Cognitive Strategy Use as an Index of Developmental Differences in Neural Responses to Feedback

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Brief report

Abstract

Developmental differences in dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC) and superior parietal cortex (SPC) activation are associated with differences in how children, adolescents, and adults learn from performance feedback in rule-learning tasks (Crone, Zanolie, Leijenhorst, Westenberg, & Rombouts, 2008). Both maturational differences and performance differences can potentially explain variance in functional brain activation. To disentangle those effects, we established strategy differences in the performance of participants on the task of Crone et al. by the application of latent mixture models (McLachlan & Peel, 2000). We found four categorically different strategies, which were divided across age groups. Both adults and adolescents were distributed among all strategy groups except for the worst performing one, whereas children were distributed among all strategy groups except for the best performing one. Strategy use was a mediator and largely explained the relation between age and variance in activation patterns in the DLPFC and the SPC, but not in the ACC. These findings are interpreted vis-à-vis age versus performance predictors of brain development.

Keywords: feedback learning, functional brain activation, development, latent mixture models, strategy use

Introduction

Learning from feedback is of crucial importance for adaptive performance. Developmental differences between adults and children in the ability to do so are evident from performance differences on tasks like the Wisconsin Card Sorting Task (WCST; Berg, 1948) and discrimination learning tasks (Kendler, 1979). In these tasks, it is essential that participants process feedback after responses to discern the correct rules. On these tasks, children (< 10 y) commit more perseverative errors, respond more slowly, and make more mistakes than adults do (Chelune & Baer, 1986; Schmittmann, van der Maas & Raijmakers, 2012; Huizinga, Dolan, & van der Molen, 2006)

Such differences in cognitive abilities have been related to differences in functional brain development, in particular activation patterns in the frontal-parietal network (Crone et al., 2008; van Meel, et al., 2012). To investigate this, Crone et al. (2008) administered a repeated rule-switch learning task, comparable to the WCST, to participants of three age groups: children, adolescents, and adults. Consistent with what is found for the original WCST, children made more perseverative errors, responded more slowly, and made more mistakes than adolescents and adults. Crone et al. (2008) concurrently measured the BOLD-signal from dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), lateral orbitofrontal cortex (lat-OFC), and superior parietal cortex (SPC). They found that DLPFC and ACC activation in adults was related to specific types of feedback. ACC activation was associated with unexpected feedback, i.e. negative feedback signaling a change of correct rule, whereas DLPFC activation was associated with expected errors such as those that occur when you search for the correct rule (see also Zanolie et al., 2008). ACC and DLPFC activation in adolescents and children, however, were equally strongly associated with both expected and unexpected negative feedback. Furthermore, they found that in children SPC activation was related to the informative value of *negative* feedback, whereas in adolescents and adults, SPC activation depended on the informative value of the *positive* feedback. Hence, the authors suggested that children might rely on SPC as compensation for the not fully developed DLPFC and ACC. The lat-OFC did not show any signs of differential activation between age groups.

The motivation for investigating these areas came from earlier studies suggesting the involvement of these areas in feedback processing and higher-order cognitive paradigms, DLPFC and ACC: (Lie, Specht, Marshall, & Fink, 2006; Carter et al., 1998); lat-OFC: (O'Doherty, Critchley, Deichmann, & Dolan, 2003); SPC: (van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008).

Together, these studies have shown that a frontal-parietal network together with the ACC is important for detecting conflict and adapting behavior to changing task demands (Kerns, 2006; Hämmerer & Eppinger, 2012).

Crone et al.'s study (2008) also revealed differences in activation patterns *within* these age groups, i.e. correlations between activation and performance. For example, the activation in DLPFC and SPC correlated positively with the number of efficient errors (successful feedback use) and negatively with the number of mistakes (errors after finding the solution). At the same time, activation in DLPFC and SPC also correlated with age. The question then arises whether the brain activation differences between age groups were primarily related to maturation or to performance differences, which are both related to age (Casey et al., 2005; Church, Petersen & Schlaggar, 2010, Durston & Casey, 2006; Galván, 2010; Schlaggar et al., 2002).

