Neuropsychologia 51 (2013) 695–703

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

On the relationship between learning strategy and feedback processing in the weather prediction task—Evidence from event-related potentials

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ARTICLE INFO

Article history:
Received 17 August 2012
Received in revised form
8 January 2013
Accepted 11 January 2013
Available online 21 January 2013

Keywords:
Declarative learning
Feedback processing
FRN
Non-declarative learning
P300

ABSTRACT

Previous work has shown that both declarative and non-declarative strategies can be engaged in probabilistic classification learning. With respect to the neural correlates of these strategies, earlier studies have focused on the classification process itself. In the present experiment, we asked whether the feedback for classification performance is processed differently by declarative and non-declarative learners. We recorded event-related potentials (ERPs) while participants performed a modified version of the weather prediction task, a well-known probabilistic classification learning task. ERP analysis focused on two ERP components typically associated with feedback processing, the feedback-related negativity (FRN) and the P300. FRN amplitude was not affected by learning strategy. The P300, however, was more pronounced in declarative learners, particularly at frontal electrode site Fz. In addition, P300 topography was different in declarative learners, with amplitude differences between negative and positive feedback being more pronounced over the frontal than the parietal cortex. Differences in feedback processing between groups were still seen after declarative learners had switched to a non-declarative strategy in later phases of the task. Our findings provide evidence for different neural mechanisms of feedback processing in declarative and non-declarative learning. This difference emerges at later stages of feedback processing, after the typical time window of the FRN.

1. Introduction

Over the past 15 years, evidence has accumulated that different memory systems contribute to probabilistic (classification) learning (PCL) which requires the incremental acquisition of probabilistic cue-outcome associations. Amnesic patients with (suspected) hippocampal or diencephalic damage have been shown to perform normally during initial learning of PCL tasks, but are impaired relative to control subjects when learning progresses, indicating that the declarative memory system does not contribute notably to early classification learning (Knowlton, Mangels, & Squire, 1996a; Knowlton, Squire, & Gluck, 1994). In contrast, patients with dysfunction of the basal ganglia (BG), which are involved in non-declarative learning, show reduced probabilistic learning from the beginning of the task (Knowlton et al., 1996b; Knowlton et al., 1996a).

Poldrack et al. (2001) examined the interplay of the medial temporal lobe (MTL)- and BG-based memory systems in PCL applying functional magnetic resonance imaging (fMRI) in healthy subjects performing the so-called weather prediction task (WPT). The WPT has been used in a variety of studies to investigate the neural correlates of declarative and non-declarative learning and memory systems (e.g., Gluck, Shohamy, & Myers, 2002; Knowlton et al., 1994; Poldrack et al., 2001). On each trial, one to three out of four different cue cards are presented and subjects have to classify them into one of two weather categories (rain or sun) based on trial-by-trial feedback. Three different learning strategies have been described that participants apply to solve the WPT: the one-cue strategy, the singleton strategy, and the multi-cue strategy (e.g., Gluck et al., 2002; Shohamy, Myers, Onlaor, & Gluck, 2004b). The responses of subjects using a one-cue strategy are based on the presence or absence of a particular cue card on a single trial. Participants who use the singleton strategy concentrate on those trials in which only one cue card is presented (singletons) and respond by chance on the other trials. Finally, subjects using a multi-cue strategy take the combination of all cue cards into account when making their choice. The one-cue strategy and the singleton strategy can be regarded as declarative learning strategies because subjects explicitly learn associations between two stimuli (cue card and outcome) and thus gain knowledge that can be consciously and intentionally recollected, which is a key characteristic of declarative memory (e.g., Cohen & Squire, 1980; Knowlton et al., 1996a; Reber & Squire, 1994; for a review, see Gabrieli, 1998). On the contrary,

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.01.009

gradual learning over many trials which is typical for the multi-cue strategy can be considered as a form of non-declarative memory because it does not require explicit knowledge and conscious awareness (Knowlton et al., 1996a; Reber & Squire, 1994; for a review, see Gabrieli, 1998). In line with this distinction, patients with BG dysfunction have been shown to engage "declarative" strategies more often than healthy controls (Shohamy et al., 2004a; Shohamy et al., 2004b). Moreover, a recent neuroimaging study showed that one-cue strategies are associated with hippocampal activity, whereas multi-cue strategies are related to striatal activity (Schwabe & Wolf, 2012). A shift from hippocampus-based one-cue to striatum-based multi-cue learning was paralleled by a decrease in explicit task knowledge, thus providing further support for the consideration of one-cue and multi-cue strategies as declarative and non-declarative, respectively. The concepts of declarative and non-declarative learning in PCL thus seem to share important features with the concepts of explicit and implicit memory, respectively (Poldrack et al., 2001; Reber, Gitelman, Parrish, & Mesulam, 2003; for a review, see Shanks & St.John, 1994).

To date, the neural correlates of PCL were mostly examined by analyzing neural activity during the decision process. For example, Poldrack et al. (2001), Poldrack, Prabhakaran, Seger, and Gabrieli (1999) showed that healthy participants relied more on the MTL region early in the WPT, while later in learning the BG were more strongly involved. These results are in line with the finding that healthy subjects often switch their learning strategy from more declarative to non-declarative during the WPT (e.g., Shohamy et al., 2004b), corroborating the concept of proceduralization (Anderson, 1982). However, it has been shown that the need to process feedback strongly affects the type of learning (declarative or non-declarative) and thus the memory systems involved. Patients with Parkinson's disease show better performance in a non-feedback version than in a feedback version of PCL tasks (Shohamy et al., 2004a), suggesting that a feedback variant engages the BG more strongly. However, as outlined above, both declarative and non-declarative approaches were seen in a feedback variant of a classification task in healthy subjects (e.g., Shohamy et al., 2004b). It is thus conceivable that declarative learners (DL) and non-declarative learners (NDL) differ in the way they process feedback in PCL tasks.

