Developmental differences in the neural dynamics of observational learning

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ABSTRACT

Learning from vicarious experience is central for educational practice, but not well understood with respect to its ontogenetic development and underlying neural dynamics. In this age-comparative study we compared behavioral and electrophysiological markers of learning from vicarious and one's own experience in children (age 8–10) and young adults. Behaviorally both groups benefitted from integrating vicarious experience into their own choices however, adults learned much faster from social information than children. The electrophysiological results show learning-related changes in the P300 to experienced and observed rewards in adults, but not in children, indicating that adults were more efficient in integrating observed and experienced information during learning. In comparison to adults, children showed an enhanced FRN for observed and experienced feedback, indicating that they focus more on valence information than adults. Taken together, children compared to adults seem to be less able to rapidly assess the informational value of observed and experienced feedback during learning and consequently up-regulate their response to both, observed and experienced (particularly negative) feedback. When transferring the current findings to an applied context, educational practice should strengthen children's ability to use feedback information for learning and be particularly cautious with negative social feedback during supervised learning.

1. Introduction

Learning through observation is a prerequisite for the acquisition of new behavior (Rendell et al., 2011) and central for educational practice (Groenendijk et al., 2013). Observational learning is of particular interest from a developmental perspective because it may serve as an important mechanism for human cognitive and social-emotional development (Marshall et al., 2011; Meltzoff et al., 2012; Nielsen and Tomaselli, 2010). Compared to learning from own experience Eppinger et al., 2009; Hämmerer et al., 2010a; van den Bos et al., 2012; van Duijvenvoorde et al., 2008), however, the underlying neural dynamics and their ontogenetic development are far less well understood. In the current study we therefore investigated developmental differences in experience-based (EL) and observational learning (OL) using an electrophysiological (i.e., event-related potential (ERP)) approach.

1.1. Neural dynamics of experience-based learning

Electrophysiological studies in adults show that the evaluation und

updating of action-outcome information during EL are reflected in the feedback-related negativity (FRN) and the feedback-related P300 (short P300 in the following). The FRN is a negative deflection in the EEG waveform that seems to be elicited in the medial prefrontal cortex (Hauser et al., 2014; Sambrook and Goslin, 2015) and that is sensitive to negative feedback (Miltner et al., 1997). The FRN is assumed to reflect an early binary evaluation of feedback along a good–bad dimension (Hajcak et al., 2006; Nieuwenhuis, 2004; Philiastides et al., 2010; von Borries et al., 2013). In addition to the FRN, performance feedback during learning is reflected in a later positive deflection, the so-called feedback-related P300, which is maximal at parietal electrodes (Polich, 2007; San Martín, 2012; Sutton et al., 1965). Recent data suggest that the P300 scales with the degree to which feedback information is used to update reward predictions during learning (Eppinger et al., 2017; Fischer and Ullsperger, 2013; Philiastides et al., 2010). Moreover, findings by Collins and Frank (2012) indicate that the updating of value predictions during learning (at least in part) depends on working memory (WM) abilities (Collins and Frank, 2012). This view is consistent with results suggesting that the P300 co-varies with individual

(A) Experimental design
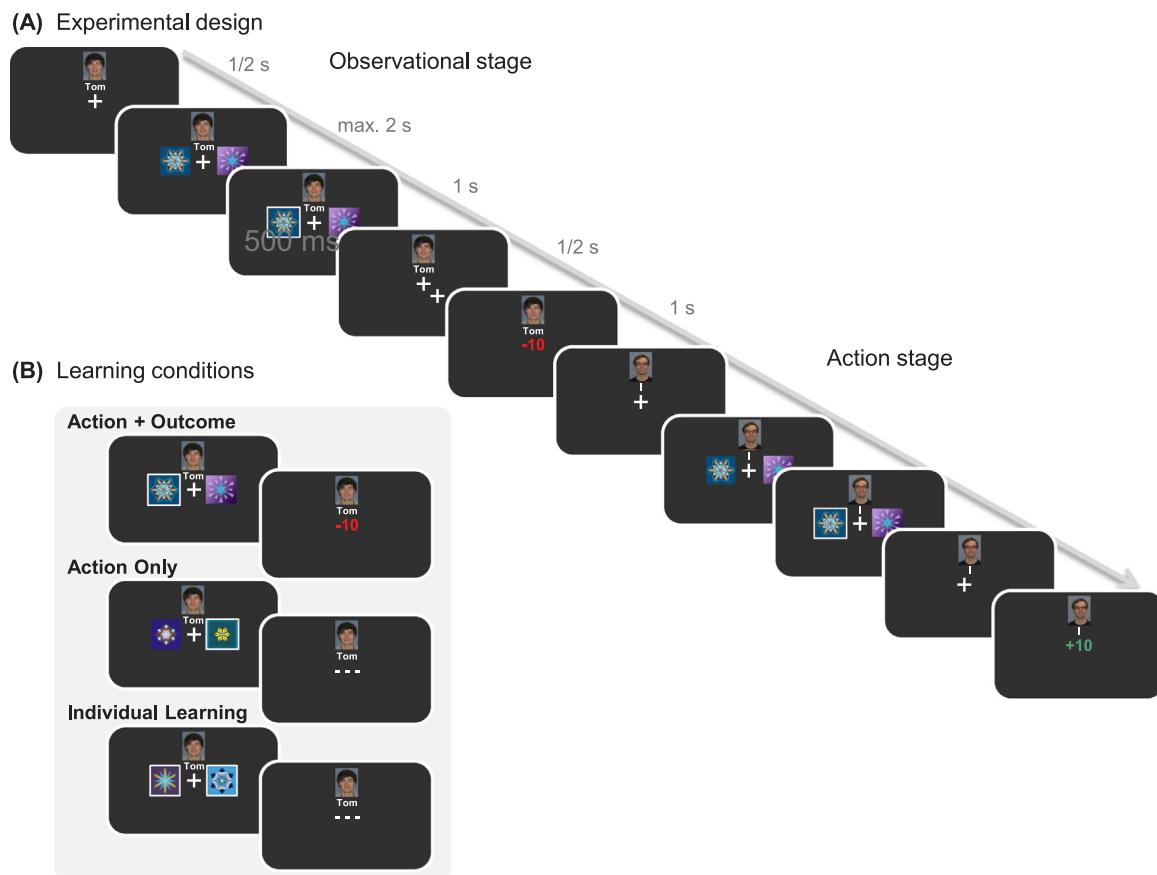
(B) Learning conditions

Fig. 1. Design. **(A)** Trial procedure. **(B)** Learning conditions: Action + Outcome (AO), Action Only (A), Individual Learning (IL).

differences in WM abilities (Bledowski, 2006; McEvoy, 1998; Morgan et al., 2008). Taken together, the P300 may reflect updating operations during reward-based learning, which seem to rely on WM.

1.2. Neural dynamics of experience-based learning across development

Developmental studies on EL suggest that, relative to adults, learning difficulties in children are associated with developmental differences in executive control (see Hämmerer and Eppinger, 2012 for review). These differences may be due to maturational changes in the prefrontal cortex (Bunge et al., 2002; Casey et al., 2005, 2000). Children (age 8–10) as compared to adults seem to have greater difficulties in extracting and using relevant (particularly negative) feedback information for learning (Crone et al., 2004; Eppinger et al., 2009; Hämmerer et al., 2010a; van den Bos et al., 2012; van Duijvenvoorde et al., 2008). Using measures of heart rate variability, Crone and colleagues (2004) showed that children have difficulties in assessing the information content of negative feedback during learning (Crone et al., 2004). In particular, their results suggest that, unlike in adults, children do not show heart rate slowing after informative compared to uninformative feedback during learning. Consistent with these findings, results of EEG studies indicate that children in comparison to adults show a reduced medial prefrontal response to incorrect choices (error-related negativity, ERN) during learning. At the same time they show an enhanced response to negative feedback (FRN) independent of whether this feedback can be used for learning or not (Eppinger et al., 2009; Hämmerer et al., 2010a). Taken together these findings suggest that the enhanced FRN in children might reflect difficulties in using negative feedback to build up an internal representation of the correct response (Eppinger et al., 2009; Ferdinand and Kray, 2014). Whereas the FRN amplitude tends to be larger in children as compared to adults, the reverse pattern is observed for the later parietal P300 component. The

parietal P300 component tends to be lower in amplitude in children as compared to adults (van Dinteren et al., 2014). Developmental differences in the P300 amplitude have been linked to changes in WM abilities with age (Polich et al., 1990). Thus, it could be that the P300 modulations in children reflect difficulties in the updating of WM representations during learning (Eppinger et al., 2017).

