



Changes in ventromedial prefrontal and insular cortex support the development of metamemory from childhood into adolescence

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Metamemory monitoring, or the ability to introspect on the accuracy of one's memories, improves considerably during childhood, but the underlying neural changes and implications for intellectual development are largely unknown. The present study examined whether cortical changes in key brain areas hypothesized to support metacognition contribute to the development of metamemory monitoring from late childhood into early adolescence. Metamemory monitoring was assessed among 7- to 12-y-old children ($n = 145$) and adults ($n = 31$). Children returned for up to two additional assessments at 8 to 14 y of age ($n = 120$) and at 9 to 15 y of age ($n = 107$) ($n = 347$ longitudinal scans). Results showed that metamemory monitoring continues to improve from childhood into adolescence. More pronounced cortical thinning in the anterior insula and a greater increase in the thickness of the ventromedial prefrontal cortex over the three assessment points predicted these improvements. Thus, performance benefits are linked to the unique patterns of regional cortical change during development. Metamemory monitoring at the first time point predicted intelligence at the third time point and vice versa, suggesting parallel development of these abilities and their reciprocal influence. Together, these results provide insights into the neuroanatomical correlates supporting the development of the capacity to self-reflect, and highlight the role of this capacity for general intellectual development.

episodic memory | metacognition | confidence | cortical thickness | intelligence

The ability to introspect on memory accuracy, or metamemory monitoring (1), is essential for guiding learning and decision making (2). If a student does not feel confident about the material for an upcoming examination, she may decide to revisit the material; similarly, an eyewitness may refrain from volunteering potentially incriminating information if he recognizes that his memory is uncertain.

Cross-sectional studies have demonstrated improvements in metamemory monitoring during the elementary school years, with older children's confidence judgments showing greater discrimination between accurate and inaccurate memories than younger children's (3–6). However, it remains an open question as to whether this development extends into adolescence when affective processes might alter or influence behavioral regulation (7). The structural brain changes that support metamemory development are also largely uncharted. This limitation is significant in the literature because understanding how metamemory develops into adolescence and how it is related to brain development can help elucidate factors that foster or limit learning and decision making at a time when children become increasingly independent learners and problem solvers.

Research in adults can help formulate predictions about the brain regions that support the development of metamemory monitoring. In adults, individual differences in metacognitive monitoring have been associated with structural differences in the anterior prefrontal cortex (APFC) (8, 9), ventromedial prefrontal

cortex (vmPFC) (10), dorsal anterior cingulate cortex (dACC) (11), or anterior insula (12), among other areas. Although the exact role of these areas is unclear, one recent proposal (13) is that prefrontal regions interact with interoceptive cortices, including insular and cingulate cortex, in support of metacognition. By this account, the insula and dACC provide inputs about ongoing cognitive performance (e.g., error signals, uncertainty signals) that are integrated with current goals and beliefs in the prefrontal cortex (PFC), resulting in introspective reports and subsequent decisions.

We examined a cohort of 145 children between 7 and 15 y of age who underwent structural magnetic resonance imaging (MRI) on up to three measurement occasions (Fig. 1A; 347 longitudinal scans). A sample of 31 adults was assessed for cross-sectional comparisons. Participants completed a memory task with an attentional manipulation during encoding, which resulted in different levels of difficulty and memory accuracy. Participants viewed a series of scenes under one of three conditions varying in attention demands (Fig. 1B). During retrieval, participants viewed novel scenes or studied scenes from the different conditions and indicated their confidence about their scene recognition judgments (Fig. 1B). Differences in confidence distributions for correct and incorrect responses may differ as a function of levels of memory accuracy across development. Thus, we accounted for these differences

Significance

Metamemory monitoring, or the ability to introspect about the accuracy of our memories, improves during childhood and is intimately connected with learning because it limits memory errors and can promote additional information gathering or review. However, the neural changes underlying this development and its relevance for general intellectual development are largely unknown. We assessed 7- to 15-year-old children on multiple occasions and showed continued longitudinal improvements in introspection on memory accuracy into adolescence. We demonstrated that introspection ability contributes to longitudinal changes in children's general intelligence and identified specific patterns of developmental changes in brain anatomy that predicted improvements in metamemory monitoring. This research highlights the mechanisms supporting metamemory development and their critical role for learning.

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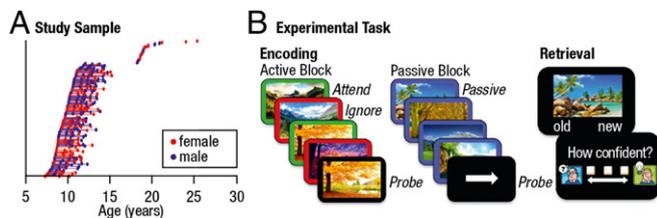


Fig. 1. Sample description and experimental design. (A) Each unique participant is represented in a different row with the participant's corresponding scans (represented by a circle) connected by a line. (B) During encoding, participants saw outdoor scenes divided into active or passive blocks. Active blocks required participants to modulate their attention: Participants were instructed to attend to scenes when they were presented on a green background and to ignore (but still view) them when they were presented on a red background. After each active block, participants were presented with a probe that was either one of the attend scenes or a novel scene, and were asked to indicate whether it had been presented in the previous block. During passive blocks, participants were instructed to view scenes presented on a blue background passively and to indicate the direction of an arrow presented as a probe. During retrieval, participants viewed studied scenes from all attention conditions (i.e., attend, ignore, passive; attend scenes used as active probes were excluded) and novel scenes, and indicated whether the scenes had been seen previously during encoding or if they were new (i.e., never seen before). After each recognition response, participants indicated their confidence in their decision on a three-point scale anchored by different faces.

in memory accuracy in our investigation of age differences and change in metamemory during the transition from childhood to adolescence.