Feedback processing is often investigated by means of event-related potentials (ERPs). In particular, the feedback-related negativity (FRN) which occurs between 200 and 300 ms after performance feedback is typically more pronounced for negative feedback (e.g., Miltner, Braun, & Coles, 1997) and has been suggested to reflect dopaminergic input to the anterior cingulate cortex (ACC), coding a reward prediction error (e.g., Bellebaum & Daum, 2008; Gehring & Willoughby, 2002; Hajcak, Moser, Holroyd, & Simons, 2007; for a review, see Holroyd & Coles, 2002).

The P300, which peaks between 300 and 500 ms after stimulus presentation, is another ERP component that is modulated by feedback- or reward-related variables such as valence, probability or magnitude. The findings concerning the type of modulation are, however, contradictory (Bellebaum & Daum, 2008; Bellebaum, Kobza, Thiele, & Daum, 2011; Bellebaum, Polezzi, & Daum, 2010; Frank, Woroch, & Curran, 2005; Hajcak et al., 2007; Sato et al., 2005; Yeung & Sanfey, 2004). The neural source of the P300 is less clear than that of the FRN (e.g., Fushimi, Matsubuchi, & Sekine, 2005; Ludowig, Bien, Elger, & Rosburg, 2010; for a review, see Linden, 2005). The longer latency compared to the FRN suggests that it reflects more declarative aspects in the context of feedback processing.

The present study aimed to systematically investigate the neural correlates of feedback processing in declarative and non-declarative learning using electroencephalography (EEG). Subjects completed a modified version of the WPT (e.g., Gluck et al., 2002; Knowlton et al., 1994). We expected declarative and non-declarative learners to differ on those aspects of feedback-related processing that are reflected by the P300 and FRN. Specifically, we expected higher FRN amplitudes in subjects who use non-declarative learning strategies to solve the WPT compared to participants who apply declarative strategies. The P300, in turn, was expected to be more pronounced in declarative learners.

2. Material and methods

2.1. Participants

Fifty-six volunteers (32 females) with a mean age of 25.20 years (SD=3.71) participated in the study. Exclusion criteria for study participation were a history of psychiatric and neurological disorders. One participant who reported a former bacterial meningitis was initially not excluded, but as he performed below chance level on the probabilistic classification task, he was excluded for analysis of performance-matched subgroups (see below for details). All participants gave written informed consent before the experiment was started. The study was approved by the Ethics Committee of the Faculty of Psychology of the Ruhr University Bochum, Germany.

2.2. The weather prediction task

2.2.1. Task procedure of the weather prediction task

Participants completed a modified version of the WPT (e.g., Gluck et al., 2002; Knowlton et al., 1994), while EEG was constantly recorded. Subjects were seated in front of a computer monitor and were asked to learn probabilistic classifications based on trial-by-trial feedback. More specifically, participants classified a stimulus set consisting of one to three cue cards as predicting one of two weather conditions (rain vs. sun) on each trial. Within 5000 ms after stimulus presentation, subjects had to respond by pressing a left (rain) or right (sun) response button. Afterwards, the chosen category was highlighted by a red circle and stayed on the computer screen for 500 ms. Following a delay of 500 ms, participants received feedback as to whether their prediction was correct or wrong (happy or sad face, respectively). The feedback stimulus was shown for 1000 ms (see Fig. 1 for details of the task). The stimuli consisted of one to three tarot cue cards (cue card 1: squares, cue card 2: diamonds, cue card 3: circles, cue card 4: triangles) (see Fig. 1, top right). The whole experiment took approximately 45 min.

As in the study by Gluck et al. (2002), fourteen stimulus patterns were used. The different patterns appeared with different frequencies throughout the experiment and each pattern was associated with a fixed probability of sun and rain outcomes (see Table 1 for details) (cf. Gluck et al., 2002).

Participants performed four blocks of trials. Each block was followed by a break. Participants could individually decide the length of the breaks. Most subjects continued with the next block after 10–20 s. Each block consisted of 100 trials, yielding 400 trials in total for each participant. Participants' responses and the accompanying outcomes were recorded and performance accuracy was determined for each individual trial. Responses were scored as correct if the category (rain or sun) with the higher probability for the particular stimulus pattern was chosen (cf. also Gluck et al., 2002).

2.2.2. Strategy analysis

As already explained in the introduction, three different learning strategies can be used to solve the WPT: the one-cue strategy, the singleton strategy, and the

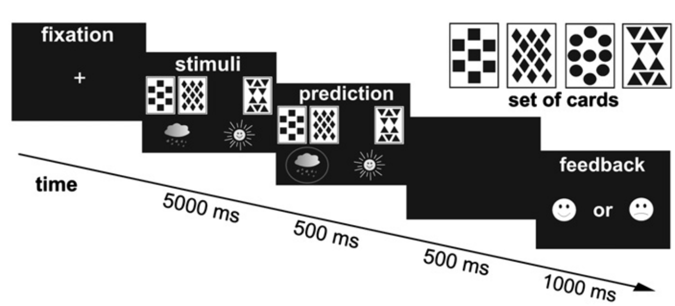

Fig. 1. Learning trials and setup of the task: On each trial, one to three cue cards were presented. Participants chose between two weather categories (rain or sun) and received feedback on prediction accuracy. Top right: The stimuli consisted of one to three tarot cue cards (cue card 1: squares, cue card 2: diamonds, cue card 3: circles, cue card 4: triangles).

Table 1
Probability structure of the WPT (according to Gluck et al. (2002)).

Pattern	Cue card 1	Cue card 2	Cue card 3	Cue card 4	*P* (pattern)	*P* (rain∣pattern)
A	0	0	0	1	14.0	14.3
B	0	0	1	0	8.0	37.5
C	0	1	0	0	9.0	11.1
D	0	1	0	1	8.0	62.5
E	0	1	1	0	6.0	16.7
F	0	1	1	1	6.0	50.0
G	0	1	1	1	4.0	25.0
H	1	0	0	0	14.0	85.7
I	1	0	0	1	6.0	50.0
J	1	0	1	0	6.0	83.3
K	1	0	1	1	3.0	33.3
L	1	1	0	0	9.0	88.9
M	1	1	0	1	3.0	66.7
N	1	1	1	0	4.0	75.0

1 means that a cue card was present. 0 means that a cue card was absent. The overall probability of rain (summing $P(\text{pattern}) \times P(\text{rain}|\text{pattern})$ for all pattern) was 50%.

multi-cue strategy (e.g., Gluck et al., 2002; Shohamy et al., 2004b). While the first two are based on explicit associations between single cue cards and outcomes (see Section 1), the multi-cue strategy is more non-declarative in nature and the subjects applying this strategy take the whole configuration of cue cards into account when making their choice.