In most functional magnetic resonance imaging (fMRI) and event-related potential (ERP) studies of the development of feedback learning it is assumed that performance differences vary continuously between individuals (e.g., vanDuijvenvoorde et al, 2008; Eppinger, Mock & Kray, 2009; Crone et al., 2008; Koolschijn et al., 2011). In contrast to this approach, category learning studies, focus on different learning strategies between individuals, such as implicit learning and rule-based hypothesis testing (Ashby & Maddox, 2010; Erickson et al., 1998; Johansen & Palmeri, 2002; Huang-Pollock, Maddox & Caralunas, 2011). Robust analyses of strategies show that age groups, including young adults, are heterogeneous in strategy use for feedback learning (Ell & Ashby, 2006; Schmittmann et al., 2006, 2012; Visser & Raijmakers, 2012; Speekenbrink et al., 2010; Johansen & Palmeri, 2002; Raijmakers, Schmittmann & Visser, 2014). Strategies in category learning were detected by modeling response patterns in the heterogeneous accuracy data into

distinct, latent categories. These strategies turned out to be either some sort of memorization strategy (e.g., exemplar-based learning) or a form of explicit hypothesis testing with different levels of efficiency. Following Rickard (2004, p. 65) and other researchers the term *strategy* is used henceforth “to denote a unique series of one or more mental steps toward a solution and does not necessarily have direct implications regarding intention or awareness” (Rickard, 2004; p. 65). Single-digit arithmetic is another illustrative example of a task that involves multiple strategies (Siegler, 1988). Young children solve a sum by counting on fingers while a proficient in arithmetic uses direct memory retrieval.

The heterogeneity in age groups is pivotal in understanding the results of the discussed imaging studies because the comparison of strategy-heterogeneous subgroups makes the interpretation of differences in activities between subgroups difficult (Church et al., 2010). Especially attributing brain activation differences between age groups to maturation is problematic if performance differences exist between age groups. Therefore, Schlaggar et al. (2002) compared accuracy- and non-accuracy-matched subgroups of children and adults while they performed a word-reading task. They found maturational differences in patterns of regional activation at the age of 10. Unfortunately, for feedback learning accuracy matching would not guarantee that performance is matched between groups. Accuracy-matched subgroups could still apply different strategies (Schlaggar et al.; Brown et al., 2005), because strategies can differ not only on the number of errors but also on the type of errors made. Hence, we followed an approach where we established strategy-matched subgroups before comparing their brain activation.

We reanalyzed the data of Crone et al. (2008) and applied latent mixture modeling (McLachlan & Peel, 2000) to make a robust description of potential categorical performance differences. The first question is: Can strategy differences be detected in the behavioral results of Crone et al.? Second, if strategy differences are correlated with functional brain activation, do they explain variance in addition to age?

In the following, we first briefly present the study of Crone et al. (2008) and the conclusions they drew from their findings. Next, latent mixture models (McLachlan & Peel, 2000) were fit to Crone et al.'s data, to reveal possible categorical strategy differences. Finally, we analyzed how categorical strategy differences correlated with differences in functional brain activation accounting for age differences at the same time.

The study of Crone et al. (2008)

Participants

Nineteen adults age 18–24 (mean age 20.3 y; 8 men, 11 women), 19 adolescents age 14–15 (mean age 14.5 y; 10 boys, 9 girls), and 17 children age 8–11 (mean age 9.5 y; 9 boys, 8 girls) were included in the current study. Participants were recruited through local advertisements and from Leiden University in the Netherlands. Participants' consent was obtained according to the Declaration of Helsinki; the Internal Review Board at Leiden University Medical Centre approved the study. Three additional children age 8–11 were tested but excluded because of excessive head movement (>2 mm of translation in any direction) or failure to perform the task. Two additional participants (one adult and one adolescent) were included in the Crone et al. (2008) analyses, but had incomplete behavioral data, which made it impossible to include them in the latent mixture modeling.

Task and Procedure

A child-friendly rule-switch task was used where the task was to help a dog find its way home (Figure 1). Participants were to respond to a stimulus (the position of the dog) and indicate the proper response (one of four doors) by a button press. Which one was the correct door was dependent on the active rule at that moment. There were three possible rules, all illustrated and explained in Figure 1. Participants had to rely on feedback to figure out the active rule. Feedback

was given after each trial indicating the accuracy of the response. After a series of 2-4 correct responses, the active rule would change without warning. Participants were told beforehand that the rule would change occasionally, but not when. The main task consisted of 3 blocks of 100 trials.

