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Longitudinal development of frontoparietal activity during feedback learning: Contributions of age, performance, working memory and cortical thickness

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Feedback learning is a crucial skill for cognitive flexibility that continues to develop into adolescence, and is linked to neural activity within a frontoparietal network. Although it is well conceptualized that activity in the frontoparietal network changes during development, there is surprisingly little consensus about the direction of change. Using a longitudinal design (N = 208, 8–27 years, two measurements in two years), we investigated developmental trajectories in frontoparietal activity during feedback learning. Our first aim was to test for linear and nonlinear developmental trajectories in dorsolateral prefrontal cortex (DLPFC), superior parietal cortex (SPC), supplementary motor area (SMA) and anterior cingulate cortex (ACC). Second, we tested which factors (task performance, working memory, cortical thickness) explained additional variance in time-related changes in activity besides age. Developmental patterns for activity in DLPFC and SPC were best characterized by a quadratic age function leveling off/peaking in late adolescence. There was a linear increase in SMA and a linear decrease with age in ACC activity. In addition to age, task performance explained variance in DLPFC and SPC activity, whereas cortical thickness explained variance in SMA activity. Together, these findings provide a novel perspective of linear and nonlinear developmental changes in the frontoparietal network during feedback learning.

1. Introduction

The ability to learn from performance feedback is crucial to flexibly adapt to a changing environment. Behavioral performance during feedback learning shows a protracted development which continues into adolescence (Huizinga et al., 2006). Several studies have investigated the neural underpinnings of feedback processing. Studies in adults have shown that learning from feedback is associated with activity in a frontoparietal network, including dorsolateral prefrontal cortex (DLPFC), supplementary motor area (SMA), anterior cingulate cortex (ACC) and superior parietal cortex (SPC) (Carter and van Veen, 2007; Mars et al., 2005; Zanolie et al., 2008). Intriguingly, developmental neuroimaging studies have reported age-related activity changes in this network during feedback processing, suggesting an important link between feedback learning and neural maturation of the frontoparietal network (Crone et al., 2008; Peters et al., 2014a; Van Duijvenvoorde et al., 2008; Velanova et al., 2008). Despite these findings, little is known about developmental trajectories in the frontoparietal network and there is surprising little consistency in the direction of change, with some studies reporting increased neural activation with age and others decreased neural activation with age (Crone and Dahl, 2012).

An important question in cognitive development concerns the shape of developmental trajectories. One possible hypothesis would be that activity in the frontoparietal network during feedback learning follows a linear trajectory, based on dual-systems models predicting steadily increasing frontoparietal recruitment from childhood to adulthood combined with an adolescent peak in socio-emotional sensitivity in subcortical systems (Ernst et al., 2006; Somerville and Casey, 2010; Steinberg, 2008). On the other hand, prior cross-sectional studies provided preliminary evidence

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for non-linear developmental patterns of frontoparietal activity during feedback learning (Peters et al., 2014a; Van den Bos et al., 2009; Van Duijvenvoorde et al., 2008). These findings indicated that young adolescents are capable of recruiting frontoparietal regions but in different situations than adults, arguing against a simple frontoparietal immaturity model with linear development in cognitive control regions.

Several recent neuroimaging studies have used longitudinal measurements of neural activity to test for neurocognitive changes over development (Ordaz et al., 2013; Paulsen et al., 2015). Longitudinal designs have critical advantages over cross-sectional designs. For instance, previous studies demonstrated important individual differences in developmental trajectories that can be overlooked in cross-sectional designs (Koolschijn et al., 2011; Ordaz et al., 2013; Shaw et al., 2013). Furthermore, longitudinal designs have increased power to detect developmental change, because testing within-individual changes reduces error related to cohort differences (Fjell et al., 2010; Koolschijn et al., 2011). In the current study, neural changes in frontoparietal cortex activity were examined by testing whether frontoparietal activity during feedback learning follows a linear pattern (i.e. monotonic development over time, no adolescent-specific changes), a quadratic pattern (i.e., adolescent-specific effects) or a cubic pattern (adolescent-emergent; e.g. stable levels during childhood, steep changes in adolescence and stabilization in adulthood) (Braams et al., 2015; Somerville et al., 2013). Our longitudinal approach allows for a more specific test of the different hypotheses concerning the pattern of developmental change in frontoparietal areas.