For learning strategy classification, we followed the analysis procedure described by Gluck et al. (2002). We constructed "ideal" data for each learning strategy and related participant's individual response profiles to these ideal profiles. The ideal data for each learning strategy reflected a choice pattern which would be expected if a subject was exclusively following this particular learning strategy. We quantified the fit of the different strategy models to individual subjects' choice data applying the following mathematical algorithm introduced by Gluck et al. (2002):

$$Score\,for\,Model\,M = \frac{\sum_P (\#sun\_expected_{P,M} - \#sun\_actual_P)^2}{\sum_P (\#presentations_P)^2}$$

(P=pattern $A \cdots N$; $\sharp presentations_P$ is the frequency with which pattern P occurs; $\sharp sun\_expected_{P,M}$ is the frequency of sun choices expected to pattern P under model M; $\sharp sun\_actual_P$ is the actual number of sun choices which the participant made to pattern P).

The result was a score between 0 and 1 for each learning strategy: The smaller the value, the better the fit to a particular learning strategy. The learning strategy which provided the best fit of choice performance was determined for each individual subject in consecutive blocks of 100 trials. This procedure yielded four classifications of learning strategy for each participant. Based on the analysis of the individual choice patterns in each block, participants were assigned to two groups: declarative learners (DL) and non-declarative learners (NDL). It is known that the processing of performance feedback is strongly affected by feedback expectation (Bellebaum & Daum, 2008; Hajcak et al., 2007; Holroyd, Krigolson, Baker, Lee, & Gibson, 2009; Holroyd & Krigolson, 2007; Pfabigan, Alexopoulos, Bauer, & Sailer, 2011). The assignment to the group of DL or NDL was therefore only based on the fits for the multi-cue and one-cue strategies because only for these strategies reward expectations can be formed for each individual trial. In contrast, singleton learners have specific expectations only for a minority of trials involving only a single cue card. Thus, the DL in the present study predominantly engaged in a one-cue strategy, while the NDL predominantly engaged in a multi-cue strategy.

2.2.3. Post-experimental questionnaire

After completion of the WPT, participants answered six questions assessing declarative knowledge about the cue-outcome associations in the WPT. Four questions required probability estimations of the outcome "sun" when only one of the four cue cards had been presented on the computer screen. Probability estimations in a range of $\pm 15\%$ of the exact probabilities were scored as correct. The two remaining questions asked for the cue card with the highest probability of sun and rain, respectively. The sum of correct answers served as a measure of declarative knowledge about the WPT.

2.3. EEG recording

During the experiment, EEG was recorded from 30 scalp sites with silver–silver chloride electrodes mounted in an elastic cap: F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8, according to the International 10–20 system. We used a Brain Products BrainAmp Standard Amplifier (Brain Products, Munich, Germany) and the appropriate software at a sample rate of 500 Hz. The average of two electrodes placed on the left and right mastoids served as reference for EEG recordings. A ground electrode was placed at Fpz. Stimulus timing was controlled by Presentation Software (Neurobehavioural Systems; http://www.neuro-bs.com). Electrode impedance was kept below 10 kΩ.

2.4. Data analysis

2.4.1. EEG data analysis

We analyzed EEG data off-line using the Brain Vision Analyser Software Package (Brain Products, Munich, Germany) and MATLAB (Mathworks, Natick, Massachusetts, USA). EEG signals were band-pass filtered with cutoffs of 0.5 and 40 Hz. To remove vertical eye movement and blink artifacts, an independent component analysis (ICA) was performed on the EEG data of each individual subject (Lee, Girolami, & Sejnowski, 1999). ICA results in an unmixing matrix which decomposes the EEG signal into a sum of temporally independent and spatially fixed components with the number of components matching the number of channels. Each subject's 30 components were screened for maps which might represent artifacts caused by eye movements and blinks. Candidate components were characterized by a symmetric, frontally positive topography. In addition, components reflecting blink artifacts typically explain a large proportion of the variance. One candidate component was then removed from the raw data by performing an ICA back transformation. Back-transformed data were then checked via visual inspection for remaining artifacts, and only if numerous artifacts were still seen, a second component was removed. To analyze feedback-related ERPs, segments were created from 200 ms before up to 800 ms after the presentation of positive or negative feedback, followed by a baseline correction relative to the 200 ms preceding the feedback stimulus. Finally, an automatic artifact detection excluded trials with data points exceeding an absolute amplitude value of 100 μV before single subject averages for positive and negative feedback were created.

FRN analysis was based on data from electrode Fz where it was most pronounced. FRN amplitude was defined as the maximum negative peak amplitude in the time window between 200 and 350 ms after feedback presentation, relative to the preceding positive peak amplitude between 150 ms after feedback onset and the latency of the negative peak. Although the FRN for positive feedback was markedly reduced, the algorithm identified a small relative negativity in the above mentioned time window also in this condition for all but one subject, for whom FRN amplitude was set to 0 μV. For the P300, the mean amplitude of the ERPs in the time window between 350 and 450 ms after feedback presentation was analyzed at Fz and Pz in order to explore strategy effects on P300 topography.

2.4.2. Statistical design and analysis

Behavioural and EEG data were analyzed with an analysis of variance (ANOVA). If sphericity was violated, Greenhouse–Geisser corrections were applied. For ANOVA results, we only report main effects and interactions involving the between-subjects factor GROUP (DL vs. NDL). Furthermore, correlation analyses (with Pearson's bivariate correlation) were performed between measures of learning strategy, derived from the response pattern (see above) or the post-experimental questionnaire, and ERP measures of feedback processing. For all analyses, the p-value was set to $p < .05$. For the resolution of significant two- or three-way interactions, post-hoc one-tailed t-tests for dependent or independent samples were performed.

