, 20) = 3.55, p = .074]. Furthermore, there was a marginally significant three-way interaction between reward, target material, and laterality $[F(2, 40) = 2.89, p = .078, \epsilon = .84]$. In line with our

hypotheses, we further examined the reward effects at each level of the Target Material and Laterality factors. The ANOVA in the target-word condition revealed a main effect of reward [F(1, 20) = 5.67, p < .05]. In the target-picture condition, we found a significant interaction between reward and laterality $[F(2, 40) = 4.15, p < .05, \varepsilon = .95]$, but no reliable effects of reward were found at left, midline, or right electrode sites (all p values > .28). These effects indicate that, in the target-word condition, high-reward items elicited more-positive ERP waveforms than did low-reward items, and that in the target-picture condition the effect was less consistent in this time window.

Fig. 5 Upper panels: Topographic maps showing the scalp distributions of the differences between neural activity elicited by new test words in the target-material conditions (material-specific retrieval orientation), in the early time window from 400 to 700 ms (left) and in the late time window from 700 to 1,000 ms (right). Lower panels: Topographic difference maps showing the scalp distributions of the differences between neural activity elicited by new test words in the high- and lowreward conditions (reward-related retrieval orientation), in the early time window from 400 to 700 ms (left) and in the late time window from 700 to 1,000 ms (right)







Reward effects were then examined in a five-way repeated measures ANOVA with the same factors as in the initial analysis, but focused on the two later time windows (1,000-1,300 ms) and (1,000-1,300 ms). This revealed a main effect of reward only (1,000-1,200 ms). This revealed a main effect confirmed that the reward-associated ERPs continued to diverge from (1,000 ms) onward, indicating a temporally protracted reward-related effect.

Discussion

The main goal of Experiment 2 was to determine whether a frontally based, reward-associated retrieval orientation effect comparable to that reported in Experiment 1 would be observed when the reward manipulation at study did not induce a strategic use of more effortful encoding and retrieval processes. We tested this in an incidental reward paradigm in which reward was directly linked to accuracy in the study task instead to later memory accuracy at test. This manipulation also elicited a reward-associated retrieval orientation effect at test, as reflected by a reliable difference between the ERPs elicited by correctly rejected new items from the high- and low-reward tasks, irrespective of the target materials. As in Experiment 1, this effect began around 400 ms, was temporally protracted, and was broadly distributed with a maximum over frontal regions. The reward effect in the 700- to 1,000-ms time window was not as robust as in Experiment 1, although it remained significant throughout the final 1,000- to 1,600-ms epoch. Finding this temporally extended reward-related effect in a retrieval task in which performance at retrieval was not related to the reward manipulation at study made it unlikely that this effect could be a reflection of a simple increase in effort related to the retrieval cue or of strategic encoding processes. Instead, we favor an account in which these effects represent the reinstatement of the nonstrategic, rewardrelated processes that were active when these items were encoded (Rugg et al., 2008).

General discussion

In the present experiments, we asked whether rewards influence retrieval processes and examined this question by using ERPs to new items as markers for retrieval orientations. In Experiment 1, we employed an intentional studytest paradigm in which a correct target response in the memory exclusion task was rewarded with a high or a low amount of money, as indicated in the study phase. By contrast, in Experiment 2, the reward manipulation at study was linked to the accuracy of the study task, and memory performance at test on the next day was no longer directly related to reward. The reward manipulations did not

modulate the classic material-specific retrieval orientation effect usually observed for contrasts of this kind, but instead led to the adoption of distinct reward-associated retrieval orientations during test.

The reward-related retrieval orientation effect took the form of a frontocentrally distributed, temporally protracted ERP effect elicited by differences in the amount of reward associated with later memory performance (Exp. 1) or with performance on the study task (Exp. 2). In the high-reward condition of the memory exclusion task, ERPs to correctly rejected new test items were more positive-going than were those in the low-reward condition from 400 ms after presentation of the retrieval cue. This reward-related retrieval orientation effect was present in both the target-picture and target-word conditions. This suggests that, irrespective of the types of targeted memory representations (either pictures or words), the retrieval of items that were linked to a high monetary reward during study was associated with distinct retrieval cue processing, as compared to when lowmonetary-reward items were to be retrieved. The presence of comparable effects in both experiments—even in Experiment 2, when the study reward manipulation was no longer related to memory test performance—makes it unlikely that these effects are a simple reflection of effort-related processing elicited by the changes in reward. Although we make this claim on the basis of the broad correspondences between the effects in the two paradigms, it is not possible to completely discount the contribution of effort-related processes in Experiment 1, and the slightly more anterior maximum of the effect in that experiment might reflect a partial contribution of processes of this kind. While this possibility cannot be entirely excluded for Experiment 1, it is difficult to make this argument for the effect in Experiment 2, and thus we take the differences between new-item ERPs from the high- and low-reward tests to reflect reward-related retrieval processes rather than changes in effort elicited by the reward manipulations.