Figure 1 around here

Classification of Feedback

For each individual, all trials were classified in one out of five types of feedback. Trials with negative feedback were classified as first warning feedback (FW), efficient feedback (EFF), or error feedback (ERR). Trials with positive feedback were classified as either first positive feedback (FP) or correct feedback (CORR). FWs are instances of negative feedback following a rule change, EFFs are instances of negative feedback that are used to find the correct rule, and ERRs are all other instances of negative feedback, including mistakes. An FP is the first positive feedback following a rule change, while CORR is all remaining positive feedback. Figure 2 illustrates and defines the five kinds of feedback in a precise manner. In the performance analysis, the number of trials of each type of feedback was the dependent variable.

Figure 2 around here

Results

In the introduction we discussed the behavioral and fMRI results reported by Crone et al. (2008). Here we present the analysis of strategy-homogeneous subgroups.

Behavioral Strategies of Individual Participants

Latent mixture modeling (LMM) offers a robust statistical technique for detecting heterogeneity in data that stems from categorical differences, i.e. strategy differences, rather than continuous differences between participants (McLachlan & Peel, 2000; van der Maas &

Straatemeier, 2008). To assess the existence of categorical differences we fitted LMMs to the performance data of Crone et al., i.e. the number of trials classified into five feedback types: FW, EFF, ERR, FP, and CORR. We used the package depmixS4 (Visser & Speekenbrink, 2010) within the statistical programming environment R (R Development Core Team, 2012) to fit LMMs with an increasing number of classes, up to six, corresponding to an increasing number of different strategies (Table 1). The dependent variable is a multinomial distribution of the number of occurrences of feedback types. To establish the number of strategies present in the data, the most parsimonious, best fitting model was selected on basis of the Bayesian Information Criterion (BIC; Schwarz, 1978). The BIC offers a statistically founded way of making a trade-off between the number of classes (more classes always results in a better or equally well fitting model) and the parsimony of the model (a model with fewer classes is more parsimonious).

As evident from Table 1, the most parsimonious, best fitting model consisted of four classes. Each class reflects one distinct strategy. The observation probabilities for each feedback type differ among classes (Table 2). Classes are strongly, but not completely, related to the number of error feedback trials (ERR). We refer to these classes as: Class 1, Class 2, Class 3, and Class 4, and ordered them such that higher class number reflected better performance on the task (Figure 3). Each individual was assigned to one of these classes, such that the posterior probability of his or her performance was maximized (Visser, 2010). Table 3 shows that age groups are distributed among the classes but with a preponderance of adults in the better performing classes and children in the worse performing classes. Age groups were not equally distributed among the classes ($\chi^2 = 25.01$, $p < 0.001$; p-value based on Monte Carlo simulation), which means that the percentage of participants in more advanced strategy classes increases with age. Moreover, there were mean differences in age between groups ($F(3,51) = 10.64$, $p < 0.001$) such that mean age increases with class. In the following sections, we will first check whether classes fully explain the relation between age and performance. Next, we will test for which brain areas classes explain the relation between age and in functional brain activation that was found in Crone et al. (2008).

Tables 1, 2, and 3 around here

Relating Age and Strategy Use to Performance

Crone et al. (2008) showed that performance, in particular the number of different feedback trials, perseveration errors, and speed, was related to age. Our goal here is to check whether classes fully explain this relation between age and performance. Evidently, strategy class will be a better predictor than age of all performance measures based the number of feedback trials because the class definition is based on these performance measures. However, the description of the behavioral data into four distinct classes is a large reduction of the behavioral data. Therefore, it is important to test whether there is a remaining contribution of age while entering both factors in describing variance in these performance measures.

Class 1 only consists of members from the children group ($N = 5$), whereas children are not part of Class 4. Because of this unbalanced design, we used mixed models (McCulloch & Searle, 2001) in SPSS instead of standard ANOVAs for the following analyses of performance, and their corresponding effect sizes: R^2_{LR} and by $R^2_{LR}^*$ (repeated measures), which were based on likelihood ratio (see Kramer, 2005).