3. Results

The main aim of the present study was to compare feedback processing between subjects using a declarative learning strategy and those using a non-declarative learning strategy in PCL. Strategy analyses revealed that most subjects engaged a non-declarative learning strategy and that the proportion of NDL further increased from block 1 to block 4. For the first 100 trials, we found that a one-cue model provided the best fit for 22 subjects (DL) (mean age=25.3 years, SD=3.7, 12 females), whereas a multi-cue model provided the best fit for 34 participants (NDL) (mean age=25.2 years, SD=3.8, 20 females). For the last 100 trials, only 7 DL remained, indicating a shift from a declarative to a non-declarative learning strategy in 15 participants (referred to as "new NDL" in the following). The opposite shift – from a non-declarative to a declarative strategy – did not occur. With respect to the ERP data, we thus focused on the first block of trials in the first step of analysis, comparing feedback-related ERPs in DL and NDL. Accordingly, behavioural data were also compared between these groups of subjects. In the second step, ERP data from the last block of trials were considered and compared with ERPs from the first block, both for subjects who switched strategy and for subjects who applied a non-declarative strategy throughout.

3.1. Behavioural data

Fig. 2 illustrates the learning performance of the 22 DL (defined according to performance in the first block) and the 34 NDL (who did not change their learning strategy during the course of the task) across the four blocks. An ANOVA with the within-subjects factor BLOCK (1–4) and the between-subjects factor GROUP (DL vs. NDL) revealed a main effect of BLOCK (linear trend: $F(1,54)=51.169$, $p<.001$). The main effect of GROUP did not reach significance ($p=.141$). A significant GROUP × BLOCK interaction ($F(2.52, 136.26)=7.175$, $p<.001$) indicated that the NDL group performed significantly better than the DL group in the first block ($t(54)=3.932$, $p<.001$), whereas there were no group differences in the following blocks (all $p>.128$), presumably because most DL changed their strategy during the course of the experiment.

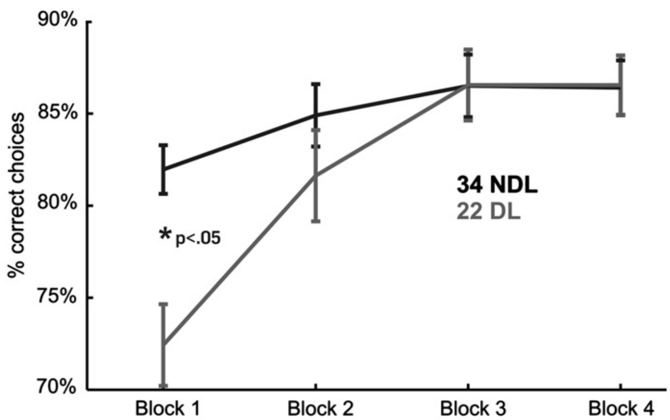

Fig. 2. Behavioural data: Percentage of correct choices in the four blocks for the 22 DL and the 34 NDL (defined based on performance in the first block). Error bars represent SEs.

The groups of DL and NDL did thus not only differ in the learning strategy, but also in overall learning success and – consequently – the frequency of positive and negative feedback. DL received positive feedback on 62.64% of the trials on average, whereas NDL received positive feedback on 66.15% of the trials in the first block, ($t(30.998)=2.068$, $p=.047$). Although the difference was numerically small, it cannot be excluded that outcome-related ERPs to some extent also reflect the between-group differences in performance accuracy and/or reward frequency (see Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003 for a modulation of the FRN by reward frequency). We thus created performance-matched subgroups by excluding an outlier with very low performance accuracy from the DL group and excluding the 13 best NDL, yielding two groups of 21 subjects each (DL: mean number of correct responses in the first block=73.61, SD=9.14; NDL: $M=77.53$, SD=6.12; $p=.110$). The 21 remaining DL received positive feedback on 63.19% of the trials on average, whereas the 21 remaining NDL received positive feedback on 64.48% of the trials in the first block ($t(30.296)=0.762$, $p=.452$), i.e., the performance-matched groups did not differ significantly in the frequency of positive and negative feedback. All ERP analyses for the first block reported below are based on the

