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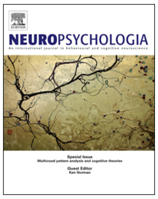

# Strategies influence neural activity for feedback learning across child and adolescent development

Sabine Peters[a,b,*], P. Cédric M.P. Koolschijn[c], Eveline A. Crone[a,b,d], Anna C.K. Van Duijvenvoorde[a,b], Maartje E.J. Raijmakers[d]

[a] Department of Developmental Psychology, Leiden University, The Netherlands
[b] Leiden Institute for Brain and Cognition, The Netherlands
[c] Department of Brain and Cognition, University of Amsterdam, The Netherlands
[d] Department of Developmental Psychology, University of Amsterdam, The Netherlands

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## ABSTRACT

Learning from feedback is an important aspect of executive functioning that shows profound improvements during childhood and adolescence. This is accompanied by neural changes in the feedback-learning network, which includes pre-supplementary motor area (pre- SMA)/anterior cingulate cortex (ACC), dorsolateral prefrontal cortex (DLPFC), superior parietal cortex (SPC), and the basal ganglia. However, there can be considerable differences within age ranges in performance that are ascribed to differences in strategy use. This is problematic for traditional approaches of analyzing developmental data, in which age groups are assumed to be homogenous in strategy use. In this study, we used latent variable models to investigate if underlying strategy groups could be detected for a feedback-learning task and whether there were differences in neural activation patterns between strategies. In a sample of 268 participants between ages 8 to 25 years, we observed four underlying strategy groups, which were cut across age groups and varied in the optimality of executive functioning. These strategy groups also differed in neural activity during learning; especially the most optimal performing group showed more activity in DLPFC, SPC and pre-SMA/ACC compared to the other groups. However, age differences remained an important contributor to neural activation, even when correcting for strategy. These findings contribute to the debate of age versus performance predictors of neural development, and highlight the importance of studying individual differences in strategy use when studying development.

## 1. Introduction

An important component of cognitive development is the ability to control and adapt behavior in response to changing environmental demands, also referred to as executive functions (Diamond, 2013; Zelazo, 2006). Executive functions are thought to consist of three core functions: inhibition, working memory and cognitive flexibility (Diamond, 2013). Higher-order executive functions such as reasoning, planning and learning from prior experiences rely upon combinations of these three core functions. The ability to adapt behavior based on prior experiences (i.e. adaptive control) shows a marked improvement during childhood and adolescence (Tamnes, Walhovd, Torstveit, Sells, & Fjell, 2013). For example, in the classic Wisconsin Card Sorting Task (WCST), there is a developmental improvement in flexibly adapting behavior based on positive and negative feedback (Huizinga, Dolan, & van der Molen, 2006) and in probabilistic feedback-learning tasks there is a developmental improvement in adapting behavior successfully based on informative versus non-informative feedback (Eppinger, Mock, & Kray, 2009; Jansen, van Duijvenvoorde, & Huizenga, 2014; van den Bos, Guroglu, van den Bulk, Rombouts, & Crone, 2009; Van Duijvenvoorde, Jansen, Griffioen, Van der Molen, & Huizenga, 2013). Despite these convincing developmental patterns, there are large individual differences in adaptive control within age ranges, i.e. not all children and adolescents are equally proficient at learning from positive and negative feedback. Why is it that some children are better at learning compared to their peers? Studying the behavioral and neural mechanisms underlying successful learning is important to advance our understanding of executive control processes and their development.

Most prior studies on the development of feedback learning have focused on performance improvements with age and the accompanying changes in brain activity. Research in adults indicated that during feedback learning, a large brain network is activated, including pre-supplementary motor area (pre-SMA)/

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[*] Corresponding author at: Institute of Psychology, Brain and Development Lab, Leiden University, Wassenaarseweg 52, 2333 AK Leiden, The Netherlands. Tel.: +31 715271844.
*E-mail address:* s.peters@fsw.leidenuniv.nl (S. Peters).

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anterior cingulate cortex (ACC) (Holroyd et al., 2004; Mars et al., 2005; Monchi, Petrides, Petre, Worsley, & Dagher, 2001; Ullsperger & von Cramon, 2003), (dorso)lateral prefrontal cortex (DLPFC) (Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Lie, Specht, Marshall, & Fink, 2006; van Veen, Holroyd, Cohen, Stenger, & Carter, 2004; Zanolie, Van Leijenhorst, Rornbouts, & Crone, 2008), basal ganglia (Monchi, et al., 2001; Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006), and superior parietal cortex (SPC) (Zanolie et al., 2008). It is thought that a dopamine-initiated alarm signal in pre-SMA/ACC signals that outcomes are worse than expected. Subsequently, the DLPFC is a primary site for implementation of adaptive control (Kerns et al., 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004).

Prior developmental studies have shown that this feedback-learning network becomes increasingly activated with age (Crone, Zanolie, Van Leijenhorst, Westenberg, & Rombouts, 2008; Peters, Braams, Raijmakers, Koolschijn & Crone, 2014, van den Bos et al., 2009; van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008). However, it is unclear whether these neural changes reflect age differences (i.e. a maturational viewpoint), or whether they are related more to performance differences rather than age (Andersen, Visser, Crone, Koolschijn, & Raijmakers, in press; Jolles & Crone, 2012; Koolschijn, Schel, de Rooij, Rombouts, & Crone, 2011).