In all the following statistical analyses, the number of different feedback trials was modeled with a mixed model with Feedback (5) as a repeated effect and Age Group (3) and Class (4) as the fixed effects. Participant ($N = 55$) was modeled as a random effect, and covariance between repeated measures was modeled as unstructured. This mixed model revealed main effects of Class ($F(3,46) = 4.10, p < 0.05, R^2_{LR} = 0.06$) and Feedback ($F(4,46) = 2531.96, p < 0.001, R^2_{LR} = 0.90$). There was no main effect of Age Group. Furthermore, there was an interaction between Class and Feedback ($F(12,46) = 22.48, p < 0.001, R^2_{LR}^* = 0.87$), but none between Age Group and Feedback and also no 3-way interaction. In an additional analysis, errors were scored as perseverative, i.e. an error when the rule from the previous trials was repeated on the trial following the first warning

feedback. Similar results were found for the number of perseveration errors where an Age Group (3) $\times$ Class (4) mixed model revealed a main effect of Class ($F(3,46) = 12.81, p < 0.001, R^2_{LR} = 0.62$). This effect was accompanied neither by a main effect of Age Group nor an interaction between Age Group and Class. In contrast to the accuracy data, reaction times did not show individual differences related to strategy in addition to age groups. There was a main effect of Age Group: ($F(2,46) = 20.10, p < 0.001, R^2_{LR} = 0.70$), but not of Class.

Figure 3 around here

In summary, the heterogeneity in the number of perseveration errors and the number of different feedback trials that was explained by age, as was reported in Crone et al. (2008), was fully captured by strategy use. Age group explained variance in reaction times better.

Relating Age and Strategy Use to Brain Activation

We related brain activation to feedback types, age groups, and strategy use to test the existence of a unique relation between age and patterns of activation and between strategy use and patterns of activation. These analyses were of special interest because they would shed light on whether Class or Age Group was the best predictor of the developmental differences in activation for the four regions of interest (ROIs) that Crone et al. tested: ACC (BA 32), right SPC (BA 7), right lateral OFC (BA 47), and right DLPFC (BA 9). For each ROI, we extracted activation levels relative to a fixation baseline for each condition and participant. As in Crone et al. the ROIs were created on the basis of an all feedback > fixation contrast across all participants. Figure 4 shows the feedback patterns of all classes for each region of interest (ROI), ACC, right SPC, right lateral OFC, and right DLPFC.

Class (4), Age Group (3), and Feedback (5) were defined as fixed effects. Feedback was modeled as a repeated effect. The covariance between the five different kinds of feedback observations was modeled as unstructured. Participant ($N = 55$) was modeled as a random effect.

The interaction effects Class $\times$ Feedback, Age Group $\times$ Feedback, and Class $\times$ Age Group $\times$ Feedback were included in addition to the main effects. However, we were only interested in the interaction effect Class $\times$ Feedback as an effect that exists in addition to the interaction effect Age Group $\times$ Feedback on BOLD-signal in ROIs. The analyses resulted in a main effect of Feedback for all areas (all areas: $F(4,46) > 14$, $p < 0.001$). No main effects for Class or Age Group were found (F 's < 1). Significant interactions were found between Class and Feedback for the SPC and DLPFC (SPC: $F(12,46) = 3.57$, $p < 0.01$; $R^2_{LR} = 0.11$; DLPFC: $F(12,46) = 2.52$, $p < 0.05$, $R^2_{LR} = 0.07$). In the presence of these interaction effects no or marginal significant interactions were found between Age Group and Feedback for these areas (SPC: $F < 1$; $R^2_{LR} = 0.04$; DLPFC: $F(8,46) = 1.89$, $p = 0.08$, $R^2_{LR} = 0.03$). For the remaining two areas significant interactions were found for neither Age Group $\times$ Feedback (ACC: $F(8,46) = 1.78$, $p = 0.11$, $R^2_{LR} = 0.07$; lat-OFC: $F(8,46) = 1.43$, $p = 0.21$, $R^2_{LR} = 0.00$) nor for Class $\times$ Feedback (ACC: $F(12,46) = 1.69$, $p = 0.10$, $R^2_{LR} = 0.08$; lat-OFC: $F(12,46) = 1.31$, $p = 0.25$, $R^2_{LR} = 0.02$). The three-way interaction was not significant. To compare brain activity patterns between each two classes (that is the Feedback $\times$ Class interaction for class 4 vs. 3, 4 vs. 2, etc.) post-hoc tests with age as a covariate were used. These tests showed that the Feedback pattern of Class 4 differed significantly from all the other classes in SPC (All p 's < 0.05 , (Holm-Bonferroni corrected, number of tests = 6; Holm, 1979). In DLPFC the Feedback pattern of Class 4 differed significantly from that of Class 3 ($p < 0.05$).