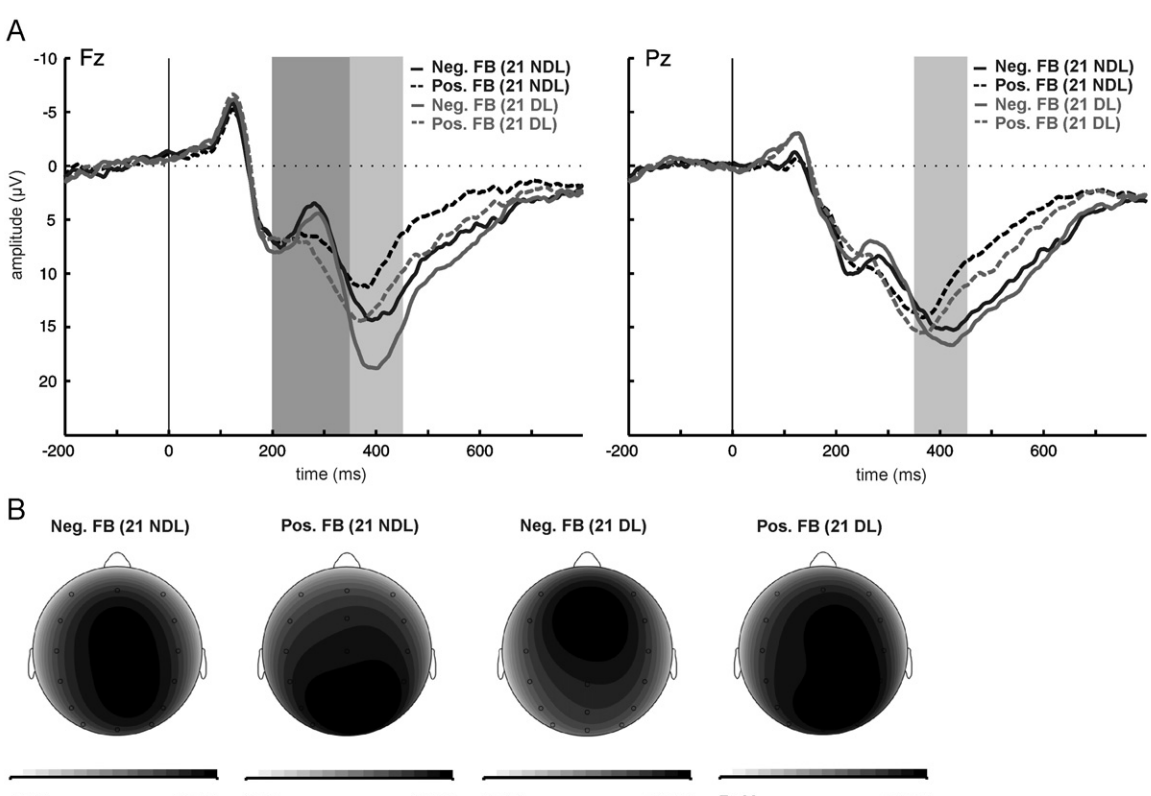

Fig. 3. ERPs at electrode sites Fz (left) and Pz (right) (A): Grand average feedback-locked ERPs following positive (pos. FB) and negative feedback (neg. FB) in the first block for the performance-matched subgroups. The time window for the FRN is shaded in dark grey. The time window for the P300 is shaded in light grey. (B) Topographic maps for positive and negative feedback processing in the time window of the P300 for the performance-matched groups.

performance-matched subgroups. The analyses involving all subjects are provided as supplemental material.

3.2. Post-experimental questionnaire

Analysis of the post-experimental questionnaire did not reveal significant differences in the number of correct answers between the 22 DL from the first block ($M=3.64$, $SD=1.68$) and the 34 NDL ($M=3.38$, $SD=1.48$) ($p=.554$). It has to be noted, however, that the questionnaire assessed declarative knowledge about stimulus-outcome associations after completion of the WPT. Differences in declarative knowledge are thus more likely to occur between subjects applying different strategies at the end of the task. Despite differences on the descriptive level, a one-way ANOVA did not reveal significant differences concerning the number of correctly answered declarative questions between the 34 NDL (see above) who applied a non-declarative strategy during the whole task, the 15 subjects who switched from a more declarative strategy to a more non-declarative strategy ($M=3.47$, $SD=1.89$), and the 7 participants ($M=4.00$, $SD=1.16$) who learned in a declarative manner from the beginning to the end of the experiment ($p=.638$).

3.3. ERP data

3.3.1. FRN in the first block

Fig. 3A (left) shows the ERPs after positive and negative feedback in the first block at electrode Fz for the performance-matched groups of 21 DL and 21 NDL. FRN amplitude of DL after positive feedback was $-3.52\ \mu V$ ($SD=2.22$) and after negative feedback $-7.30\ \mu V$ ($SD=3.16$). NDL showed an FRN amplitude of $-3.82\ \mu V$ ($SD=3.31$) after positive feedback and of $-7.43\ \mu V$ ($SD=4.79$) after negative feedback.

An ANOVA on FRN amplitude with the within-subjects factor FEEDBACK TYPE (positive vs. negative) and the between-subjects factor GROUP (DL vs. NDL) revealed a main effect of FEEDBACK TYPE ($F(1,40)=35.280$, $p<.001$) with higher FRN amplitudes after negative than positive feedback, whereas the main effect of GROUP and the interaction GROUP × FEEDBACK TYPE did not reach significance (both $p>.808$).

For the analysis of all 56 subjects (34 NDL vs. 22 DL), the same pattern of findings was found, with only the main effect of FEEDBACK TYPE reaching significance (see Supplementary Fig. S1 (left) and Supplementary Table S1). The lower p-value for the main GROUP effect compared to the analysis of the performance-matched subgroups ($p=.120$) appears to indicate, however, that the frequency of positive and negative feedback had a greater influence on the FRN amplitude than the specific learning strategy.

3.3.2. P300 in the first block

Fig. 3A illustrates the ERPs after positive and negative feedback in the first block of trials at electrodes Fz (left) and Pz (right) for the 21 DL and the 21 NDL (see Table 2 for P300 amplitudes). ANOVA with the within-subjects factors FEEDBACK TYPE (positive vs. negative) and ROW (frontal vs. parietal) and the between-subjects factor GROUP (DL vs. NDL) revealed a significant main effect of FEEDBACK TYPE (higher amplitudes for negative feedback; $F(1,40)=31.397$, $p<.001$), while the main effects of ROW and GROUP did not reach significance (both $p>.129$). The interaction GROUP × FEEDBACK TYPE was not significant ($p=.833$). The two-way interaction GROUP × ROW ($F(1,40)=4.335$, $p=.044$) and the three-way interaction GROUP × FEEDBACK TYPE × ROW ($F(1,40)=5.223$, $p=.028$) reached significance. Compared to NDL, DL showed higher frontal P300 amplitudes ($t(40)=-1.897$, $p=.033$), while no significant group difference emerged for parietal P300 amplitudes ($p=.167$). Furthermore, P300 amplitude differences between negative and positive feedback were similarly pronounced at frontal ($t(20)=-6.402$, $p<.001$) and parietal electrodes in NDL ($t(20)=-5.008$, $p<.001$). In DL, significantly larger P300 amplitudes for negative than positive feedback also emerged at both electrode sites, but were more pronounced at Fz ($t(20)=-3.960$, $p<.001$) than Pz ($t(20)=-2.127$, $p=.023$; see also Fig. 3B for topographies of the P300). The nature of the above mentioned three-way interaction also becomes apparent when comparing P300 amplitudes between electrode sites Fz and Pz, separately for positive and negative feedback and for DL and NDL (see also Table 2). While for NDL parietal amplitudes are generally higher (positive feedback: $t(20)=-7.216$, $p<.001$; negative feedback: $t(20)=-2.880$, $p=.005$), this pattern, albeit not significant, is seen only for positive feedback in DL ($p=.150$). For negative feedback, a strong trend for a higher frontal P300 emerges ($p=.054$).