1.3. Neural dynamics of observational learning

Compared to EL the neural dynamics underlying OL and their developmental changes are far less well understood. In adults, the two ERP components described in EL (i.e., FRN and P300) can also be observed during OL (referred to as observational FRN (oFRN) and observational P300 (oP300), respectively; Bellebaum et al., 2010; Rodriguez Buritica et al., 2016; Yu and Zhou, 2006). However, so far, only one study investigated developmental differences in these ERP components (Rodriguez Buritica et al., 2016). In this research we examined how the similarity between the observer and the observed individual may affect learning (and the associated ERP correlates) in 8–10 year-old children (Rodriguez Buritica et al., 2016). Our findings suggest that in children the oFRN is sensitive to observed positive and negative feedback during learning. Furthermore, the degree of similarity between the observer and the observed individual influenced children's choice behavior and their oFRN amplitude. Children chose the same options selected by a child model more consistently than those selected by an adult model and their oFRN amplitude was larger after they observed a child as compared to an adult model. However, in this study, the age variable was only manipulated with respect to the to-be-observed models, but not with respect to the observers. It was therefore not possible to investigate whether and how ERP correlates of experienced and observed feedback during learning may differ between children and adults.

1.4. The current study

In this study we examined whether children and younger adults differ in their abilities to learn from experienced and observed feedback and whether these developmental differences in learning are associated with separable underlying neurophysiological mechanisms. To address these questions we used a probabilistic reward-based observational learning paradigm (Burke et al., 2010; Rodriguez Buritica et al., 2016) in combination with EEG in 8–10 year-old children and 20–30 year-old adults (see supplement for justification of the age-ranges). To vary the degree to which subjects could learn from social information, we manipulated the amount of observable information across the three learning conditions (Fig. 1B). In the individual learning (IL) condition participants had to learn their own action outcomes, that is, they received no social information. In the action only (A) condition they could learn from their own action outcomes and, in addition, could observe the actions of the other individual. Finally, in the action +outcome (AO) condition subjects could learn from their own action outcomes, as well as from the actions *and* outcomes of the other individual. To separately assess how observed actions and outcomes may affect subject's actions, we included two different observational learning conditions (i.e., A and AO). The IL condition served as a baseline condition (i.e., did not involve social information).

Based on prior work (Burke et al., 2010; Rodriguez Buritica et al., 2016), we predicted that learning performance should scale with the amount of observable information.[1] Learning performance should be lower in children as compared to adults. Furthermore, we expected that learning in children should be associated with a greater sensitivity to observed as well as experienced negative feedback, as reflected in enhanced medial prefrontal (FRN) activity (Ferdinand and Kray, 2014). Based on our own prior work using the same paradigm, we predict that in children medial prefrontal brain responses to external feedback information should *not be* modulated by its relationship to one's own action (Rodriguez Buritica et al., 2016). In contrast, in adults medial prefrontal brain responses to external feedback information should vary with its relationship to one's own action (Bellebaum et al., 2010; Yu and Zhou, 2006). Thus, the FRN and oFRN should not differ in amplitude in children, whereas in adults the oFRN should be reduced compared to the FRN. Based on previous results of a meta-analysis on the life-span development of the P300 (van Dinteren et al., 2014), we expected smaller P300 components during the processing of observed and experienced feedback in children compared to adults. Furthermore, in line with the work by Collins and Frank (2012) as well as Polich and colleagues (1990) we expected that learning related changes in the P300 should be associated with WM abilities in both age groups.

2. Methods

2.1. Participants

Twenty-three adults between 20 and 30 years of age and 24 children between 8 and 10 years of age participated in the study (see supplements for justification of the sample size). Data of one child were excluded from further analyses, due to technical problems during data collection. Data from another child had to be excluded because the individual event-related potential (ERP) components of interest differed more than three standard deviations from the group mean. The effective sample of the study consisted of 23 adults (11 female, mean age = 23.52, SD = 2.81) and 22 children (10 female, mean age = 9.05, SD = 0.79). All participants were right-handed (Oldfield, 1971), had normal or corrected-to-normal vision and no neurological or psychological disorders. Prior to the experiment we obtained informed consent

from the participants and their parents (in case of children). The study was approved by the Ethics Committee of the Max-Planck-Institute for Human Development, Berlin. Subjects participated in two experimental sessions: a behavioral group session (together with same-aged participants) in which we assessed psychometric covariate measures and an individual EEG session in which we assessed observational learning performance. The participants received a compensation of 14 Euro for the first and 24 Euro for the second session.

To ensure the age representativeness of our sample, general cognitive abilities were assessed using two psychometric tests that have been used in previous large scale assessments of fluid and crystallized abilities across the lifespan (Li et al., 2004). Processing speed (a measure of fluid abilities) was assessed using the Identical Pictures Test (Ekstrom et al., 1976). Verbal knowledge was assessed using a modified version of the Spot-the-Word Test (Lehrl, 2005; Lindenberger et al., 1993). In addition to these measures we used a modified version of the spatial n-back task described in detail by Li et al. (2008) to investigate WM abilities (Li et al., 2008). In this task, a sequence of black circles appeared on a three-by-three grid. Participants were asked to respond with one key press if the position of the circle matched the one they saw two/three trials before and another key if there was no match. For further details see by Li et al. (2008). Finally, reasoning abilities were assessed Raven's Progressive Matrices for adults and the Colored Progressive Matrices for children (Raven et al., 1998). Children differed from adults in accuracy on the WM test (children: $M = 0.64$ (SD = 0.21), adults: $M = 0.84$ (SD = 0.08); $F(1, 43) = 18.47$, $p < .001$, $\eta_p^2 = .3$). Children had lower scores than adults on the Identical Pictures (children: $M = 20.32$ (SD = 2.95), adults: $M = 32.83$ (SD = 3.63); $F(1, 43) = 160.24$, $p < .001$, $\eta_p^2 = .79$) and Spot-the-Word test (children: $M = 2.09$ (SD = 1.49), adults: $M = 17.57$ (SD = 6.77); $F(1, 43) = 100.55$, $p < .001$, $\eta_p^2 = .7$).[2] These age differences are consistent with previous findings from larger population-based lifespan samples (Li et al., 2004). One-way analysis of variance (ANOVA) yielded no age differences in the mean IQ percentiles, $F(1, 43) = 0.72$, $p = .4$, $\eta_p^2 = .02$ (children: $M = 63.23$ (SD = 30.53), adults: $M = 70.61$ (SD = 27.71)). Estimated mean intelligence (Ravens) scores were 105 for the 8- to 10-year-olds and 108 for the 20- to 30-year-olds.

2.2. Experimental design and procedure

2.2.1. Design

The task (controlled by using the psychtoolbox for Matlab; psychtoolbox, Brainard, 1997) involved three learning conditions: AO, A and IL. As shown in Fig. 1A, participants were asked to choose one of two abstract stimuli (generated with Vector Snowflake Application; Windell, 2008) that may result in a positive or negative feedback.