The Class $\times$ Feedback effect was found for BOLD-signal in SPC and DLPFC. A more stringent test of the importance of Class in addition to Age Group in explaining variance in BOLD-signal is a test within age groups. For the DLPFC, there was a marginal Class $\times$ Feedback interaction for the adults ($F(8,16) = 2.278$, $p = 0.08$), an interaction for the adolescents ($F(8,16) = 5.794$, $p < 0.001$), and no interaction for the children. For the SPC, there was a Class $\times$ Feedback interaction for the adults ($F(8,16) = 3.261$, $p = 0.021$), and the adolescents ($F(8,16) = 5.201$, $p = 0.003$), but not for the children.

In summary, strategy use is a unique predictor of patterns in brain activation related to feedback types in the SPC and DLPFC, i.e. in addition to age group as a predictor. According to Cohen (1988), the effect sizes reported here are in the medium range for Class. Also in age homogenous groups, strategy differences are a predictor of patterns in brain activation for the DLPFC and SPC. For the other areas, ACC and lat-OFC, both strategy and age are not uniquely explaining variance of the activation patterns related to feedback type. Note that there is a significant overlap between age and strategy use, which means that these results are not in conflict with the developmental differences that were found by Crone et al. (2008).

Figure 4 around here

Strategy as mediator of the relation between Age and Brain Activation.

Above, we tested differences in activation patterns between strategy classes only in the ROIs where significant interactions between Feedback and Class were found, i.e., SPC and DLPFC. Results of the analyses above suggest that the relations between Age and BOLD-signal in SPC and DLPFC as was found by Crone et al. (2008), were mediated by Class. We test this mediation effect for the difference in BOLD-signal between trials with negative feedback (FW, EFF, ERR) and trials with positive feedback (FP, CORR). We applied the method of causal mediation analysis (Imai, Keele & Tingly, 2010; Imai et al., 2010). In the analysis Age is a direct predictor (continuous scale) and Class is the mediator variable, and difference in BOLD-signal is the dependent variable. According to this method a mediation effect is only present if 1) Age predicts BOLD-signal (path c), 2) Age predicts Class (path a), 3) Class predicts BOLD-signal in a model with Age entered simultaneously as a predictor (path b), and 4) the effect of Age on BOLD-signal decreases substantially if Class is entered simultaneously as a predictor (path c'; Preacher & Hayes, 2008). Path a is the same for all the following linear models and is a significant relation (path a: $B = .12$, p

< .001; B). The reported regression coefficients are unstandardized coefficients. In addition we will report a proportion mediated, which is the size of the average causal mediation effect relative to the total effect. We will only analyze Class as a mediator of the effect between Age and BOLD-signal for those ROIs for which we did find an effect of Class. That is, the difference in BOLD-signal between positive and negative feedback in SPC and DLPFC.

We started with testing for collinearity problems between Age and Class. According to the literature, collinearity is indicated by a tolerance value less than 0.1 (Menard, 1995), a Variance Inflation Factor (VIF) greater than 10 (Myers, 1990), and condition indices greater than 10 (Belsley, Kuh, & Welsh, 1980). In the analyses below, tolerance values are .62, VIF is 1.6, and condition indices are 9.4.

In SPC, the mediation model of the difference in BOLD-signal between negative and positive feedback showed that the effect of Age (path c': $B = .005$, $p = .84$; path c: $B = .05$, $p = .03$) was largely mediated by Class (path b: $B = .05$; $p = .01$; proportion mediated = .86; Figure 5A).

In DLPFC, the mediation model of the difference in BOLD-signal between negative and positive feedback showed that the effect of Age (path c': $B = .03$, $p = .21$; path c: $B = .12$, $p < .001$) was largely mediated by Class (path b: $B = .04$; $p = .01$; proportion mediated is .57; Figure 5B).

In summary, we applied mediation modeling to reveal the relation between age and strategy use in explaining variance in brain activation. Both in SPC and DLPFC the relation between age and the difference in brain activation after negative feedback and positive feedback was largely mediated by strategy use. That is, more advanced strategies went together with a larger difference in brain activation in SPC and DLPFC between trials with negative and positive feedback.