We investigated how structural changes in the anterior insula, dACC, vmPFC, and APFC contribute to the development of metamemory monitoring in late childhood and adolescence. Research has shown that development in the insular cortex follows a roughly linear trajectory, with cortical thinning starting earlier during childhood (14), whereas lateral and medial PFC development is characterized by an initial increase in thickness until around 9 y of age, followed by subsequent thinning (15). Thus, one may predict that earlier maturing insular regions involved in error or performance monitoring may contribute to metamemory monitoring earlier in development than later maturing PFC regions, which support more elaborate control operations. This prediction is consistent with the idea that PFC areas may show only weak relations with metamemory change at younger ages, reflecting the later onset of cortical thinning.

Alternatively, developmental improvements in metamemory monitoring may emerge as a function of the specific trajectories of regional cortical change. If so, thinning in insular regions and thickening in medial and lateral PFC regions (in which gray matter thickness continues to increase during childhood) should contribute to metamemory development. This alternative prediction is consistent with the idea that optimal development emerges from the contribution of all relevant regions across development, albeit in ways that are constrained by their specific pattern of cortical change (16).

The present study also offered the opportunity to garner evidence for the relevance of metamemory monitoring for cognitive development beyond memory accuracy (1). If the capacity to introspect on memory accuracy is relevant for learning, it might be more broadly important for intellectual development. To date, no study has addressed this question. To fill this gap, we examined the cross-sectional and longitudinal relations between metamemory monitoring and intelligence (IQ) in late childhood and adolescence.

Results

Age Differences and Change in Recognition Accuracy over Time. Longitudinal analyses were conducted using multilevel models and included data from children at all available time points (*Materials and Methods*). Longitudinal improvements in recognition accuracy were investigated using a model that included the intercept centered at 9.6 y along with linear and quadratic change over time. Cross-

sectional age differences in recognition accuracy at the first time point (T1) are reported elsewhere (17). Longitudinally, we found significant linear ($b = 0.061$, $P < 0.05$) and quadratic ($b = -0.014$, $P < 0.05$) effects of time, demonstrating that recognition accuracy improved over time, but changes were greater earlier compared with later in time (Fig. S1).

Furthermore, we assessed whether the manipulation of task difficulty resulted in the expected differences in recognition accuracy. Across all children and time points, accuracy in the attend condition was higher than in the ignore condition [$b = 0.124$, $P < 0.05$, Bonferroni-corrected P (P_{Bonf}) < 0.05], which, in turn, was higher than in the passive condition ($b = 0.050$, $P < 0.05$, $P_{Bonf} < 0.05$) (Fig. S1). Longitudinal improvements in the attend condition were larger relative to the passive condition at a trend level ($b = 0.020$, $P < 0.05$, $P_{Bonf} = 0.09$), but not relative to the ignore condition ($P > 0.54$). The passive and ignore conditions did not differ from each other, ($P > 0.13$). No remaining interactions were significant at the $P < 0.05$ level (all P s > 0.08). Overall, recognition accuracy improved across conditions over time, with the largest improvements in the attend condition.

Age Differences and Change in Metamemory Monitoring over Time.

For an initial assessment of age differences in metamemory monitoring at T1, we first compared average confidence for correct and incorrect responses across children and adults (Fig. 2A). Effective metamemory monitoring is reflected in higher confidence judgments for correct than incorrect responses (2). Age differences in confidence judgments at T1 were examined via an age group (younger children vs. older children vs. adults) \times condition (attend vs. ignore vs. passive) \times recognition accuracy (correct vs. incorrect) mixed ANOVA.

We found a significant age group \times accuracy interaction [$F(2,169) = 11.32$, $P < 0.05$, partial η^2 (η_p^2) = 0.12], such that confidence was higher when participants responded correctly than incorrectly on the recognition test. This difference was significantly greater in adults relative to both younger ($P < 0.05$, $P_{Bonf} < 0.05$) and older ($P < 0.05$, $P_{Bonf} < 0.05$) children. Older and younger children did not differ from each other ($P = 0.10$, $P_{Bonf} = 0.30$). These age differences in the ability to introspect on memory accuracy were driven by lower confidence for incorrect responses in adults compared with both younger and older children [$F(2,169) = 5.90$, $P < 0.05$, $\eta_p^2 = 0.07$]. In contrast, there were no age differences in confidence for correct responses [$F(2,169) = 0.34$, $P = 0.71$, $\eta_p^2 = 0.00$]. Critically, this age group \times accuracy interaction in confidence judgments remained significant when recognition accuracy was included as a covariate [$F(2,168) = 9.78$, $P < 0.05$, $\eta_p^2 = 0.10$], suggesting that age differences in metamemory were unlikely to be driven by age differences in memory accuracy.