Within each stimulus pair, one stimulus was associated with a high probability (80% rewards, 20% losses) and one associated with a low probability (20% rewards, 80% losses) of gaining points. In the two observational learning conditions (i.e., A and AO), prior to making their own choices, the computer program presented the participants a picture of the face of a randomly chosen sex- and age-matched "model player"[3] (i.e., another participant who took part in the same first group session of cognitive covariate assessments together with the to be tested participant). The participants were told that the other player had already performed the task and that they would observe recorded choices of this

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[1] We defined learning performance as the accuracy difference between the averaged first five trials and the averaged last five trials within each block.

[2] Identical Pictures and Spot-the-Word scores (see Table S1 in the supplemental material) were comparable to what has been obtained in previous studies (see Hämmerer et al., 2010b; Störmer et al., 2014).

[3] We assessed participants' subjective ratings regarding the model player in a post-questionnaire after the main experiment. Participants had to rate feelings of similarly and sympathy regarding the model player (on a scale ranging from 1 to 3). We did not find significant age-differences in these ratings (Mann-Whitney Test: p's > 0.1).

other player. In fact, however, the to be observed behavior was computer-generated (see supplemental information and Fig. S1 for further details). The participants were debriefed about the cover story after the experiment.

2.2.2. Trial procedure

As shown in Fig. 1A, the participants first saw in the *observational stage* the picture and the name of the model player for 500 ms. They were told that they had to press the response key within 2 s (in all three learning conditions) to see the information of the model player (to ensure that they paid attention during the task). Then the model player's choice was indicated using a colored frame (1 s), which was followed by a fixation cross for 500 ms and the outcome (i.e., reward/ loss of 10 points) for 1 s. The position of the stimuli was randomized across and within trials and blocks. The amount of information about the model behavior differed between the three different learning conditions: In the AO condition, full information about the choices and outcomes of the model players was provided (see Fig. 1B). In the A condition, information about the choices of the model players was shown but not information about the associated choice outcomes (see Fig. 1B). In the IL condition, no information about the model player's choices and the outcomes was given (see Fig. 1B). The observational stage was followed by an *action stage* indicated by the picture of the participant (displayed for 500 ms). Here, participants had to decide between the same pair of stimuli within 2 s. Then the participants' choice was indicated for 1 s using a colored frame, followed by a fixation cross for 500 ms and the outcome (i.e., reward/loss of 10 points) for 1 s. Each block included 10 trials per learning condition. Each condition involved one stimulus pair (i.e., 3 different pairs per condition and block) resulting in 30 trials per block. The order of the learning conditions was pseudo-randomized across the 12 blocks.

2.3. Electrophysiological recording

While the participants performed the task EEG was recorded continuously (Brain Amp DC, BrainVision Recorder software) from 64 Ag/ AgCl electrodes (American Electroencephalographic Society, 1994) in an elastic cap (Braincap, BrainVision). The sampling rate was 1000 Hz, with a bandpass filter (0.01–100 Hz) applied. EEG recordings were referenced online to the right mastoid. Vertical and horizontal eye movements were recorded from electrodes placed next to each eye and below the eye. Impedances were kept below 5 kΩ.

2.4. Data analysis

2.4.1. Behavioral data

The analysis of variance was based on accuracy (proportion correct [i.e., how often the 80% reward option was selected]) and statistical analyses were performed using SPSS (IBM Corp. Released, 2013). To analyze learning effects, we split each learning block into two halves[4] (i.e., first 5 trials and last 5 trials) and averaged the block halves across the 12 blocks and separately for each condition. This procedure resulted in a total trial number of 60 trials (i.e., 5 trials × 12 blocks) per subject and per block half. Responses faster than 100 ms (children: 4.22%, adults: 0.09%) and exceeding the response deadlines (2 s) in the action stage (children: 5.31%, adults: 1.38%) were excluded from further analyses. The remaining accuracy data involved an average of $M = 54.16$, $SD = 3.53$ trials per block half in children and of $M = 59.13$, $SD = 1.88$ trials per block half in adults. Accuracy was analyzed using a repeated-measures analysis of variances (ANOVA) with the between-

subject factor age group (adults, children), and the within-subject factors learning condition (AO, A, IL) and block half [first (BH1), second (BH2)].

2.4.2. EEG Data

The recorded data were re-referenced offline to averaged mastoids and further analyzed using Brain Vision Analyzer software (Brain Products, Germany). The data were bandpass-filtered in a range of 0.01–20 Hz (according to suggestions of Luck, 2005) and segmented into epochs (−200 to 700 ms) after the observed and experienced feedback onset. Ocular artifacts were removed using a linear regression approach (Gratton et al., 1983). Additional artifacts were rejected based on a maximum admissible voltage step (50 μV), and by a maximum admissible difference between 2 values on a segment (200 μV). The data were baseline corrected (200 ms pre-stimulus). For eight participants, the data from one to seven malfunctioning electrodes (AF7, AF8, FP1, FP2, FPz, FP2, F8, FT8, P1, P2, PO7, O1, O2, Oz) were replaced via spherical spline interpolation (Perrin et al., 1989).[5] ERPs were averaged separately for all channels per condition and per participant first, and then averaged across participants. The FRN was determined in all three learning conditions (i.e., AO, A and IL). The oFRN was measured in the AO condition. As suggested by the results of a meta-analysis we analyzed the FRN component at electrode FCz (Sambrook and Goslin, 2015). In line with findings of a recent meta-analysis across the lifespan, P300 amplitudes were measured at electrode Pz (see van Dinteren et al., 2014). Difference waves were calculated by subtracting the ERPs following rewards from those following losses.

As shown in Figs. 3A and 5A FRN and oFRN peak latencies differed between age groups. To evaluate these effects we determined the peak latencies of FRN and oFRN for each participant and each valence (i.e., reward, loss). We then compared latencies differences for FRN and oFRN using separate repeated-measures ANOVA designs with the between-subject factor age group (adults, children), and the within-subject factors valence (reward, loss). The analysis revealed main effects of age group (p's < 0.001, η_p^2's > 0.3) for both components, but no main effects of valence (p's > 0.1). To account for the significantly different peaks of childrens' and adults' FRN and oFRN we adjusted the time windows accordingly. The components were measured and analyzed as mean amplitudes within an age-group specific 50 ms time window centered on the peaks of the components (Reinhart and Woodman, 2014) at electrode FCz (adults: FRN (248–298 ms) & oFRN (275–325 ms); children: FRN (317–367 ms) & oFRN (327–377 ms)).

Similar to the FRN/oFRN, visual inspection of the EEG waveforms of the P300 and oP300 (see Figs. 3B and 5B) suggested differences in peak latencies between groups and additionally between valences. To verify this result we compared individual peak latencies of P300 and oP300 using separate repeated-measures ANOVA designs with the between-subject factor age group (adults, children), and the within-subject factors valence (reward, loss). The analyses showed main effects of age (p's < 0.001, η_p^2's > 0.3), and of valence (p's < 0.01, η_p^2's > 0.2) for both components (although P300 and oP300 when directly compared, they did not differ in age and valence from it each other).[6] To account for the significantly different peaks for rewards and losses in the P300

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[4] Please note that the block half procedure was necessary to maintain a reasonable number of trials for the individual averages of the event-related ERPs (Larson et al., 2010; Marco-Pallares et al., 2010; Pontifex et al., 2010; Olvet and Hajcak, 2009).

[5] Exclusion of the data of the eight participants with malfunctioning electrodes leads to qualitatively similar results as reported in the paper (see supplements for further details). Our results for all ERPs and oERPs are unaffected by the exclusion of the data of the eight participants with malfunctioning electrodes (see supplements for further details).