Effects of performance versus age are only scarcely investigated in developmental feedback learning studies. Moreover, most studies have assumed that performance differences are continuous, implying that all participants within an age group perform the task using the same strategy. However, performance is not constant within age groups; some children perform at levels similar to adults, whereas others never seem to reach the highest performing levels. It is possible that these individual differences in performance can be described by differences in strategy use. Such differences in performance and strategy use within age groups pose a considerable problem for traditional ways of analyzing developmental data, because these are based on the assumption of homogenous strategy use within age groups.

A robust approach for analyzing individual differences is a categorical latent variable model, which allows for detection of different strategies based on individuals' responses across trials. Such techniques have been applied by a number of studies that distinguished distinct learning strategies within age groups (Andersen et al., in press; Raijmakers, Dolan, & Molenaar, 2001; Schmittmann, van der Maas, & Raijmakers, 2012; Schmittmann, Visser, & Raijmakers, 2006; Speekenbrink, Lagnado, Wilkinson, Jahanshahi, & Shanks, 2010). For instance, Schmittmann et al. (2006) showed that two distinct learning strategies (resulting in relatively fast or slow learning) could be distinguished in a category-learning task. The fast and slow strategy groups both employed a learning strategy based on hypothesis-testing (as opposed to incremental, associative learning), but participants in the slow group were less efficient in their hypothesis testing compared to the fast group. This difference in efficiency was categorical. That is, with age, children were increasingly likely to belong to the faster strategy group; they were not simply less efficient in employing the same strategy. In the current study, we applied these methods to a feedback-learning task and investigated whether distinct learning strategies were also observable at the neural level.

In the current paradigm, we built on prior studies on the development of feedback learning such as a rule switch task used by Crone et al. (2008) and a rule search and application task used by van Duijvenvoorde et al. (2008), and constructed a paradigm in which correct responses could be inferred through a process of hypothesis-testing. In addition, different deductive reasoning steps could be applied to use a more efficient hypothesis testing strategy. This made the task suitable for differentiating between categorically different strategies, rather than simply assessing performance differences within one strategy. We asked 268 participants ranging from 8 to 25 years to sort stimuli in one of three locations by using positive and negative feedback. An efficient way of solving this task was to not only focus on feedback for the current stimulus but also to remember the locations for the other two stimuli. We recorded trial-by-trial data on learning efficiency and analyzed this with latent variable modeling approaches (Markov models and finite mixture models), to investigate if latent strategy groups could be detected (van der Maas & Straatemeier, 2008). As a further addition to prior research, we investigated if underlying strategy groups could be distinguished at the neural level (see also Andersen et al. (in press)). We hypothesized that age differences in neural activity for feedback learning are largely attributable to differences in strategy use. Thus, we tested whether age differences in neural activity were influenced by strategy use, or if there was also neural activity related to maturational processes per se, independent of strategy use. The main developmental effects have previously been reported by Peters et al. (2014). This dataset presents a unique opportunity for analyzing strategy-related versus age-related neural changes in feedback learning given the large-sample size across a broad developmental range.

## 2. Methods

### 2.1. Participants

The sample included 268 participants (138 females) between 8.01 and 25.95 years old ($M = 14.22$, $SD = 3.63$), who were recruited through local schools and advertisements. See Table 1 for the number of participants per age and per sex. Adult participants (18–25 years) were grouped together.

A chi square test indicated that the proportion of males to females was similar across age groups ($\chi^2(10) = 9.20$, $p = .514$). IQ scores were estimated with two subtests of the WAIS-III or WISC-III (Similarities and Block Design). Estimated IQ scores ranged from 80 to 143 ($M = 110.25$, $SD = 10.62$) and showed no correlation with age ($r = -.09$, $p = .155$). None of the participants reported a history of neurological or psychiatric disorders or current use of psychotropic medication. All anatomical MRI scans were reviewed and cleared by a radiologist. The study was approved by the Institutional Review Board at the Leiden University Medical Center and all participants (or participant's parents for minors) provided written informed consent. Adults received payment for participation, and children and their parents received presents and a fixed payment for travel reimbursement.

### 2.2. Exclusion criteria

Twenty-five participants were excluded (not included in Table 1) from further analyses after participation for the following reasons: 19 participants were excluded because movement in the MRI scanner exceeded 3.0 mm in any direction, three participants were excluded because of technical problems and three participants were excluded because they were outliers (more than three times

**Table 1**
Number of participants per age and sex.

| Age | *N* Female | *N* Male | *N* Total |
|---|---|---|---|
| 8 | 6 | 4 | **10** |
| 9 | 14 | 5 | **19** |
| 10 | 11 | 12 | **23** |
| 11 | 13 | 14 | **27** |
| 12 | 19 | 11 | **30** |
| 13 | 16 | 20 | **36** |
| 14 | 10 | 17 | **27** |
| 15 | 10 | 11 | **21** |
| 16 | 11 | 9 | **20** |
| 17 | 12 | 11 | **23** |
| 18–25 | 16 | 16 | **32** |
| ***N* Total** | **138** | **130** | **268** |