Condition (attend vs. ignore vs. passive) was included as a factor in the ANOVA to assess whether the attentional manipulation at encoding contributed to age differences in metamemory monitoring at T1. We observed a significant condition \times accuracy interaction, [$F(2,338) = 9.96$, $P < 0.05$, $\eta_p^2 = 0.06$]. Confidence for correct responses was higher in the attend than ignore condition ($P < 0.05$, $P_{Bonf} < 0.05$), which, in turn, was higher than in the passive condition ($P < 0.05$, $P_{Bonf} < 0.05$). Confidence for incorrect responses did not differ across conditions ($P > 0.47$). This pattern of condition effects was observed in all age groups and did not differ across age groups ($P = 0.37$). No remaining interactions were significant (P s > 0.24).

Together, although confidence for correct responses was modulated by condition, in line with more mnemonic evidence available in the attend condition, these effects did not depend on age group. Thus, for all subsequent analyses, we collapsed across conditions and examined the development of metamemory monitoring across the entire task to increase the reliability of our index of metamemory monitoring (9).

To examine longitudinal changes in metamemory monitoring, we calculated metamemory resolution as the area under the type 2 receiver operating characteristic curve (AUCROC2) collapsed across conditions. This measure captures how well participants can discriminate between correct and incorrect responses, and it is

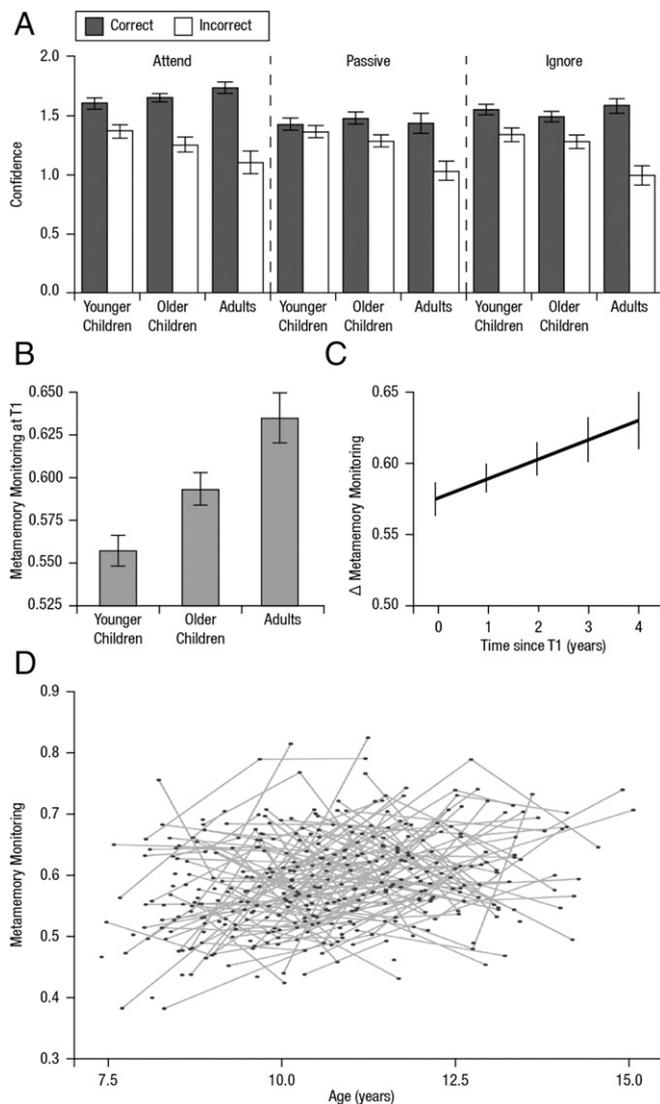


Fig. 2. Confidence judgments and metamemory monitoring. (A) Average confidence for each condition and age group at T1. Errors bars: ± 1 SEM. (B) At T1, there were reliable age differences in metamemory monitoring (i.e., AUCROC2) among all three groups [$F(2,173) = 10.8, P < 0.05$], which persisted after accounting for memory accuracy. Errors bars: ± 1 SEM. (C) Predicted change in metamemory monitoring (i.e., AUCROC2) over time. Error bars: maximum and minimum values. (D) Individual trajectories of metamemory monitoring (i.e., AUCROC2) in children. Lines represent unique participants with their corresponding data points represented by a circle.

not affected by metacognitive bias, or an individual's tendency to report high confidence (18). Longitudinal improvements in metamemory resolution were investigated using a model with an intercept centered at 9.6 y and linear change over time. Metamemory resolution was higher in older than younger children at the initial assessment [$b = 0.010, P < 0.05$; a cross-sectional comparison with adults at T1 is provided in Fig. 2B]. The linear effect of time was also significant ($b = 0.014, P < 0.05$), demonstrating a time-related increase in metamemory resolution (Fig. 2C and D). Time-related improvements in metamemory resolution persisted ($b = 0.012, P < 0.05$) when recognition accuracy was included in the model, indicating that longitudinal increases in metamemory monitoring are unlikely to reflect merely improvements in recognition accuracy. These results were replicated with an alternative measure of metamemory sensitivity, meta d' , which is based on signal detection theory (19) (SI Results and Fig. S2).