Figure 5 around here

Differences in Brain Activation within Strategies. To reveal brain activation patterns that are specific for each strategy, we tested differences in brain activation elicited by the

different kinds of feedback within classes. Holm-Bonferroni correction was used (no. of tests = 10; reported $p < 0.05$).

For SPC, no differentiation was found in Class 1 between positive and negative feedback and no significant activation above baseline was found for any type of feedback (note that $N = 5$). In Class 2, EFF elicited more activation than all the other kinds of feedback, and also ERR elicited activation above baseline. In Class 3, EFF, ERR, and FP elicited more activation than CORR. All feedback-types except CORR showed activation above baseline. Finally, in Class 4, FW and EFF both showed more activation above baseline and more than CORR.

For DLPFC, no differentiation was found in Class 1 and no significant activations were found (note that $N = 5$). In Class 2, EFF and ERR showed more activation than positive feedback and all negative feedback showed more activation than baseline. In Class 3, all negative feedback elicited more activation than CORR; EFF and ERR also elicited more activation than FP and above baseline. In Class 4, all negative feedback showed more activation than positive feedback, but with only FW and EFF showing more than baseline activation and CORR showing below baseline activation.

The general picture for the SPC is specificity for the EFF for only class 2. Class 3 shows specificity for EFF, ERR, and FP. Moreover, only class 4 shows activation specifically for the informative errors (FW, EFF). The general picture for the DLPFC is one of greater differentiation of informative versus non-informative trials with more advanced strategies. This sensitivity is mainly related to EFF and ERR for classes 2 and 3. Only the best performing class, Class 4, is set apart by their DLPFC showing specific sensitivity to FW in addition to EFF.

Discussion

The findings we report here show that heterogeneity in feedback learning for the task at hand could be characterized by a number of different behavioral strategies. Here we use the term

strategy without direct implications regarding intention or awareness (cf, Rickard, 2004). The strategies differed from one another on the number of trials completed, the number of perseveration errors, and the distribution of feedback observations (i.e., first warning feedback, efficient feedback, error feedback, first positive feedback, correct feedback). Behavioral strategies were most strongly related to the number of error feedback trials. Error feedback, and hence the difference between strategies, is associated most likely with several control processes, including expectation violations, hypothesis testing, and uncertainty (Crone et al., 2008). Heterogeneity in feedback learning was found between age groups but also within age groups. More advanced strategies were used more frequently by older participants. However, only 42% of the adults and 16% of the adolescents used the most advanced strategy. From the adults 42% used the second best strategy and 58% of the adolescents and 24% of the children used the second best strategy. The present article shows that the behavioral strategies could explain an important part of the relation between age and patterns of brain activation during feedback learning (Crone et al., 2008).

To test the existence of a unique relation between age and patterns of activation and between strategy use and patterns of activation, we related brain activation in four ROIs, right SPC, right DLPFC, right lateral OFC, and ACC, to feedback types, age groups, and strategy use. Strategy use was uniquely related to activation patterns in SPC and DLPFC, but not to activation patterns in lat-OFC and ACC. Activation patterns in Class 1 were difficult to interpret because of a small number of participants ($N = 5$). Especially, the most advanced strategy (class 4) stood out with a pattern different from the other strategies (classes 1, 2, and 3). Thus, strategy differences were uniquely related to patterns of functional brain activation. This will be explicated in greater detail below.

We addressed the question whether age is a unique predictor of performance. We did not find any unique relations between age and activation patterns for these four areas. Strategy differences, in contrast, did uniquely explain variance in activation in SPC and DLPFC, i.e. above age. For the other areas, lat-OFC and ACC, no variance was uniquely explained by either age or

strategy differences. Hence, for these areas results were indecisive. This result can be understood in relation to the age effects found by Crone et al. (2008) given that both factors, age and strategies, are partly overlapping in the present analyses.

Crone et al. (2008) suggested that adults rely on DLPFC and ACC when processing performance feedback and adapting behavior to changing task demands, whereas children additionally recruit the SPC. These findings were interpreted to suggest that, optimal performance goes together with specialization of ACC and DLPFC, reacting respectively to first warnings and efficient errors. Prior studies have shown that with development children show a pattern of diffuse to focal activation in the frontoparietal network when performing cognitive control tasks (Durstun et al, 2006). These findings are also consistent with recent models that suggest that cortical brain development is associated with a process of increased interactive specialization of task relevant networks in the brain (Johnson, 2011).