[6] To investigate whether the valence specific time windows within P300 and oP300 differ in latency, we analyzed P300 and oP300 latencies using a valence (reward, loss) × agency (P300, oP300) ANOVA design with age groups as the between subject factor. Neither main effects nor interactions reached significance ($p \geq .05$). Thus, there are no statistically significant latency differences between age groups and valences for the P300 and oP300.

and oP300 we adjusted the time windows accordingly. The components were measured and analyzed as mean amplitudes (please see supplements for a different approach) within an age-group and valence specific 100 ms time window centered on the peaks of the components (adults: reward P300 (309–409 ms) & loss P300 (325–425 ms); reward oP300 (313–413 ms) & loss oP300 (366–466 ms); children: reward P300 (443–543 ms) & loss P300 (472–572 ms); reward oP300 (484–584 ms) & loss oP300 (472–572 ms)) (see Figs. 3B and 5B).

Statistical analyses of the EEG data were performed using SPSS (IBM Corp. Released, 2013). To account for differences in the frequencies of rewards and losses we equated the trial numbers by randomly selecting subsets of trials (per learning condition and block half in every subject). ERP averages for the FRN and P300 involved 22 trials, whereas ERP averages for the oFRN and oP300 involved 19 trials. Given that we were interested in valence-dependent learning effects in the ERPs rather than overall amplitude changes with learning, we focused the analyses of ERP components on interactions including the factor valence. To understand the resulting interactions separate ANOVAs and paired samples t-tests were conducted. Effect sizes (partial eta squared, η_p^2) are reported, and Pearson's r was computed for correlation analysis. The Greenhouse-Geisser correction for non-sphericity (Geisser and Greenhouse, 1958) and Bonferroni-corrections were applied when necessary and the corrected p-values are reported.

3. Results

3.1. Behavioral results

Accuracy was analyzed using a condition (AO, A, IL) x block half (BH1, BH2) ANOVA design with age group (adults, children) as the between-subject factor.[7] Both age groups benefited (in terms of accuracy) from integrating the observed information into their own choices (learning condition: $F (2, 86) = 27.09, p < .001, \eta_p^2 = .39$). As shown in Fig. 2, accuracy was greater in the AO than the other learning conditions (two-tailed t-test, p's < 0.001; Bonferroni-corrected). However, accuracy did not differ significantly between the A and IL condition ($p > .1$). Across age groups, performance increased in the second as compared to the first block half (block half: $F(1, 43) = 72.39, p < .001, \eta_p^2 = .63$).

Between age groups, adults performed significantly better than children (age group: $F (1, 43) = 28.94, p < .001, \eta_p^2 = .40$) and, across conditions, showed greater learning effects (i.e., by comparing the first and the second block half; age group × block half: $F(1, 43) = 15.42, p < .001, \eta_p^2 = .26$). Performance in the two age groups differed from chance in both block halves (one-sampled t-Tests: p's < 0.001).

Most interestingly, we found a significant three-way interaction between age group, learning condition and block half ($F (2, 86) = 8.18, p < .001, \eta_p^2 = 0.16$). Separate analyses for each age group showed that learning effects differed between conditions in adults, (learning condition x block half: $p = .001, \eta_p^2 = 0.27$), but not in children, (learning condition × black half: $p = .14$). As displayed in Fig. 2 and in contrast to children younger adults showed greater accuracy in the AO in the first block half as compared to the other two learning conditions. No further main effects or interactions reached significance (p's > 0.1).

3.2. ERPs to experienced feedback

ERPs to experienced feedback were analyzed in a condition (AO, A, IL) x valence (reward, loss) × block half (BH1, BH2) ANOVA design with age group (adults, children) as the between-subject factor. The results for the FRN and P300 will be reported separately in the following.

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[7] The results of a mixed-effects logistic regression analysis (see supplements and Table S1) qualitatively resembled the results of the repeated-measures ANOVA based on block halves.

3.2.1. FRN

As shown in Fig. 3A, across age groups, the FRN was significantly larger (i.e., more negative going) for losses than for rewards (valence: $F (1, 43) = 25.14, p < .001, \eta_p^2 = .37$), and across conditions, FRN amplitudes were larger for children than adults (age group: $F (1, 43) = 42.65, p < .001, \eta_p^2 = .49$). No further main effects or interactions reached significance (p's > 0.18).

3.2.2. Feedback-related P300

Comparing P300 and oP300 across age groups, we found significant main effects of valence (i.e., larger P300/oP300 for losses as compared to rewards; $F(1, 43) = 6.53\ p < .01, \eta_p^2 = .13$). The difference between losses and rewards varied, however, between conditions (condition × valence, $F(2, 86) = 7.12, p = .002, \varepsilon = 0.93, \eta_p^2 = .14$). Separate analyses for reward and loss trials showed a condition effect for both trial types ($p = .009, \varepsilon = 0.95, \eta_p^2 = .11$, for reward trials and $p = .004, \eta_p^2 = .12$, for loss trials). T-tests between conditions that were performed separately for the two valences showed that the P300 to rewards decreases with increasing amounts of observable information (two-tailed t-test, AO – (A + IL): $p = .02$; A – IL: $p = .047$), whereas as the P300 response to losses increases, two-tailed t-test, AO – (A + IL): $p = .023$; A – IL: $p = .018$. Thus, the P300 difference between losses and rewards increased with the amount of information that could be used for learning (see Fig. 4A).

As shown in Fig. 3B, the P300 was larger for adults compared to children (age group: $F(1, 43) = 23.12, p < .001, \eta_p^2 = .35$). Moreover, as for performance, we obtained a significant interaction between the factors age group, valence, and block half ($F(1, 43) = 8.91, p = .005, \eta_p^2 = .17$). Separate analyses for the factor valence revealed a significant interaction between block half and age group for rewards ($p = .001, \eta_p^2 = .25$), but not for losses ($p = .3$). As displayed in Fig. 3B, comparisons between block halves revealed a decrease in the P300 to rewards as accuracy between the block halves increases in adults (two-tailed t-test, $p < .001$), but not in children ($p = .15$). No further main effects or interactions reached significance (p's > 0.1).

3.2.3. Correlational effects

As shown in 4B, the P300 difference between losses and rewards correlated positively with accuracy in both age groups (adults: $r (23) = 0.46, p = .03$, children: $r(22) = 0.5, p = .01$). No such effects were observed for the FRN (p's > 0.4). This result suggests that the P300 but not the FRN reflects the degree to which individuals update outcome predictions. Moreover, in adults greater P300 amplitude differences to rewards between block halves were correlated with better behavioral learning performance (i.e., accuracy difference between block halves) ($r(23) = -0.51, p = .01$) (see Fig. 4C) and higher WM scores (accuracy) ($r(23) = -0.49, p = .02$) (see Fig. 4D).

In children the correlations were not significant, neither for behavioral learning effects ($r(22) = 0.02, p = .94$) nor for WM scores ($r (22) = 0.23, p = .31$). Fisher's Z test showed that the correlation coefficients between both age groups were significantly different from each other (two-tailed test for learning: $z = -1.82, p = .068$ & WM: $z = -2.4, p = .02$).

3.3. ERPs to observed feedback

ERPs to observed feedback were analyzed in the AO condition as a valence (reward, loss) x block half (BH1, BH2) ANOVA with age group (adults, children) as the between-subject factor. The results for the oFRN and oP300 will be reported separately in the following.