Table 2
Means with standard deviations (in brackets) for P300 mean amplitudes (in μV) in the first block.

Group	Fz		Pz	
	Pos. feedback	Neg. feedback	Pos. feedback	Neg. feedback
21 NDL	9.68 (4.00)	13.35 (5.40)	12.15 (4.26)	14.48 (5.00)
21 DL	12.80 (6.52)	17.41 (8.97)	13.85 (4.30)	15.71 (6.58)

ANOVA for 34 NDL vs. 22 DL (see Supplementary Fig. S1 and Supplementary Table S2) revealed a similar pattern of results indicating that the three-way interaction existed independently of performance matching. Furthermore, significant main effects of FEEDBACK TYPE and GROUP emerged for the analysis of all subjects.

3.3.3. Comparison of P300 in the first and last block

To further examine the relationship between learning strategy and feedback processing, ERPs in the first and last block of the WPT were analyzed in the 15 participants who switched their learning strategy during the experiment (named “new NDL”) and compared to ERPs in those 34 subjects who applied a non-declarative strategy throughout the whole experiment (NDL). For this analysis, all 34 NDL were considered because there were no performance differences between NDL and DL in the last learning block and because the three-way interaction GROUP × FEEDBACK TYPE × ROW existed for the analyses of all 56 subjects as well as for the performance-matched subgroups.

Fig. 4 illustrates the ERPs after positive and negative feedback in the first block (Fig. 4A) and last block (Fig. 4B) at electrodes Fz and Pz for the 34 NDL and the 15 “new NDL” (see Table 3 for P300 amplitudes). An ANOVA with the factors mentioned above and the additional factor BLOCK (1 vs. 4) yielded significantly higher P300 amplitudes after negative than positive feedback ($F(1,47)=71.526$, $p<.001$) and at parietal compared to frontal electrodes ($F(1,47)=4.543$, $p=.038$). In addition, a significant main effect of BLOCK emerged ($F(1,47)=46.537$, $p<.001$), indicating higher P300 amplitudes at the beginning of the task. The 15 “new NDL” showed overall higher P300 amplitudes than the 34 NDL ($F(1,47)=6.149$, $p=.017$). Again a significant three-way interaction GROUP × FEEDBACK TYPE × ROW emerged ($F(1,47)=6.245$, $p=.016$). All other interactions with the factor GROUP did not reach significance (all $p>.136$). The resolution of the three-way interaction revealed a similar pattern as for the analysis of the ERPs from the first block. Although the comparison of P300 amplitudes for positive and negative feedback (pooled over the first and last block) yielded highly significant differences for electrode sites Fz and Pz in both NDL (Fz: $t(33)=-6.300$, $p<.001$; Pz: $t(33)=-7.225$, $p<.001$) and DL (Fz: $t(14)=-5.431$, $p<.001$; Pz: $t(14)=-5.122$, $p<.001$), the descriptive