Besides investigating age-related patterns of neural activity, a second goal of this study was to investigate other factors influencing time-related changes in frontoparietal activity in addition to age. There are multiple processes closely related to advancing age that may drive changes in neural activity. That is, an increase in age could be the sole factor explaining time-related increases or decreases in activity, but other factors might also play a role. The factors investigated in this study were task performance, working memory and structural brain development. Task performance has been shown to influence neural activity, and there is evidence that a portion of developmental changes attributed to advancing age are related more to changes in performance (Church et al., 2010; Dumontheil et al., 2010; Koolschijn et al., 2011). Here we tested whether performance on a feedback learning task partly explained changes in neural activation over time. Working memory has previously been argued to be a core prerequisite for cognitive development (Case, 1992) and cognitive control functions (Huizinga et al., 2006), and as such was investigated as an important contributor to changes over time in neural activity during feedback learning. That is, we aimed to study whether a portion of changes in neural activity during feedback learning was explained by individual differences in working memory. A final factor that was investigated is cortical thickness. Several cross-sectional studies have suggested a link between functional activity and structural gray matter in adults (Harms et al., 2013; Hegarty et al., 2012) and children (Dumontheil et al., 2010; Lu et al., 2009; Wendelken et al., 2011). It is likely that developmental changes in neural activity are at least partly influenced by structural development of these brain regions, although the longitudinal relation between structural maturation and development of brain function is not well understood.

Taken together, in this study, we tested developmental trajectories of activation in the frontoparietal network during feedback learning in a large longitudinal fMRI sample across a wide age range (N = 208, 8–27 years) with a two year interval between the first and second time point (see Peters et al., 2014a,b). Our aims were (1) to examine growth trajectories of core areas in the frontoparietal network (DLPFC, SMA, ACC and SPC) and to define the shape of age-related changes, (2) to test the additional contributions of task performance, working memory and structural development to changes over time in neural activity for feedback learning.

2. Methods

2.1. Participants

At time point 1 (TP1), a total of 299 participants between ages 8–27 years underwent an MRI scan, of which 293 participants completed the feedback learning task in the MRI scanner. Of these, 25 participants were excluded from further analyses because of excessive movement (movement >3.0 mm: n = 19), artifacts (n = 3) or because they were extreme outliers in task performance (>3x the interquartile range: n = 3). In total, 268 participants were included at TP1 (*Mean* Age = 14.52 years, *SD* = 3.55; published in Peters et al., 2014a). At time point 2 (TP2), a total of 254 of the initial 299 participants were scanned again approximately two years later (mean time = 1.99 years, SD = 0.10 years, range = 1.66–2.47 years). Reasons for not collecting a scan at TP2 (n = 45) were braces (n = 32) or no interest in participating again (n = 13). Further exclusions at TP2 were because of excessive movement at TP2 (n = 9), scanner artifacts (n = 5), loss of signal (n = 3) or extreme outliers (>3x the interquartile range) on task performance (n = 2).

Only those participants who were included at both TP1 and at TP2 were included in the analyses (N = 208). All analyses were performed on these 208 participants, except for the analyses including working memory and cortical thickness. For working memory, data were incomplete for five participants at TP1 and for two participants at TP2. For the analyses involving structural MRI data, visual quality control led to exclusion of 28 out of 208 participants: Three exclusions for insufficient quality data at both TP1 and TP2, 16 for TP1 and nine for TP2. These participants were only excluded from the analyses where cortical thickness was a factor. Taken together, the analyses with fMRI in the model contained a total of 208 participants (105 females and 103 males), the analyses with working memory a total of 201 participants and the analyses with structural MRI in the model contained a total of 177 participants.

IQ was estimated with two subtests of the WAIS-III or WISC-III (Similarities and Block Design at TP1, Vocabulary and Picture Completion at TP2). The estimated IQ-scores of the 208 included participants were within the normal range at TP1 (85–143, *Mean* = 110.91, *SD* = 9.74) and TP2 (80–147, *Mean* = 108.92, *SD* = 10.18). The study was approved by the Institutional Review Board at the Leiden University Medical Center and all participants (or participants' parents in case of minors) provided written informed consent. Adults received payment for participation and children and their parents received small presents and payment for participation. Participants did not report psychiatric or neurological diagnosis, and no current use of psychotropic medication. All anatomical MRI scans were reviewed and cleared by a radiologist.

2.2. Feedback learning task

Participants performed a child-friendly feedback learning task in the MRI scanner described in detail earlier (Peters et al., 2014a,b). In short, on each trial, participants viewed a screen with three boxes at the top part of the screen (Fig. 1a). At the bottom part of the screen, a stimulus picture was presented, which was one of three possible stimuli. Participants were informed that all pictures belonged in one of the three boxes and that they had to find the correct box for each picture. Performance feedback was provided in the form of a plus-sign ('+') for correct choices (positive feedback) and a minus-sign ('−') for incorrect choices (negative feedback). Stimuli were presented in a pseudorandom order (maximum two identical pictures in a row). The sequence ended after 12