In the present analyses, these results could be confirmed to some degree. Class 2 showed SPC-characteristics similar to those Crone et al. (2008) argued that children recruited, i.e. reacting most strongly to efficient feedback (Figure 4B). Classes 3 and 4 showed a pattern in SPC activation more similar to that of adults and adolescents in Crone et al. (2008), i.e. negative feedback eliciting more activation than correct feedback (Figure 4B). Moreover, Class 4 showed also specific sensitivity for the informative value of negative feedback. If the SPC compensates for suboptimal function of DLPFC and ACC, such as Crone et al. suggested the present results suggest that the application of the SPC is directly related to strategy use, rather than age. Similarly, DLPFC for Class 4 also depended on the *informative* value of feedback, both positive and negative, while DLPFC of classes 2 and 3 were active in response to all negative feedback (Figure 4D). Finally, in SPC and DLPFC class 4 subjects showed greater sensitivity to first warnings than any of the other classes. These results imply that the developmental changes in feedback processing and associated activity in the frontoparietal network are part of a larger set of changes, including changes in strategies use over time.

Taken together, different results were found depending on whether age groups or latent performance classes were contrasted with one another. When only age group was included as an explanatory grouping variable (Crone et al., 2008), results suggested that only DLPFC and ACC of adults show specialized activation, but not adolescents and children. That is, for adults the ACC was specifically related to detecting rule changes, and the DLPFC was specifically related to detecting efficient errors. For children, in contrast, the detecting of efficient errors was specifically related to the SPC. Adding strategy use as an explanatory grouping variable changes these interpretations. The present results indicate that heterogeneity in DLPFC and SPC activation was better explained by differences in strategy use than by age differences. Applying an optimal strategy goes together with the DLPFC and SPC being the areas becoming active only to informative negative feedback, i.e. first warnings and efficient errors; the ACC being the area to detect mistakes for most participants. From this perspective, the different specialized activations of DLPFC and SPC for feedback learning found by Crone et al. (2008) could result from grouping participants using different strategies together. However, to be able to generalize the findings of the present study it would be necessary to repeat the study with a balanced number of participants per strategy.

Casey et al. (2005; Durston & Casey, 2006) and Church et al. (2010) previously dissociated effects of age and effects of performance. Durston and Casey (2006) suggested using a parametric manipulation of task difficulty (e.g., with a go no-go paradigm, Durston et al., 2002). This kind of manipulation allows for post hoc comparisons between age groups at different levels of task difficulty, while controlling for task performance. However, for feedback learning such a manipulation introduces the possibility that different strategies are used for different task difficulties, which does not solve but might enlarge the problem of strategy heterogeneity. Church et al. (2010) discuss the method of comparing performance-matched age groups as a way to look at the effect of maturation on brain activation. The way we matched performance was by detecting latent classes, which were based on the distribution of different trial types instead of sum scores. In

this way we created strategy-matched subgroups. We showed for the SPC and DLPFC that variance in activation patterns that was found to be related to age (Crone et al., 2008) could be better described by strategy differences. Nevertheless, these results do not give a definite answer to the question whether patterns of brain activation were related to strategy and not to maturation; it only shows that multiple interpretations are possible (cf. discussion in Brown et al., 2005, p. 286). However, given the large age differences within strategy-matched groups it is a convincing alternative. A next step in disentangling the effects of maturation and strategy-use would be a training-study design (cf. Patel et al., 2013).

Conclusions

The findings we report here show that developmental differences in task performance can be characterized by a number of different strategies with considerable individual differences within age group. That is, the percentage of children with more advanced strategy use increased with age but was not perfectly related to age. Strategy use was a mediator and largely explained the relation between age and activation patterns in the DLPFC and the SPC, but not in the lat-OFC and the ACC. Unique functional brain activation of DLPFC and SPC was found for participants following the optimal strategy. For these participants activation in the DLPFC and the SPC was specifically related to all informative negative feedback (first warnings and efficient errors). Comparing strategies, for participants using the optimal strategy, the activation in the DLPFC and the SPC after first warnings was stronger than for participants following any other strategy. Among the four strategies revealed, adults and adolescents were represented in three of them. This suggests that heterogeneity in functional brain activation of SPC and DLPFC are better explained by differences in strategy use than by age differences.