Age Differences and Change in Cortical Thickness over Time. Cortical thickness was extracted from anatomical regions of a priori interest (ROIs) in several frontal subregions, including the left and right anterior insula, vmPFC, APFC, and dACC, which have been implicated in metacognition in adults (a detailed ROI definition is provided in *Materials and Methods*). First, we examined cross-sectional age differences in cortical thickness among younger children, older children, and adults at T1 (Fig. 3). Reliable age differences were found in all ROIs ($P_{Bonf} < 0.05$), such that in all ROIs, thickness was lower in adults compared with both younger and older children ($P_{Bonf} < 0.05$), who did not differ from each other ($P_{Bonf} > 0.05$). These results suggest protracted cortical development of the regions supporting metamemory monitoring.

Next, we examined longitudinal change in cortical thickness among children using a model that included the intercept centered at 9.6 y and linear change over time. Parameter estimates and statistical tests for each ROI are presented in Fig. 3 and Table 1 (individual data points are presented in Fig. S3). In the left hemisphere, the main effect of T1 age was significant in the insula and at a trend level in the vmPFC after correction for multiple comparisons. In both areas, older children displayed lower cortical thickness than younger children at the initial assessment. The linear effect of time was significant in the insula, but not in the APFC, vmPFC, or dACC (Fig. 3). Follow-up analyses comparing change across left ROIs confirmed that cortical thinning in the anterior insula was significantly greater than change in the dACC ($P < 0.05, P_{Bonf} < 0.05$); vmPFC ($P < 0.05, P_{Bonf} < 0.05$); and, at a trend level, APFC ($P < 0.05, P_{Bonf} = 0.09$).

In the right hemisphere, the linear effect of time was significant in the insula and vmPFC, but not in the dACC and APFC (Fig. 3 and Table 1). Whereas the insula demonstrated reliable

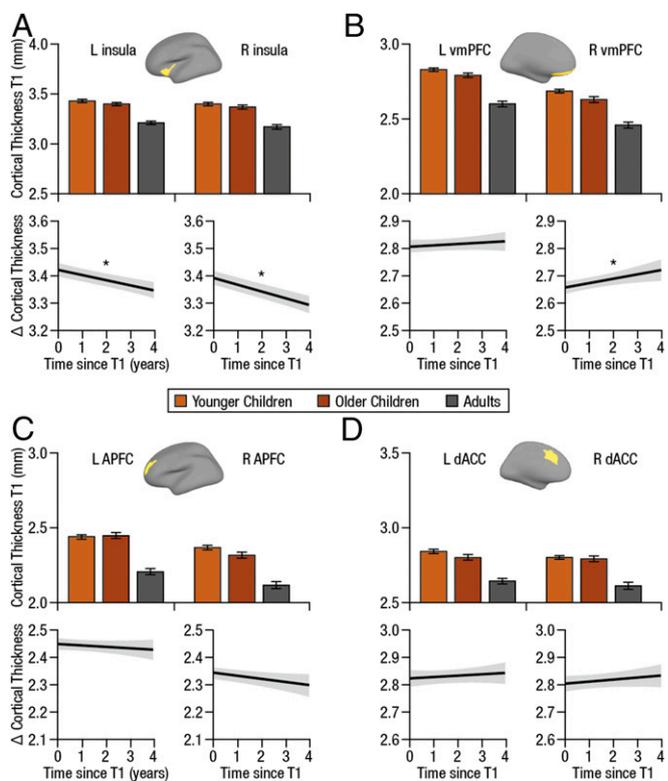


Fig. 3. Cross-sectional age differences and longitudinal change in cortical thickness in bilateral anterior insula (A), vmPFC (B), APFC (C), and dACC (D). (Top) Age differences in cortical thickness among groups at T1 for each ROI. Errors bars: ± 1 SEM. (Bottom) Predicted cortical change (in millimeters) in children over time. Confidence bands indicate maximum and minimum values. $*P < 0.05$. L, left; R, right.

Table 1. Longitudinal change in cortical thickness across ROIs in children

ROI	Intercept (SE)	Age T1, y (SE)	Time since T1, y (SE)
L APFC	2.45 [†] (0.01)	-0.004 (0.01)	-0.005 (0.01)
R APFC	2.34 [†] (0.02)	-0.012 (0.01)	-0.011 (0.006)
L vmPFC	2.81 [†] (0.01)	-0.020* (0.01)	0.004 (0.005)
R vmPFC	2.66 [†] (0.01)	-0.019* (0.01)	0.016 [†] (0.01)
L insula	3.42 [†] (0.01)	-0.026 [†] (0.01)	-0.019 [†] (0.004)
R insula	3.39 [†] (0.01)	-0.013 (0.01)	-0.023 [†] (0.004)
L dACC	2.85 [†] (0.02)	-0.011 (0.01)	0.005 (0.006)
R dACC	2.80 [†] (0.01)	-0.010 (0.01)	0.007 (0.006)

Gender effects were reliable only in the left dACC, with lower thickness in males relative to females ($b = -0.06$, $SE = 0.02$). L, left; R, right.

* $P < 0.05$, uncorrected.