We favor an account that claims that the differences in ERPs between items associated with high and low reward reflect the reengagement of nonstrategic reward-related encoding processes at retrieval. We assume that the reward manipulation at study influenced the encoding of a subsequent study episode, perhaps by increasing the strength of highly rewarded memory representations and/or by leading to distinct kinds of representations according to whether items were associated with a high- or low-reward cue. The recovery of such information, including the associated reward cue, might then lead participants to reengage processes analogous to those employed during the initial encoding phase. This reasoning is in line with the cortical-reinstatement hypothesis (Rugg et al., 2008) and the associated principle of transferappropriate processing (Morris et al., 1977), which emphasize the interdependent nature of encoding and retrieval processes.



The incidental nature of the study phase in Experiment 2 is likely to have reduced the contribution of deliberate learning processing during this task, thus ensuring that any processes recapitulated at test were principally related to reward and not to explicit learning strategies. The present data thus provide the first demonstration that reward-related processing at study modulates the retrieval processes engaged during test.

One way to test a recapitulation account of this kind would be to compare processing from retrieval phases in which all old items are associated with one kind of perceptual context that is, pictures versus spoken words. If the consistent recovery of a particular class of information in each test phase leads to the engagement of processing that facilitates the further recovery of such information on successive trials, this should be observable in new-item ERP contrasts from the two phases. Moreover, these contrasts should differ from the frontal modulation observed in the present reward-related contrasts. An alternative approach would be to make comparable fMRI contrasts, in order to examine whether material-specific brain regions are activated for new items in each test phase (see Hornberger et al., 2006b). Regardless of whether the rewardrelated processes observed here can be unequivocally shown to reflect the reengagement of those processes engaged during study, the present data comprise the first demonstration of a change in strategic processing, indexed by new-item ERPs at retrieval, that comes about not because of explicit changes in task requirements, but because of a change in the kinds of content or processes associated with old items in each test phase. This observation highlights the sensitivity of retrieval orientations to inherent task features and introduces the notion that retrieving different kinds of information during a test phase can elicit the engagement of related strategic retrieval processes, presumably because this might facilitate the recovery of similar classes of information (Bridger et al., 2009).

The extent to which the engagement of these processes directly contributes to behavioral reward-related memory benefits is not yet clear, however, because while we observed a reward-related ERP effect that was not modulated by the target material, the behavioral reward effect was specific to the target-picture test blocks. In both experiments, high monetary incentives during learning promoted memory performance after a delay, relative to low incentives, but only when pictures served as the targets. This reward effect for the target-picture block came about primarily because of an increase in the correct-rejection rate for nontargets (words) that had been studied with high reward. We assume that this occurred in part because the format of the nontargets in this target designation was perceptually identical at test to the words' format at study (copy cues), a factor that is known to boost the accuracy of responding to old items (Hornberger et al., 2004; see also Herron & Rugg, 2003). This means that, while high-reward cues may provide better memory representations for both picture and word items, the retrieval of these representations is likely to be further boosted for words in light of the perceptual overlap from study to test. This reasoning cannot entirely account for the present findings, however, because we did not find a comparable boost in responding for these items when they were designated as targets, indicating that the extent to which copy cue presentation is beneficial depends on the particular target designation. In order to outline how changes in the current retrieval requirements might influence this, we will first describe the differences between new-item ERPs from the two target designations and the ways in which these can inform understanding of the retrieval processes engaged in the two tasks.