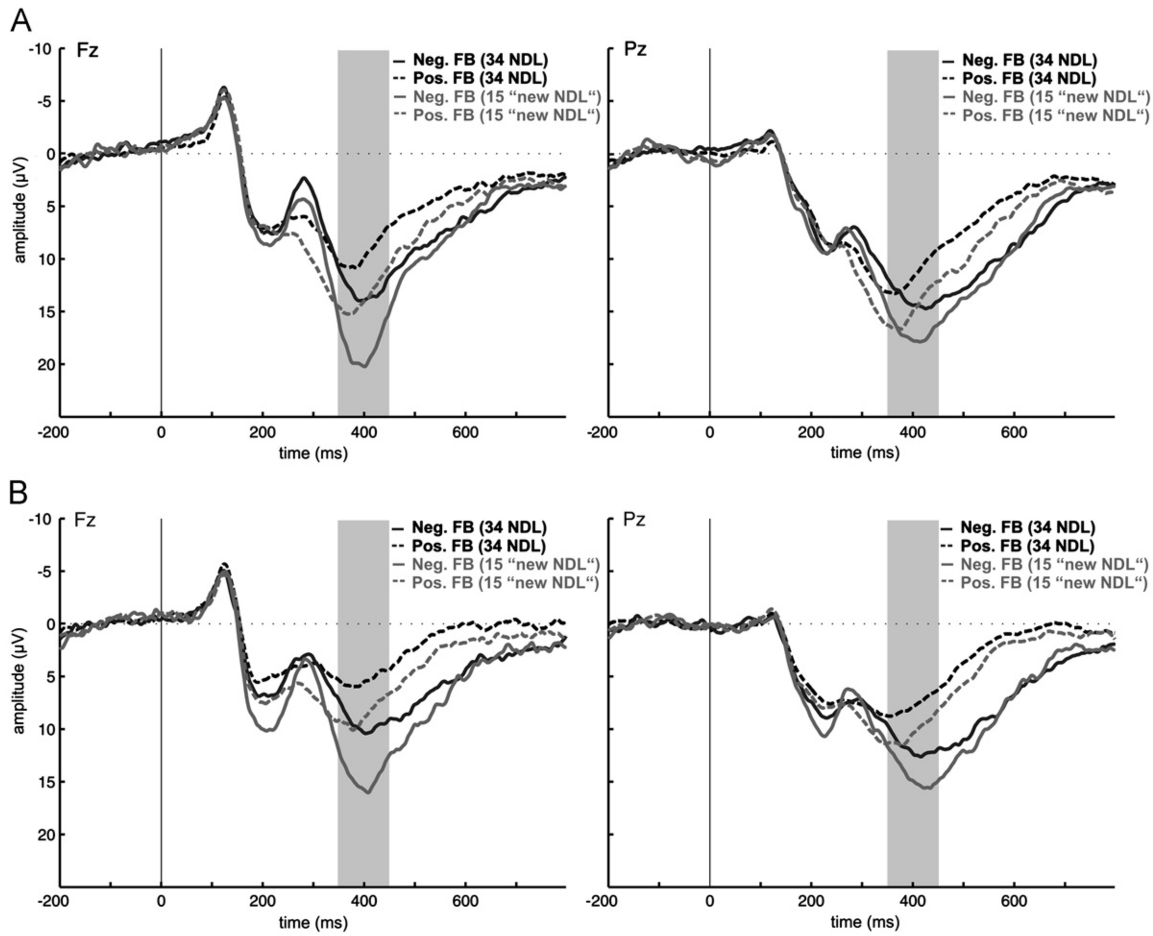

Fig. 4. ERPs at electrode sites Fz (left) and Pz (right): Grand average feedback-locked ERPs following positive (pos. FB) and negative (neg. FB) feedback in the first block (A) and the last block (B) for the 34 NDL and the 15 “new NDL” who changed strategy from the first to the last block. The time window for the P300 is shaded in light grey.

Table 3
Means with standard deviations (in brackets) for P300 mean amplitudes (in µV) in the first and last block.

First block	**Fz**		**Pz**	
Group	**Pos. feedback**	**Neg. feedback**	**Pos. feedback**	**Neg. feedback**
34 NDL	9.54 (4.55)	13.00 (5.79)	11.67 (4.27)	13.82 (4.84)
15 “new NDL”	13.69 (5.61)	18.41 (5.91)	14.87 (3.78)	16.96 (4.52)
Last block	**Fz**		**Pz**	
Group	**Pos. feedback**	**Neg. feedback**	**Pos. feedback**	**Neg. feedback**
34 NDL	5.34 (5.39)	9.41 (8.94)	7.79 (4.79)	11.71 (7.05)
15 “new NDL”	8.64 (5.60)	14.44 (6.83)	10.37 (4.42)	14.27 (6.06)

pattern again shows that the frontal P300 is larger than the parietal P300 only for negative feedback in the 15 “new NDL” (see Table 3).

3.4. Correlation analyses of strategy measures and ERP data

The post-experimental questionnaire assessed declarative knowledge about feedback probabilities in the WPT after completion of the task. We therefore correlated questionnaire data with strategy-data derived from choice performance and ERPs from the last block of trials only. For this purpose, the difference between the fit score for the non-declarative strategy and the fit score for the declarative strategy was computed for each subject (see Section 2.2.2 for details on strategy analysis). Negative values in this difference measure indicate a non-declarative strategy, whereas positive values indicate a declarative strategy, with larger absolute values indicating a stronger preference for the respective strategy.

Over all 56 subjects a weak but significant positive correlation was found between the difference score for block 4 and the sum score in the questionnaire ($r=.321$, $p=.016$), suggesting that subjects applying a more declarative strategy indeed had more explicit knowledge about the WPT. Correlation analyses between the number of correctly answered questions in the questionnaire and the frontal or parietal positive or negative P300 amplitude of the last block did not reveal any significant correlations (all $p>.190$).

Correlation analyses between strategy difference scores for the first block and frontal and parietal P300 amplitude revealed a near significant correlation with the frontal P300 amplitude after positive feedback in the first block ($p=.055$) and a near significant correlation for the parietal P300 amplitude after positive feedback in the first block ($p=.065$), but not for negative feedback (both

$p > .118$). These correlations indicate a relationship between the predominance of declarative learning and the P300 amplitude for the first block. No significant correlations were found between the difference scores for the last block and the P300 amplitudes in the last block (all $p > .370$).

4. Discussion

The present study analyzed the neural correlates of feedback processing in declarative and non-declarative learners in PCL. Subjects completed a modified version of the WPT (e.g., Gluck et al., 2002; Knowlton et al., 1994), while EEG was recorded. Based on their individual choice patterns, participants were classified as declarative and non-declarative learners, respectively. Changes in the engaged learning strategy over the course of the experiment were also taken into account. Behavioural and EEG Data were analyzed for the beginning (first block of the WPT) and the end (last block of the WPT) of the experiment and related to each other.

Participants who predominantly applied a non-declarative learning strategy were generally more successful than those subjects who engaged a declarative strategy. They responded correctly and received positive feedback more often. Contrary to our assumption, FRN amplitude was not affected by learning strategy. DL did, however, show higher frontal P300 amplitudes than NDL. In addition, P300 topography was different in DL and NDL. While the P300 was generally higher for negative feedback in both NDL and DL, the difference was more pronounced at frontal than parietal electrodes in DL but not NDL. Interestingly, some group differences in feedback coding as reflected by the P300 also appeared to persist or were even more pronounced in later stages of PCL, when the DL switched to a non-declarative learning strategy. When both the first and the last block of trials were considered, subjects who started with a declarative strategy showed a generally enhanced P300 amplitude, irrespective of electrode site. Furthermore, the pronounced P300 for negative feedback over the frontal cortex persisted throughout the task in these subjects. Across all participants, the relative contribution of the declarative learning strategy correlated positively with explicit knowledge about the WPT and tended to correlate with P300 amplitude.

Two ERP components, the FRN and the P300, have been linked to the processing of performance feedback in probabilistic learning tasks (e.g., Hajcak et al., 2007; Miltner et al., 1997). One potential reason for the lack of strategy influences on the FRN in the present study may relate to the definition of DL and NDL. In accordance with the procedure applied in previous studies (e.g., Gluck et al., 2002), learning strategy was determined based on the degree of deviation from a response pattern which would be expected for the "pure" application of a particular strategy, that is subjects differed with respect to the relative preference for one strategy over the other, but may also have used aspects of both strategies to solve the task. Similar classification procedures were also applied in a range of previous studies using the WPT (e.g., Hopkins, Myers, Shohamy, Grossman, & Gluck, 2004; Shohamy et al., 2004b). Schwabe and Wolf (2012), for example, also distinguished between two types of strategies, "simple" (corresponding to declarative in the present study) and "complex (non-declarative)" (cf. also Thomas & LaBar, 2008). Other investigators added further strategies, such as the multi-match strategy, which assumes that participants' choice frequency of a particular outcome for a particular combination of cue cards matches the outcome probability, rather than assuming optimal responding (in terms of always choosing the more probable outcome) as in the "classical" multi-cue strategy (Lagnado, Newell, Kahan, & Shanks, 2006). Intermediate strategies represent a mixture of strategies focusing on one cue card and those involving all cue cards (Meeter, Myers, Shohamy, Hopkins, & Gluck, 2006). With respect to the present FRN findings, it might be that the addition of a third, mixed strategy and the comparison of (then) more extreme groups of clear DL and NDL would have yielded FRN differences.