[†] $P < 0.05$, corrected (in bold).

thinning over time, the effect of time was positive in the vmPFC, suggesting that cortical thickness in this area increased over time within individuals. In addition, a trend toward thinning was observed in the APFC ($P = 0.05$, before correction for multiple comparisons). A direct comparison of the right ROIs confirmed reliable differences in the developmental trajectory between the insula and vmPFC ($P < 0.05$, $P_{Bonf} < 0.05$) and between the vmPFC and APFC ($P < 0.05$, $P_{Bonf} < 0.05$), but not between the vmPFC and dACC ($P = 0.07$, $P_{Bonf} = 0.21$). The quadratic effect of time and the higher order interactions were not reliable in any ROI in the left or right hemisphere.

Together, these longitudinal analyses demonstrate distinct developmental trajectories across cortical areas, with thinning in the insula, thickening in the vmPFC, and no reliable change in the dACC or APFC over the studied time period.

Cortical Changes Predict Metamemory Monitoring Improvement over Time. Having provided evidence for cortical development over time in children, we examined whether these cortical changes predicted change in metamemory monitoring. To this end, we examined whether initial thickness and change in thickness in our ROIs over time predicted improvements in metamemory resolution, measured as the AUCROC2. In the left hemisphere, children with more pronounced insula thinning over time ($b = -0.160$, $P < 0.05$; Fig. 4A), as well as those children who showed more pronounced increase in vmPFC thickness over time ($b = 0.158$, $P < 0.05$; Fig. 4B), exhibited a higher rate of metamemory monitoring improvement over time. Change in the APFC ($b = 0.023$, $P = 0.63$) or dACC ($b = 0.017$, $P = 0.68$) did not predict change in metamemory resolution over time. Additional control analyses demonstrated that the rate of increase in metamemory resolution was still related to change in the left vmPFC ($b = 0.13$, $P = 0.02$) and left anterior insula ($b = -0.14$, $P = 0.01$) after controlling for recognition accuracy (SI Results).

In the right hemisphere, greater insular thinning over time emerged as a predictor of overall metamemory resolution at a trend level ($b = -0.090$, $P = 0.05$) and was not related to the rate of metamemory change over time. A model collapsing across hemispheres revealed similar results as those results observed in the left hemisphere (SI Results).

Together, these results demonstrate that cortical development in frontal subregions contributes to improvements in children's ability to introspect on their memory accuracy. However, the way in which different cortical regions contribute to metamemory monitoring depends on their unique pattern of cortical change. Our results suggest that the rate of increase in monitoring ability in the transition to adolescence is related to insular thinning and an increase in vmPFC thickness over time.

Relation of Metamemory Monitoring to Intellectual Ability. Metamemory monitoring ability is thought to support the regulation of learning (1). Thus, we asked whether metamemory

development was related to change in IQ, which is related to the general capacity to learn (20). IQ measures were available only at two time points: T1 and T3. Thus, path modeling (Fig. S4) was used to examine the concurrent relations among metamemory resolution (indexed by AUCROC2), recognition accuracy, and IQ, as well as their longitudinal relations. The model showed a good fit [$\chi^2(6) = 3.46$, comparative fit index (CFI) = 1.00, rms error of approximation (RMSEA) = 0.00, 90% confidence interval = 0.00–0.09]. There were trend-level relations between IQ and metamemory resolution at T1 ($r = 0.19$, $P = 0.05$) and at T3 ($r = 0.17$, $P = 0.07$). Critically, IQ at T1 predicted metamemory resolution at T3 ($\beta = 0.24$, $P < 0.05$), and metamemory resolution at T1 predicted IQ at T3 ($\beta = 0.26$, $P < 0.05$). Thus, metamemory resolution and IQ were not only related concurrently but also demonstrated reciprocal influences on each other over time, of similar magnitude in both directions. These relations between metamemory monitoring and intellectual ability are unlikely to reflect a common relation to memory ability, because both the cross-sectional and longitudinal relations between the two measures were present with memory accuracy included in the model (Fig. S4).

Discussion

Developmental scientists have long been interested in the development of metacognition (2), including introspection and control of ongoing information processing (21). We provide longitudinal evidence that children's ability to calibrate their subjective confidence to their objective memory accuracy continues to improve into adolescence, and that these changes do not simply reflect improvements in overall accuracy. Our findings align well with the extensive literature on continued development of executive functioning and decision making into adolescence (7, 22). Given that the ability to introspect on memory accuracy forms the basis for making effective decisions and for regulating behavior (1, 23), future research should examine the extent to which adolescents can effectively harness their metamemory judgments to control learning and memory retrieval actively, and whether these findings extend to socially relevant contexts, which can influence adolescents' risk taking and decision making (24). Critically, we provide a demonstration of the cortical changes supporting metamemory improvements during development and their relation to intellectual development.

The results of the present study shed light onto the neural mechanisms supporting the development of metamemory monitoring. Changes in the anterior insula and vmPFC predicted improvements in metamemory over time. These brain regions have been implicated in metacognition by structural and functional neuroimaging studies of young (25, 26) and

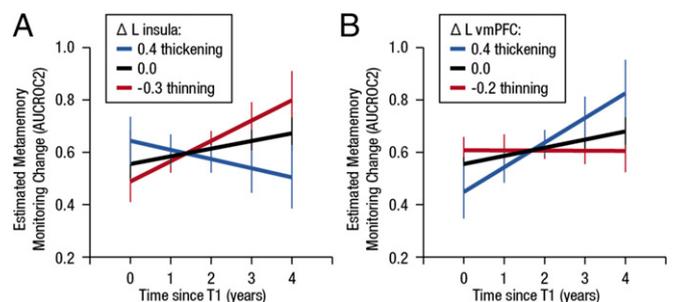


Fig. 4. Results of models testing the relation between cortical thickness change and metamemory monitoring improvement. Plots show interaction effects as predicted metamemory monitoring (y axis) over time (x axis) for three fixed values (lines) of change in cortical thickness in the left anterior insula (A) and left vmPFC (B). Fixed values of cortical thickness change were chosen to demonstrate maximal increase in thickness (blue), no change in thickness (black), and maximal decrease in thickness (red) in the anterior insula and vmPFC to visualize the interactions between time and cortical change. Error bars indicate maximum and minimum values.

older (27) adults. Additionally, there is evidence that vmPFC damage is associated with deficits in metamemory monitoring and control (10).