3.3.1. OFRN

As shown in Fig. 5A we found significant main effects of age group and valence (p's ≤ 0.009, η_p^2's > 0.15) as well as a significant age group by valence interaction, $F(1, 43) = 6.55, p = .01, \eta_p^2 = .13$. The oFRN was larger for losses than rewards in children ($t(21) = -3.83$,
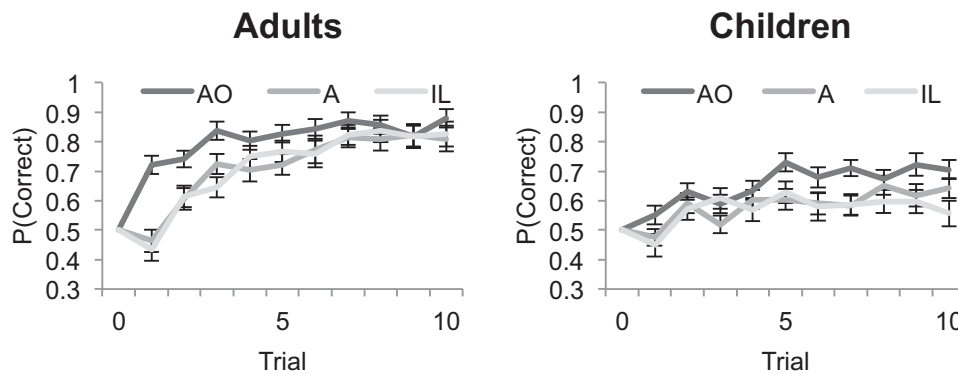
Adults

Children

Fig. 2. Behavioral learning & condition effects. Accuracy in proportion correct separately for age group and learning condition displayed per trial.

$p = .001$), but not in adults, $(p = .59)$ (see Fig. 5A). No further main effects or interactions reached significance (p's > 0.5).

3.3.2. Feedback-related oP300

Similar to the P300 we found a significant interaction between the factors age group, valence, and block half (see Fig. 5B) in the oP300 (F (1, 43) = 4.57, $p = .04$, $\eta_p^2 = .1$). Separate analyses for the factor valence showed a significant interaction between block half and age group for rewards ($p = .06$, $\eta_p^2 = .08$), but not for losses ($p = .4$). As shown in Fig. 5B, in adults the P300 to rewards decreased from block half 1 to block half 2, suggesting that the component decreases as performance increases during learning, two-tailed t-test, $p = .01$. This was not the case in children ($p = .41$). As shown in Fig. 5B, comparisons between block halves revealed a decrease in the oP300 to rewards as a function of learning in adults (two-tailed t-test, $p = .01$), but not in children ($p = .41$). No further main effects or interactions reached significance (p's > 0.2).

3.3.3. Correlational effects

As shown in Fig. 6 the learning effects in the oP300 to rewards (i.e., amplitude difference between block halves) were positively correlated with behavioral learning effects (i.e., accuracy difference between block halves) in the AO condition ($r(23) = -0.59$, $p = .003$) in adults, but not in children ($r(22) = 0.15$ $p = .5$). For the oFRN no significant correlations were observed (p's > 0.15). Similar to our findings in the P300 to experienced feedback this result suggests that the oP300 (but not the oFRN) reflects the degree to which individuals can use information during OL to update feedback predictions (see Fig. 6). Correlation coefficients for the reward oP300 differed significantly between the two age groups (Fisher's Z, two-tailed: $z = -2.61$, $p = .009$).

3.4. Comparison between ERPs to experienced and to observed feedback

In a final analysis step we compared ERPs to experienced feedback (FRN, P300) and ERPs to observed feedback (oFRN, oP300). ERPs to experienced and observed feedback were analyzed as a valence (reward, loss) x agency (FRN, oFRN)/ agency (P300, oP300) ANOVA design with age group as the between-subject factor.

3.4.1. FRN vs. oFRN

FRN and oFRN were both larger for losses as compared to gains (valence: $F(1, 43) = 43$, $p < .001$, $\eta_p^2 = .41$) and for children as compared to adults (age group: $F(1, 43) = 26.46$, $p < .001$, $\eta_p^2 = .38$). Moreover, age group and agency interacted significantly, $F(1, 43) = 17.53$, $p = .001$, $\eta_p^2 = .29$. Separate analyses for the two age groups showed larger FRNs to experienced than observed feedback in adults (p's < 0.001), but not in children (p's > 0.21). Moreover, we found an significant age group x valence interaction, $F(1, 43) = 8.18$, $p = .007$, $\eta_p^2 = .16$. Separate comparisons for the factor valence showed larger

(experienced and observed) FRN responses for children compared to adults for rewards ($p < .001$, $\eta_p^2 = .31$) as well as losses ($p < .001$, $\eta_p^2 = .4$). Children showed a larger (experienced and observed) FRN response to losses than rewards as compared to adults (t-Test on differences between losses and rewards, $p = .007$).

3.4.2. P300 vs. oP300

Comparing P300 and oP300 across age groups, we found significant main effects of valence (i.e., larger P300/oP300 for losses as compared to rewards; $F(1, 43) = 6.53$ $p < .01$, $\eta_p^2 = .13$), age ($F(1, 43) = 6.53$ $p < .01$, $\eta_p^2 = .19$) and agency ($F(1, 43) = 50.97$ $p < .001$, $\eta_p^2 = .54$). Moreover, age group and agency interacted significantly for the P300/ oP300, $F(1, 43) = 25.64$, $p < .001$, $\eta_p^2 = .37$. Separate analyses for the two age groups showed larger P300 than oP300 for adults ($p < .001$), but not for children ($p = .26$).

4. Discussion

In this age-comparative study we used an observational learning paradigm (Burke et al., 2010; Rodriguez Buritica et al., 2016) to compare behavioral and electrophysiological markers of experience-based and observational learning in 8–10 year old children and younger adults. Although both age groups benefitted from information about the other's actions and outcomes during learning, adults learned much faster from vicarious information (see Fig. 2). The ERP results indicate that these age differences in observational learning are associated with a developmental shift in the processing of experienced and observed feedback during learning: Children are less able than adults to use experienced feedback during learning. This effect is further exaggerated when learning from observed information. In contrast, young adults are more efficient in integrating experienced and observed feedback information during learning.