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Table 1: Fit statistics of the latent mixture models

No. of classes	# pars	Log-likelihood	BIC
1	4	-1081.56	2179.14
2	9	-818.84	1673.75
3	14	-724.64	1505.38
4	19	-705.41	1486.97
5	24	-700.02	1496.22
6	29	-695.35	1506.91

Note: Fit statistics of 6 explorative LMM with increasing number of classes. # pars is the number of parameters estimated. The model with 4 classes and 19 parameters estimated is the best model as judged by BIC (Bayesian Information Criterion).

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Table 2 – The probability of observing each of the five possible kinds of feedback per latent class

	FW	EFF	ERR	FP	CORR
Class 1	.12	.02	.31	.22	.33
Class 2	.16	.05	.16	.23	.39
Class 3	.19	.08	.09	.22	.42
Class 4	.21	.10	.03	.22	.44

Note: The classes have been ordered such that a higher class reflects a better performance.

Abbreviations: FW = First Warning Feedback, EFF = Efficient Feedback, ERR = Error Feedback,

FP = First Positive Feedback, and CORR = Correct Feedback.

Table 3 – Percentage (N) of participants in each class per age group.

	Adults	Adolescents	Children	Age (sd)
Class 1	0 (0)	0 (0)	29 (5)	9.8 (1.1)
Class 2	16 (3)	26 (5)	47 (8)	12.8 (4.0)
Class 3	42 (8)	58 (11)	24 (4)	15.4 (4.0)
Class 4	42 (8)	16 (3)	0 (0)	19.4 (3.1)

Figure 1: Adapted from Zanolie, Leijenhurst, Rombouts and Crone (2008). (A) During scanning, participants viewed a 500ms fixation cross, followed by a 2500ms stimulus display. The stimulus required a left index, left middle, right middle or right index finger response, according to three rules that were learned prior to scanning. The stimulus display was followed by a feedback display which was presented for 1000 ms. Random jitter of 2000, 4000, 6000 or 8000ms was added to all trials. (B) Response-rules: participants were instructed to respond to the stimuli according to three rules. Each response (each door) was mapped to one specific finger: left middle finger (1) to left door, left house; left index finger (2) to right door, left house; right index finger (3) to left door, right house; and right middle finger (4) to right door, right house. Relative to the dog's position the correct response according to rule A was same door, same house. To rule B, it was same house, but opposite door. To rule C, it was same door, but opposite house. Positive (+) and negative (–) feedback was shown on the door participants chose as the dog's home according to the correctness of their choice.

Example 1

Example 2

Figure 2: Adapted from Crone et al. (2008). Illustration of the classification of feedback: negative feedback is classified as First Warning (FW) when the formerly correct rule is applied for the first time immediately following a rule change (Example 1, second application). It is classified as Efficient negative feedback (EFF) when the wrong one of the remaining two rules is applied after an FW, but *only* if it is then followed by positive feedback (Example 1, third application). *All* other instances of negative feedback are classified as Errors (ERR) (Example 2, third application). The first instance of positive feedback following a rule change is classified as First Positive (FP) (Example 1, third and fourth applications). All other instances of positive feedback are classified as Correct (CORR).

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Figure 3: Distributions of feedback for the three age groups. Error bars are standard errors of the mean. A main effect for Class Membership was found, but not for Age Group. No interaction between Class Membership and Age Group was found.

Figure 4: ROIs (A) ACC, (B) SPC, (C) lat-OFC, (D) DLPFC. Significant interactions between

Feedback and Class were found in SPC (B) and DLPFC (D). Post-hoc tests showed that the activation pattern of Class 4 differed from all other classes in SPC, but only from Class 3 DLPFC. Error bars are standard errors of the mean. Asterisks (only for the analyzed SPC and DLPFC) signify that the BOLD-signal is significantly different from the baseline (Holm-Bonferroni corrected). N = 5, 16, 23, and 11 for Class 1, 2, 3, and 4 respectively.

Figure 5: Linear models for the effect of age on BOLD-signal differences between trials with negative and positive feedback. B: unstandardized coefficients; * $p < .05$; ** $p < .01$. Path a is the effect of age on strategy use. Path b is the effect of strategy use on BOLD-signal differences with age entered simultaneously as a predictor; Path c is the direct effect of age on BOLD signal; Path c' is the remaining direct effect of age on BOLD-signal differences with strategy use entered simultaneously as a predictor. Fig. 5A shows the model for SPC and Fig. 5B shows the model for DLPFC.