The present study linked patterns of cortical change and behavioral improvement in metamemory during childhood and adolescence. The anterior insula and vmPFC showed distinct patterns of cortical change; whereas thickness in the insula decreased, thickness in the vmPFC increased over time. Insular thinning is largely consistent with the literature (14, 15), and the thickening pattern in the vmPFC is consistent with previous research examining children between 5 and 11 y of age (28). The longitudinal finding among children paired with the cross-sectional results demonstrating a thinner vmPFC in adults suggests a more prolonged developmental period of increase in vmPFC thickness.

Consistent with these divergent patterns of change in the two regions, thinning in the anterior insula and thickening in the vmPFC over time predicted the rate of improvement in metamemory monitoring. Thus, the contributions of these regions to metamemory development reflect the unique direction of developmental cortical change in each region. These results offer initial insights into the dynamic nature of the cortical mechanisms supporting metamemory. Future research is needed to test a critical prediction emerging from the current findings, namely, that the direction of the relation between vmPFC thickness and metamemory monitoring is reversed later in adolescence when the vmPFC starts thinning.

The anterior insula and cingulate are engaged in performance and error monitoring processes, and provide inputs for the monitoring and control of cognitive processing by frontal and parietal regions (13, 29). This account is consistent with the anatomy of the anterior insula: It is highly interconnected to multiple brain regions and has a high concentration of von Economo neurons, which may enable fast communication among regions (30). Consequently, the anterior insula has been implicated in various processes, including changes in bodily states, emotional and self-awareness, as well as cognition and decision making (30, 31).

It is tempting to hypothesize that the earlier starting thinning process in the anterior insula may be functionally important in providing the initial building blocks of the capacity to self-reflect: Performance or error monitoring processes supported by the insula may constitute an important stepping stone for development of the ability to introspect on memory accuracy and uncertainty. Indeed, in a functional MRI study, we showed that insular activity during failure to retrieve episodic detail on a source memory task, regardless of whether children were aware that they were failing, predicted longitudinal increases in APFC activity associated with decisions to report memory uncertainty (32). No direct evidence exists, however, supporting the necessity of this earlier mechanism for the development of effective metacognitive ability, and future research should establish whether it is indeed a necessary precursor.

Our results corroborate previous research implicating the vmPFC in metamemory and metacognition more generally (10, 33). The specific computational function in this region has been linked to the assignment of value to different choice options, integrating choice value with confidence (33), an initial “feeling of rightness” assessment in memory (34), or reward-based choices. Whether and how these different operations are already in place in childhood should be examined in future research. Our result that vmPFC change predicted metamemory improvement is consistent with neuroimaging studies showing age differences in medial PFC activity among adolescents (7) in tasks requiring other forms of self-reflection.

We note that the relation between change in vmPFC thickness and metacognitive improvement persisted when memory accuracy was accounted for, either at the individual level using meta d'/d' (SI Results) or as part of the modeling of longitudinal change with the inclusion of memory accuracy in the model. In

contrast, the relation between insular thinning and metamemory was reliable only when recognition accuracy was accounted for in the longitudinal model. The attenuated relation when using meta d'/d' (SI Results) suggests that the developmental effects of the anterior insula may not be specific to metacognitive processes, consistent with the idea that this region contributes to error and uncertainty monitoring processes that are used as inputs by various higher order systems (29).

In the current study, we did not find reliable relations between APFC and dACC thickness and metamemory monitoring. However, we observed limited cortical change in these regions, which may preclude our ability to detect brain–behavior relations. Of note, a few studies in adults found that the APFC was related to the monitoring of perceptual, but not memory, decisions (e.g., ref. 9). An important question for future research is how cortical changes in frontal subregions contribute to metacognitive development in other domains. Areas in the posterior parietal lobes have also been implicated in metacognition (9, 26) and could be investigated in the future. Additional exploratory ROI and whole-brain analyses indicated that these regions were not related to metamemory improvement in the present study (SI Results).

It should be noted that one important difference between previous research and our study is that the former has primarily used object pictures (in younger children) or words (mostly in older children) to investigate metacognitive monitoring. Our use of outdoor scenes likely limited the use of elaborative strategies during encoding, which may magnify age differences. The improvements reported with these stimuli suggest that increases in metamemory monitoring occur regardless of elaborative encoding strategies.