### 4.1. Benefits of observing others' feedback for learning

In line with previous developmental studies (Crone et al., 2004; Eppinger et al., 2009; Hämmerer et al., 2010a; van den Bos et al., 2012; van Duijvenvoorde et al., 2008), adults performed better than children and showed more learning than children across all conditions (see also Fig. 2). As hypothesized, both age groups benefited from observing the actions *and* outcomes of the other player (i.e., in the AO condition), in line with previous studies (Burke et al., 2010; Rodriguez Buritica et al., 2016). However, this effect was exaggerated in younger adults, who showed rapid learning in the AO condition, whereas children did not show this effect. In line with recent findings on developmental differences in behavioral learning strategies (Decker et al., 2016), children might be less able than adults to use the full information of the other player in the AO condition to form and test hypotheses about their own outcomes. Previous studies refer to this type of learning as goal-directed
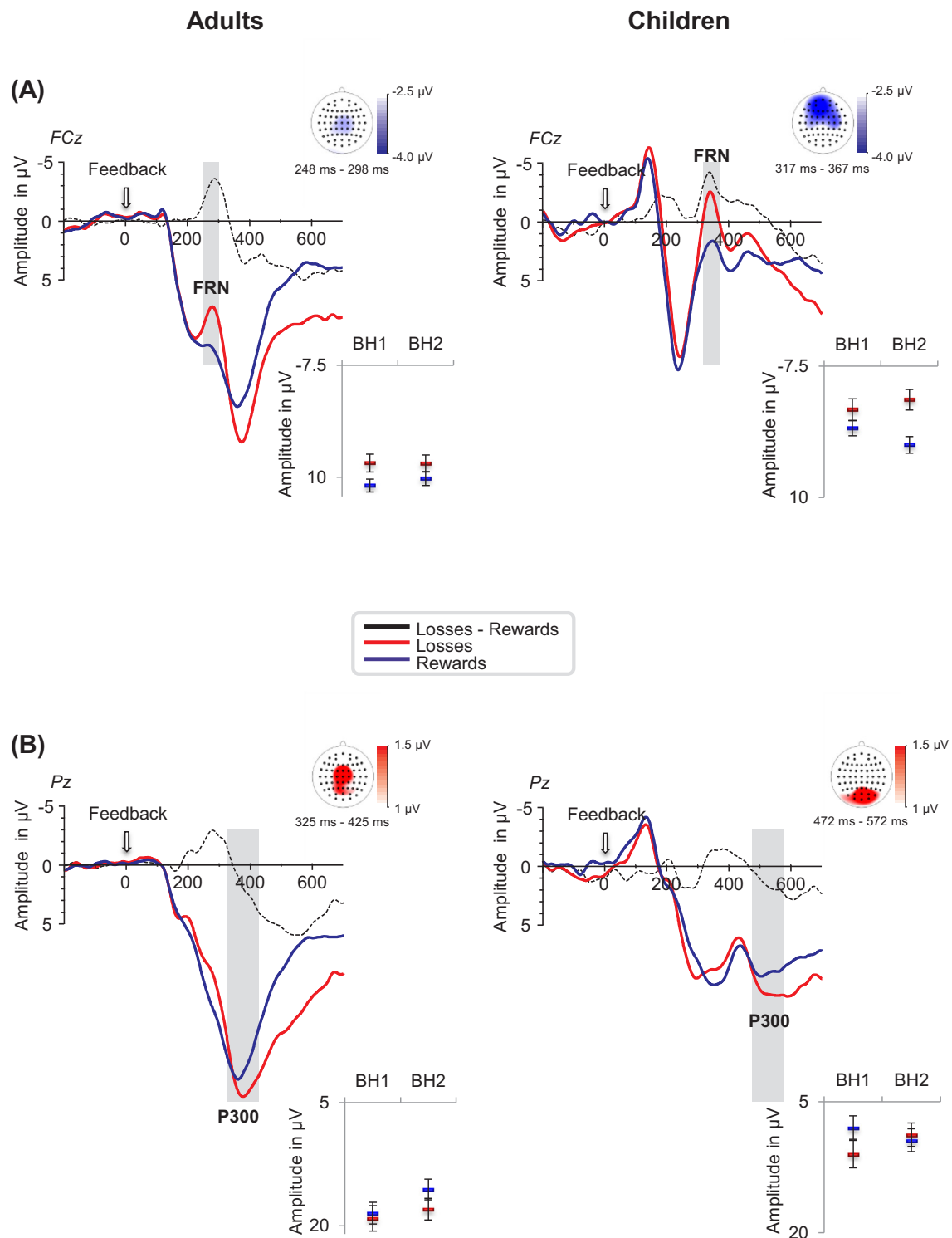
Fig. 3. ERPs associated with experienced feedback. Grand averages shown for losses (red line) and rewards (blue line) for **(A)** the FRN displayed at FCz and **(B)** the P300 displayed at Pz separately for both age groups, as well as learning related changes for losses and rewards separately for both block halves (BH1 and BH2). The topographic maps display the difference (black line) between losses and rewards for the FRN (within 50 ms) and P300 (within 100 ms).

or model-based learning (Daw et al., 2011; Eppinger et al., 2013; Otto et al., 2013). This type of learning is driven by internal goal representation, which include knowledge of the environmental structure that can be used for learning (Daw et al., 2005; Doll et al., 2012). The findings by Decker and colleagues (2016) suggest that the ability to use such learning strategies emerges around adolescence (see also Li and Eppinger, 2016). One cognitive ability that has been linked to model-

based learning is WM capacity (Eppinger et al., 2013; Otto et al., 2013). In line with these findings it could be argued that developmental differences in WM functions (Fry and Hale, 1996; Kwon et al., 2002) might be one of the primary sources of the developmental differences in OL.

Adults

Children

P300 valence effects

(A)

(B)

P300 learning & WM effects

(C)

(D)
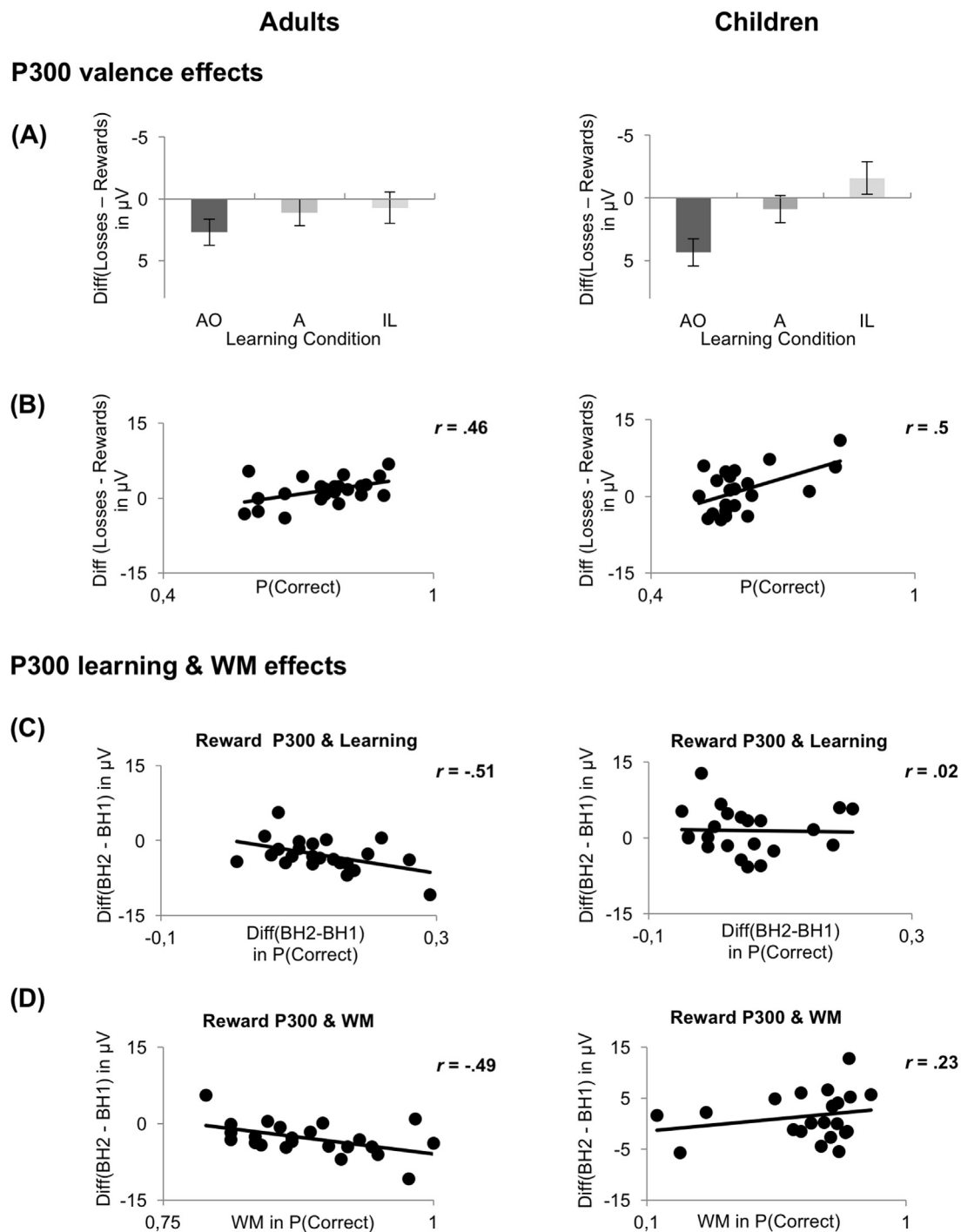
Fig. 4. (A) & (B) P300 valence effects. **(A)** Amplitude difference for the P300 between losses and rewards separately per age group and learning condition. **(B)** Scatter plots illustrating the correlation of proportion of correct choice on the x-axis and the mean P300 amplitude difference between losses and rewards on the y-axis separately for the two age groups. **(C) & (D)** P300 learning & WM effects. Scatter plots illustrating the correlation between **(C)** difference score of proportion of correct choice (second – first block half) & **(D)** proportion correct in the WM task on the x-axis and the difference score of the mean P300 amplitude to rewards (second – first block half) on the y-axis separately for the two age groups.