Different aspects have been shown to be responsible for modulations of the FRN amplitude in reward processing. For example, many studies have shown decreases in FRN amplitude with learning (e.g., Eppinger, Kray, Mock, & Mecklinger, 2008; Luque, Lopez, Marco-Pallares, Camara, & Rodriguez-Fornells, 2012), possibly reflecting decreases in motivational significance (Sailer, Fischmeister, & Bauer, 2010). The NDL of the present study showed very good performance accuracy from the beginning of the task and thus it cannot be excluded that the feedback stimuli were not very salient any more, yielding reduced FRN amplitudes. A recent study reported strategy influences on the FRN (Warren & Holroyd, 2012). However, the experimental manipulation differed from that in the present study as not differences in the type of learning, but in task involvement were examined. FRN amplitude modulations were highest in tasks involving active decision learning compared with passively watching feedback (see also Yeung, Holroyd, & Cohen, 2005).

Instead, the results of the present study may suggest that there is no strong link between implicit feedback processing and the learning strategy. Upon feedback presentation, the DA system may be automatically recruited, and the dopaminergic signals carrying reward information are propagated to the BG and the ACC (Gaspar, Berger, Febvret, Vigny, & Henry, 1989; Williams & Goldman-Rakic, 1993; for reviews on anatomical connections, see Berger, Gaspar, & Verney, 1991; Smith & Bolam, 1990). A similar suggestion has been made in a recent review on the FRN by Walsh and Anderson (2012). They distinguish between a goal-directed and habitual system controlling actions and suggest that DA neurons code prediction errors irrespective of the system controlling actions for a task at hand. The FRN as an indirect indicator of DA neuron activity only coincides with performance, however, when the habitual system is more strongly involved.

Whether or not a subject uses declarative processes in PCL may be determined by additional recruitment of other structures. For example, direct and indirect DA projections are supposed to be sent from the midbrain to the hippocampus and to the prefrontal cortex (for reviews, see Lisman & Grace, 2005; Thierry, Gioanni, Degenetais, & Glowinski, 2000). Accordingly, the P300, which has been described as an indicator of conscious cognitive processes (Ridderinkhof, Ramautar, & Wijnen, 2009; Sommer & Matt, 1990; Sommer, Matt, & Leuthold, 1990) and reflects a later and therefore probably more declarative stage of feedback processing, was larger in DL than in NDL of the present study, most prominent over the frontal cortex. This result pattern fits to findings of frontal involvement during declarative as well as classification learning (Boettiger & D'Esposito, 2005; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Halsband et al., 1998; Lupyan, Mirman, Hamilton, & Thompson-Schill, 2012; Wagner et al., 1998) and is consistent with findings on a role of prefrontal cortex in P300 generation (Parvaz, Konova, Tomasi, Volkow, & Goldstein, 2012). Prefrontal brain structures and the hippocampus are anatomically connected and interact in long-term memory formation, in the encoding and retrieval of memory contents (Cohen, 2011; for reviews, see Simons & Spiers, 2003; Thierry et al., 2000). It has to be noted, however, that, the P300 cannot generally be assigned to a single neural structure. Both amplitude and topography vary considerably depending on the task at hand (for a review, see Linden, 2005): The P300 may also be composed of different subcomponents (P3a and P3b) with different topographies (for reviews, see Hruby & Marsalek, 2003; Linden, 2005; Polich, 2007). Although it is possible that the feedback-locked P300 shares more features with one of the two subcomponents, no such distinction has been made in the context of reward processing (e.g., Bellebaum & Daum, 2008; Sailer et al., 2010; Wu & Zhou, 2009).

The described P300 differences between DL and NDL were seen during the first phase of the experiment. In accordance with previous studies on PCL (e.g., Shohamy et al., 2004b), most subjects who started with a declarative strategy in the present study switched to a non-declarative strategy during the course of the experiment. However, some differences in feedback processing between subjects persisted: The P300 was elevated in those participants who applied a declarative strategy at the beginning and then switched compared to subjects who applied a non-declarative strategy from the beginning on, albeit now over frontal and parietal cortex. It is reasonable to assume that declarative knowledge about stimulus-outcome associations was still available in subjects who switched strategy and that non-declarative aspects of learning were applied in addition. This interpretation is supported by studies showing that the BG and MTL memory systems can work in parallel during probabilistic learning (Dickerson, Li, & Delgado, 2011; Mattfeld & Stark, 2011).

Taken together, this study provides first evidence for different neural mechanisms of feedback processing in declarative and non-declarative PCL. Strategy effects were seen in ERP correlates of feedback processing, which provide a measure of brain activation with high temporal resolution. Differences between declarative and non-declarative learning did not emerge for an early BG-based ERP component, but at later, more declarative processing stages. The topography of the ERP differences may suggest a stronger prefrontal mediation of negative feedback processing in declarative learning which also persists, when subjects further optimize responding by switching to a non-declarative strategy during late phases of the task. A potential differential role of the prefrontal cortex in declarative and non-declarative feedback processing needs to be studied in the future applying techniques with a higher spatial resolution for the assessment of brain activation.

Acknowledgments

We thank the Ministry of Innovation, Science and Research of the federal state of Nordrhein-Westfalen, Germany, for supporting this research (Ministerium für Innovation, Wissenschaft und Forschung des Landes Nordrhein-Westfalen; MIWF—grant number 334-4).

Appendix A. Supplementary Information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.01.009.

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