The development of the capacity to introspect on memory accuracy was closely related to change in overall cognitive ability. IQ at T1 predicted future monitoring ability at T3, and monitoring at T1 predicted future IQ at T3; together, these results suggest that metamemory monitoring and IQ might mutually influence each other during development. This finding is consistent with the traditional notion that metacognition is one of the key predictors of cognitive development (2). Despite its intuitive appeal, this notion had not been subjected to empirical testing with longitudinal designs. Our results provide evidence for these reciprocal relations in the transition from childhood into adolescence. We note that a recent cross-sectional study that examined monitoring of perceptual decisions did not find any relations to IQ in 11- to 17-y-olds (35). Although there are notable differences between the two studies, including participants' age range, stimuli, and experimental procedures, these different results raise an intriguing question concerning the generality versus domain specificity of the relation between metacognitive monitoring and IQ. Discrepancies in the associations between cortical structure and behavior discussed earlier also point to possible differences between monitoring of memory and perception. It is possible that relations with IQ are restricted to, or stronger in, domains in which introspection is directed to higher order cognitive functions like memory. This possibility should be examined in future research.

In conclusion, the present study represents a first step toward understanding the neural mechanisms supporting metamemory development, which is important for learning and decision making. Our results demonstrate that metamemory monitoring continues to develop beyond middle childhood, supported by structural changes in the anterior insula and the ventromedial PFC, and that its development is reciprocally related to changes in general intellectual ability. A better understanding of the neurocognitive mechanisms supporting metamemory, and metacognition in general, may be particularly critical in the context of education, where finding effective ways to foster metacognitive monitoring and its utilization for metacognitive control may facilitate instruction and improve self-regulated learning and problem solving.

Materials and Methods

Participants. At T1, 145 children provided behavioral data [$M(SD) = 9.57(1.09)$ y, 74 females] and 141 provided structural MRI data. T1 also included behavioral and structural MRI data from 31 adults [$M(SD) = 19.46(1.61)$ y, 18 females]. T2 occurred ~ 1.4 y later and included 120 children with behavioral data [$M(SD) = 10.88(1.22)$ y, 57 females] and 117 children with structural MRI data. T3 occurred ~ 1.3 y later and included 107 children with behavioral data [$M(SD) = 12.22(1.3)$ y, 48 females] and 89 with structural MRI data (*SI Materials and Methods*). The study was approved by the Institutional Review Board of the University of California, Davis. Informed consent was obtained from all participants and their parents.

Recognition Memory Task. Participants were each presented with 24 blocks of four outdoor scenes that were assigned to either an active encoding condition (16 blocks) or a passive encoding condition (eight blocks) (Fig. 1*B*). Each scene was presented for 3 s, and the order of passive and active blocks was counter-balanced across participants. Probes were included after each block to ensure that participants followed instructions and viewed the stimuli. After encoding, participants were given a self-paced recognition test involving studied scenes from all blocks ($n = 48$) or novel scenes ($n = 32$). After each old/new recognition decision, participants provided confidence ratings on a three-point scale.

MRI Acquisition and Analysis. A high-resolution, whole-brain, magnetization-prepared rapid gradient-echo scan was acquired (*SI Materials and Methods*), and reconstruction was performed using Freesurfer 5.3 following standard procedures (36). Cortical thickness was extracted from the following ROIs based on the Destrieux atlas (37): vmPFC, defined as the orbital gyrus, orbital sulcus, and gyrus rectus; insula, defined as the anterior insula sulcus and short insular gyrus; APFC, defined as the middle frontal sulcus containing a majority of the coordinates reported in association with metacognitive

ability in adults (9, 18); and dACC, corresponding to the middle anterior cingulate gyrus and sulcus.

Statistical Analyses. Cross-sectional analyses at T1 compared children, median-split into younger children (7.41–9.59 y, $n = 72$) and older children (9.61–12.04 y, $n = 73$) and adults. Recognition accuracy was calculated as the difference between hit and false alarm rates (38). Metamemory resolution was calculated as the area under the AUCROC2 collapsed across all conditions. This measure captures how well observers can discriminate between correct and incorrect responses in their confidence judgments and is estimated by plotting varying levels of cumulative confidence pairs for of correct vs. incorrect responses and calculating the area under the AUCROC2 (18). Longitudinal analyses were conducted using multilevel models implemented in lme4 (39) (a model description is provided in *SI Materials and Methods*). First, we examined longitudinal change in recognition accuracy, AUCROC2, and cortical thickness by testing for linear and, if necessary (*SI Materials and Methods*), quadratic effects of time in children. Second, we examined the relation between cortical change across ROIs and change in the AUCROC2 over time. To ensure that our results were not dependent on the precise measure of metamemory, we also calculated meta d' as a model-based measure of metamemory monitoring (19) (*SI Results*).