4.2. Developmental differences in the reactivity to feedback

In line with previous developmental findings we observed a larger FRN for losses compared to rewards and for children compared to adults (see Fig. 3A), suggesting that children react more strongly to external feedback than adults (Eppinger et al., 2009; Hämmerer et al., 2010a).

Although the FRN has been reported to have larger amplitudes in response to infrequent compared to frequent stimuli (see San Martín, 2012 for a review), this view is inconsistent with our current data: If our FRN effects were _only_ related to the probability of the outcomes, we would expect, given the difference in performance in the two groups and the resulting trial numbers, to see greater FRN amplitudes for losses as compared to gains in adults than children, as the higher performance in adults resulted in receiving more rewards than losses as compared to children. This is clearly not the case for the FRN (see Fig. 3A). Additionally, we found no evidence for valence by condition or age by condition interactions in the FRN. This corroborates several previous
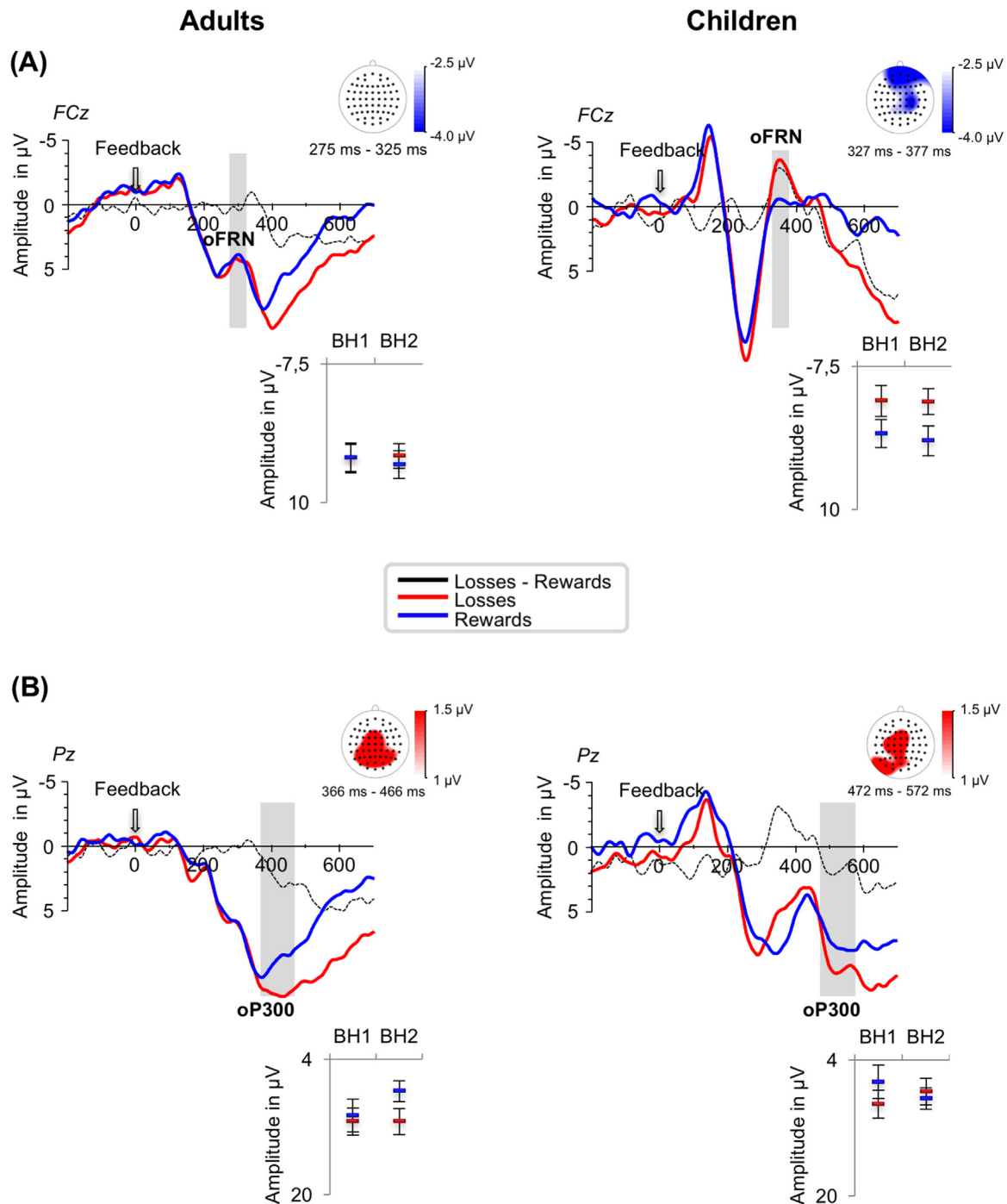
Fig. 5. ERPs associated with observed feedback. Grand averages shown for losses (red line) and rewards (blue line) for **(A)** the oFRN displayed at FCz and **(B)** the oP300 displayed at Pz separately for both age groups, as well as learning related changes for losses and rewards separately for both block halves (BH1 and BH2). The topographic maps display the difference (black line) between losses and rewards for the oFRN (within 50 ms) and oP300 (within 100 ms).

results indicating that the FRN reflects a rapid and relatively coarse evaluation of events along a valence (good vs. bad) dimension (Eppinger et al., 2008; Hajcak et al., 2006; Hämmerer et al., 2010a). In line with the findings in the FRN, children showed a larger oFRN than adults when observing the outcomes of others' actions. When comparing oERPs to ERPs, children's ERP responses to observed outcomes were similar in magnitude to their ERPs to experienced feedback (see Figs. 3 and 5). In contrast, in adults the ERPs to observed outcomes were overall significantly smaller than the ERPs to experienced feedback (Bellebaum et al., 2010). These findings are consistent with the general notion that children compared to adults are more susceptible to

external (and especially to negative) feedback information during learning than adults (Crone et al., 2004; Eppinger et al., 2009; Ferdinand and Kray, 2014; Hämmerer et al., 2010a; Rodriguez Buritica et al., 2016; van den Bos et al., 2012; van Duijvenvoorde et al., 2008). Moreover, they extend this notion by suggesting that this greater sensitivity to external feedback in children is also found when they observe feedback that other individuals receive (Rodriguez Buritica et al., 2016). Most interestingly, the oFRN in children differentiated between losses and rewards (see Fig. 5A). This was not the case in adults, indicating that the valence information of observed feedback is less salient to them (see Fig. 5A). Previous findings in adults and children
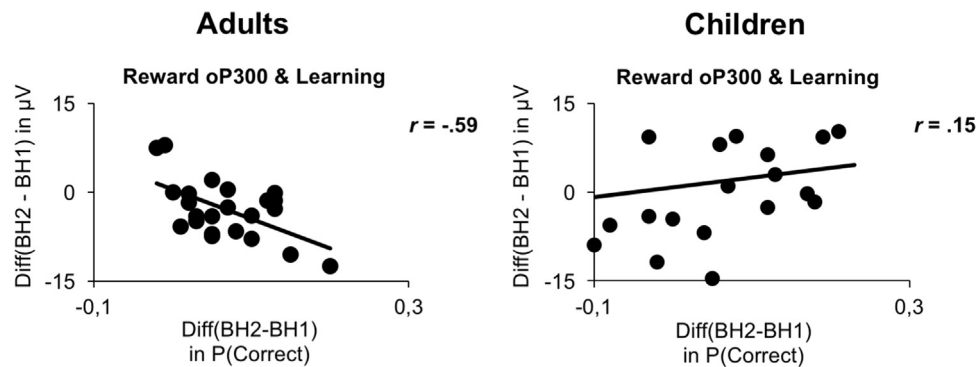
Adults