Consistent with several other studies (Dzulkifli & Wilding, 2005; Herron & Rugg, 2003; Hornberger et al., 2004; Hornberger et al., 2006a; Robb & Rugg, 2002), our findings confirmed the view that different retrieval orientations are adopted as a function of the targeted memory representation. ERPs to correctly rejected new items in the target-picture condition were more negative-going, relative to ERPs in the target-word condition. This materialspecific retrieval orientation effect was present from 400 to 700 ms poststimulus and was most pronounced at central scalp sites in Experiment 1, with a somewhat more anterior distribution and temporal extension in Experiment 2. Notably, while there was some indication that the effect showed a more anterior distribution in high-reward blocks in Experiment 1, neither its magnitude nor its temporal characteristics differed between the two reward conditions in either experiment, indicating that the requirement to adopt a material-specific retrieval orientation was only minimally influenced by reward.

In line with observations made in previous ERP studies, one possibility is that this effect reflected the adoption of processes that helped increase the resemblance between retrieval cues and the targeted memory representations in each test phase (Hornberger et al., 2004). In the case of low retrieval-cue-target overlap, as when words serve as retrieval cues to target pictures, retrieval cue processing is thought to be constrained to conceptual features of the retrieval cue, because these are the only features shared by the retrieval cue and the targeted memory representations (Hornberger et al., 2004). Such processing is not necessary in the targetword condition, where all old items can, in principle, be correctly responded to on the basis of the success or failure of perceptual matching. An account that posits a change in the relative emphasis on the processing of conceptual aspects of items is in line with the temporal and topographic correspondences between the present effect and the N400 component, a robust and centralized negativity around 400 ms poststimulus, elicited in conditions that require greater semantic processing of items (see Kutas & Federmeier, 2011, for a review). Reasoning of this kind has been outlined elsewhere (e.g., Hornberger et al., 2004; Hornberger et al.,



2006a), but one additional possibility relevant to the present data is that an increased emphasis on the conceptual features of items in the target-picture condition (as compared to the target-word condition) might also bolster the recollection of nontarget items in this retrieval condition. This, combined with the benefits that arise from the presentation of copy cues for nontarget words in this condition (see above), might therefore account for the specificity of the behavioral reward-related boost to these items.

Not all data points from this paradigm, however, are in line with the notion that these retrieval orientation correlates relate to changes in the extent to which processes are constrained to the semantic level. Hornberger et al. (2006b) also reported data from an analogous fMRI study in which new items were contrasted from test phases in which old items had been studied either as pictures or as aurally presented words. New items in each test phase elicited activity in the brain regions previously associated with the to-be-sought for information that is, greater left fusiform activity was observed when visual information was sought for, whereas greater activation occurred in bilateral inferior parietal regions (previously associated with imagining speech; Shergill et al., 2001) in the test phases in which mnemonic information was auditory. The authors interpreted this pattern of data in line with the principle of transfer-appropriate processing (Morris et al., 1977). Aspects of this data set might also be consistent with a conceptual-constraint account, however, because significant changes in activation also occurred in the left middle temporal gyrus, an area associated with semantic processing that is thought to be a candidate region for generating the N400 (Lau, Phillips, & Poeppel, 2008). Notwithstanding these alternative (but not necessarily mutually exclusive) interpretations, Hornberger and colleagues' (2006b) data highlight the possibility that the present 400–700 ms (material-specific) ERP effect might not reflect changes in the strength with which the same process is activated, but instead may come about because of changes in the exact brain regions activated in each test phase. Although it may not be appropriate to make strong functional claims about material-specific ERP effects, it remains clear that these robust effects are temporally and functionally dissociable from the retrieval orientation processes associated with reward.

We have considered possible reasons for the absence of a clear association between the ERP and behavioral reward-related memory effects observed in the experiments reported here, but empirically it remains to be shown whether this discrepancy occurs because the reward-related ERP effects do not directly facilitate the recovery of information at test or because the long study—test interval combined with the high mnemonic demands employed here may have obscured such a relationship. The findings of the present study provide the first evidence that participants can adopt distinct retrieval orientations, not only as a function of the targeted information

(material-specific retrieval orientation effect), but also as a function of reward (reward-associated retrieval orientation effect). This suggests that incentives during learning facilitate the adoption of a reward-associated retrieval orientation in a delayed memory test in order to retrieve the perceptual details of highly motivational information.

Author note This research was supported by grants from the German Research Foundation (Grants IRTG 1457 and ME 1588/5-1). We thank Julia N. Schuler and Leon P. Makelis for their help with data acquisition.

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