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- Koriat A, Goldsmith M (1996) Monitoring and control processes in the strategic regulation of memory accuracy. *Psychol Rev* 103:490–517.
- Flavell JH (1979) Metacognition and cognitive monitoring: A new area of cognitive-developmental inquiry. *Am Psychol* 34:906–911.
- Roebbers CM, Howie P (2003) Confidence judgments in event recall: Developmental progression in the impact of question format. *J Exp Child Psychol* 85:352–371.
- Ghetti S, Castelli P, Lyons KE (2010) Knowing about not remembering: Developmental dissociations in lack-of-memory monitoring. *Dev Sci* 13:611–621.
- Ghetti S, Mirandola C, Angelini L, Cornoldi C, Ciarra E (2011) Development of subjective recollection: Understanding of and introspection on memory states. *Child Dev* 82:1954–1969.
- Fandakova Y, Shing YL, Lindenberger U (2013) Differences in binding and monitoring mechanisms contribute to lifespan age differences in false memory. *Dev Psychol* 49:1822–1832.
- Blakemore SJ, Robbins TW (2012) Decision-making in the adolescent brain. *Nat Neurosci* 15:1184–1191.
- Fleming SM, Weil RS, Nagy Z, Dolan RJ, Rees G (2010) Relating introspective accuracy to individual differences in brain structure. *Science* 329:1541–1543.
- McCurdy LY, et al. (2013) Anatomical coupling between distinct metacognitive systems for memory and visual perception. *J Neurosci* 33:1897–1906.
- Hebscher M, Barkan-Abramski M, Goldsmith M, Aharon-Peretz J, Gilboa A (2016) Memory, decision-making, and the ventromedial prefrontal cortex (vmPFC): The roles of subcallosal and posterior orbitofrontal cortices in monitoring and control processes. *Cereb Cortex* 26:4590–4601.
- Baird B, Cieslak M, Smallwood J, Grafton ST, Schooler JW (2015) Regional white matter variation associated with domain-specific metacognitive accuracy. *J Cogn Neurosci* 27:440–452.
- Sinanaj I, Cojan Y, Vuilleumier P (2015) Inter-individual variability in metacognitive ability for visuomotor performance and underlying brain structures. *Conscious Cogn* 36:327–337.
- Fleming SM, Dolan RJ (2012) The neural basis of metacognitive ability. *Philos Trans R Soc Lond B Biol Sci* 367:1338–1349.
- Vandekar SN, et al. (2015) Topologically dissociable patterns of development of the human cerebral cortex. *J Neurosci* 35:599–609.
- Shaw P, et al. (2008) Neurodevelopmental trajectories of the human cerebral cortex. *J Neurosci* 28:3586–3594.
- Shaw P, et al. (2006) Intellectual ability and cortical development in children and adolescents. *Nature* 440:676–679.
- Wendelken C, et al. (2015) White matter tracts connected to the medial temporal lobe support the development of mnemonic control. *Cereb Cortex* 25:2574–2583.
- Fleming SM, Lau HC (2014) How to measure metacognition. *Front Hum Neurosci* 8:443.
- Maniscalco B, Lau H (2012) A signal detection theoretic approach for estimating metacognitive sensitivity from confidence ratings. *Conscious Cogn* 21:422–430.
- Kline P (1991) *Intelligence: The Psychometric View* (Routledge, London).
- Schneider W, Pressley M (1997) *Memory Development Between Two and Twenty* (Lawrence Erlbaum Associates, Mahwah, NJ).
- Luna B, Padmanabhan A, O'Hearn K (2010) What has fMRI told us about the development of cognitive control through adolescence? *Brain Cogn* 72:101–113.
- Hembacher E, Ghetti S (2014) Don't look at my answer: Subjective uncertainty underlies preschoolers' exclusion of their least accurate memories. *Psychol Sci* 25:1768–1776.
- Crone EA, Dahl RE (2012) Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat Rev Neurosci* 13:636–650.
- Chua EF, Schacter DL, Rand-Giovannetti E, Sperling RA (2006) Understanding metamemory: Neural correlates of the cognitive process and subjective level of confidence in recognition memory. *Neuroimage* 29:1150–1160.
- Fleck MS, Daselaar SM, Dobbins IG, Cabeza R (2006) Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cereb Cortex* 16:1623–1630.
- Cosentino S, et al. (2015) The right insula contributes to memory awareness in cognitively diverse older adults. *Neuropsychologia* 75:163–169.
- Sowell ER, et al. (2004) Longitudinal mapping of cortical thickness and brain growth in normal children. *J Neurosci* 24:8223–8231.
- Menon V, Uddin LQ (2010) Saliency, switching, attention and control: A network model of insula function. *Brain Struct Funct* 214:655–667.
- Craig AD (2009) How do you feel—now? The anterior insula and human awareness. *Nat Rev Neurosci* 10:59–70.
- Singer T, Critchley HD, Preusschoff K (2009) A common role of insula in feelings, empathy and uncertainty. *Trends Cogn Sci* 13:334–340.
- Fandakova Y, et al. (2016) The importance of knowing when you don't remember: Neural signaling of retrieval failure predicts memory improvement over time. *Cereb Cortex*, 10.1093/cercor/bhw352.
- De Martino B, Fleming SM, Garrett N, Dolan RJ (2013) Confidence in value-based choice. *Nat Neurosci* 16:105–110.
- Moscovitch M, Winocur G (2002) The frontal cortex and working with memory. *Principles of Frontal Lobe Function*, eds Stuss DT, Knight R (Oxford Univ Press, New York), pp 188–209.
- Weil LG, et al. (2013) The development of metacognitive ability in adolescence. *Conscious Cogn* 22:264–271.
- Fischl B, Dale AM (2000) Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proc Natl Acad Sci USA* 97:11050–11055.
- Destrieux C, Fischl B, Dale A, Halgren E (2010) Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *Neuroimage* 53:1–15.
- Snodgrass JG, Corwin J (1988) Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *J Exp Psychol Gen* 117:34–50.
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1(7). *J Stat Softw* 67:1–48.