Reward oP300 & Learning

Children

Reward oP300 & Learning

Fig. 6. oP300 correlational effects. Scatter plots illustrating the correlation between difference score of proportion of correct choice (second – first block half) on the x-axis and the difference score of the mean oP300 amplitude to rewards (second – first block half) on the y-axis separately both age groups.

indicate that the differentiation between rewards and losses in the FRN decreases as task performance increases (Eppinger et al., 2008, 2009). Eppinger et al., (2008, 2009) suggested that this modulation indicates that the more participants represent the correctness of their choices the less they have to rely on the external feedback. Consistent with these results, our findings suggest that children as compared to adults are less able to rapidly assess the information value of (particularly negative) feedback (i.e., how much the feedback should guide learning) and are less able to use external (particularly negative) feedback for learning (van Duijvenvoorde et al., 2008). This interpretation is in line with findings showing that children as compared to adults are less capable to differentiate between response-dependent and uninformative negative feedback (Crone et al., 2004). As a consequence of this children may up-regulate their response to (observed and experienced) negative feedback. fMRI studies link difficulties of children in using negative feedback for learning to functional changes in prefrontal areas (Christakou et al., 2013; Crone et al., 2008; Hauser et al., 2015, 2014; van den Bos et al., 2012; van Duijvenvoorde et al., 2008). Van Duijvenvoorde et al. (2008) showed that developmental differences in learning from negative feedback are related to developmental differences in BOLD activity in areas linked to executive control, such as the dorsolateral prefrontal cortex (DLPFC) and superior parietal cortex, regions that are not fully developed in children (e.g., Gogtay et al., 2004; Lenroot and Giedd, 2006). Thus, children's difficulties in using negative feedback during learning may be due to functional changes in areas associated with executive control (see also Hämmerer and Eppinger, 2012 for review).

4.3. Developmental differences in learning from feedback

In contrast to the FRN, the P300 valence effects varied as a function of learning condition (Rodriguez Buritica et al., 2016). As shown in Fig. 4A across age groups the P300 difference between losses and rewards was larger in the AO compared to the other learning conditions. Thus, the P300 effect increases with increasing amounts of observable information. We think that this result might reflect the fact that with better performance the probability of positive feedback increases whereas the likelihood of negative feedback decreases. That is, rewards may be experienced as more expected whereas negative outcomes may be experienced as more surprising (Mars et al., 2008; Neville et al., 1986). Consistent with this interpretation the P300 differentiation between losses and rewards correlated with behavioral performance (see Fig. 4B). That is, the more subjects expect themselves to be correct, the greater the P300 for losses and the smaller the P300 for rewards. Our P300 results also point to specific developmental differences: In line with prior research (Polich et al., 1990; van Dinteren et al., 2014), adults showed a larger P300 than children (see Fig. 3B). Moreover, the P300 to rewards decreased as a function of learning in adults but not in children and this learning-related decrease in the P300 correlated with behavioral learning effects (see Fig. 4C) as well as WM (see Fig. 4D).

One could assume that changes in the P300 with learning only reflect the frequency of feedback and that they have nothing to do with the actual learning process. We argue, however, that this view is inconsistent with our results. First, in *both* age groups the P300 differentiation between losses and rewards correlated with behavioral (learning) performance across all learning conditions (see also Rodriguez Buritica et al., 2016). Second, in the younger adults the P300 difference measure (i.e., averaged amplitudes in the second compared to the first block half) correlates with performance. Both findings indicate that there is a tight coupling of the underlying neurobiological processes and learning. Furthermore, this view is inconsistent with recent findings from model-informed EEG studies that clearly show that the amplitude of the P300 is not only sensitive to surprise but, in addition, reflects processes involved in value updating during learning (Eppinger et al., 2017; Fischer and Ullsperger, 2013; Philiastides et al., 2010). We think that these results suggest that the P300 (rather than the FRN) in adults may reflect the updating of reward predictions (Eppinger et al., 2017; Fischer and Ullsperger, 2013; Philiastides et al., 2010; Ullsperger et al., 2014) and that this effect depends on WM abilities (Collins and Frank, 2012). Thus, our electrophysiological findings suggest that WM abilities might be a limiting factor for reward-based (probabilistic) learning in children compared to adults.

Similar to the findings in the P300 to experienced feedback, in adults, but not in children the P300 to observed rewards decreased with learning (see Fig. 5B). Moreover and similar to the findings in the P300 to experienced feedback, in adults, but not in children the oP300 valence effect was positively related to learning effects in the AO condition (see Fig. 6). Thus, consistent with the interpretation for the P300 to experienced feedback our results suggest that adults are able to use the observed information to update reward predictions. In contrast, children seem to be stuck in processing the valence of the observed feedback but are unable to determine how much they should learn from this information.

Taken together, the current results suggest that the P300/oP300 reflects the degree to which individuals can use information from own and observed experience to update reward predictions during reinforcement learning (Eppinger et al., 2017; Fischer and Ullsperger, 2013; Philiastides et al., 2010; Ullsperger et al., 2014) and that this effect depends on WM abilities (Collins and Frank, 2012). Thus, the P300 may reflect the computational mechanisms that determine the degree to which behavior should be updated based on a given prediction error and that this process may in part depend on WM abilities (Nassar et al., 2016). According to such an interpretation the absence of this effect in children may reflect difficulties in determining (or adjusting) the optimal rate of learning in a given environment (McGuire et al., 2014; Nassar et al., 2012) as well as developmental differences in WM functions (Fry and Hale, 1996; Kwon et al., 2002). On a more general level such an interpretation suggests that developmental differences in learning may not be the consequence of differences in

prediction error signaling per se (Cohen et al., 2010; Hauser et al., 2015) but rather in determining how much to learn from a given prediction error (McGuire et al., 2014; van den Bos et al., 2012).

5. Limitations

Our findings provide first insights into developmental differences underlying OL. However, it is important to note that in our experiments children and adults learn indirectly from other individuals (i.e., using computer-generated information). We created a social learning setting, where participants were told that they could learn from another real participant they met in a previous session. In our previous study (Rodriguez Buritica et al., 2016), using the same social learning setting and task, we showed that similarity in age (same-aged child vs. young adult) between the observed player and the observer influenced both behavior and ERPs in 8–10 year old children. Based on these findings we argue that it is likely that the participants perceived the OL conditions as social learning conditions rather than conditions in which they simply received more information (see also Fig. S2 and supplements for further information). Future studies should, however, validate such "indirect" OL effects in comparison to more direct OL (e.g., "directly" observing others' choices in presence of the other player). Additionally, OL should be investigated in more "natural" social learning settings. In school for instance, OL rarely takes place by a contingently observation of other's behavior (i.e., where teachers or peers make errors and observers can use this information on a trial-by-trial basis). If we want to understand and design programs to enhance OL from, for instance, others' errors and negative feedback in children, we have to study OL in classroom-settings with more real-world designs.

6. Conclusion

Taken together, our results indicate a developmental shift in the processing of experienced and observed feedback during learning: Although both age groups benefitted from observational information during learning, adults learned much faster compared to children in the age of 8–10 years. Thus, children are less efficient in integrating other's and their own (particularly negative) outcomes into their behavioral strategies than adults. Our electrophysiological results show that children react more to external (particularly negative) feedback during learning than adults and are less able to use observed and experienced feedback for learning. As a consequence, they might generally up-regulate their response to external negative feedback, independently of who receives the feedback. Adults are more efficient in using the additional information in the fully observational (AO) condition, which is in line with their accelerated learning effects in this condition. These developmental differences may reflect a more general developmental trend in the ability to use observed and experienced feedback for goal-directed learning. When transferring the current findings to an applied context one tempting interpretation of our results is that educational intervention programs designed to enhance learning in children should focus in enhancing their ability to use experienced and social feedback for learning.

Acknowledgments

Declarations of interest

None.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2018.07.022.

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