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Development of relational reasoning during adolescence

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Abstract

Non-linear changes in behaviour and in brain activity during adolescent development have been reported in a variety of cognitive tasks. These developmental changes are often interpreted as being a consequence of changes in brain structure, including non-linear changes in grey matter volumes, which occur during adolescence. However, very few studies have attempted to combine behavioural, functional and structural data. This multi-method approach is the one we took in the current study, which was designed to investigate developmental changes in behaviour and brain activity during relational reasoning, the simultaneous integration of multiple relations. We used a relational reasoning task known to recruit rostrolateral prefrontal cortex (RLPFC), a region that undergoes substantial structural changes during adolescence. The task was administered to female participants in a behavioural (N=178, 7-27 years) and an fMRI study (N=37, 11-30 years). Non-linear changes in accuracy were observed, with poorer performance during mid-adolescence. fMRI and VBM results revealed a complex picture of linear and possibly non-linear changes with age. Performance and structural changes partly accounted for changes with age in RLPFC and medial superior frontal gyrus activity but not for a decrease in activation in the anterior insula/frontal operculum between mid-adolescence and adulthood. These functional changes might instead reflect the maturation of neurocognitive strategies.

Keywords

Frontal pole; Adolescence; Cognitive control; Development; fMRI; Raven's matrices

Running title

Relational reasoning development

Introduction

Previous studies have reported non-linear developmental changes in performance on cognitive tasks, including face processing and match-to-sample tasks, during adolescence (e.g. Carey, Diamond & Woods, 1980; Diamond, Carey & Back, 1983; McGivern, Andersen, Byrd, Mutter & Reilly, 2002). Typically, a dip in performance is observed around the start of puberty (age 11-12 years old) and its timing can differ between genders (McGivern *et al.*, 2002). Non-linear developmental changes in brain structure, in particular grey matter volumes (Giedd *et al.*, 1999; Shaw *et al.*, 2008), and in brain function during face processing and go-nogo tasks (Hare, Tottenham, Galvan, Voss, Glover & Casey, 2008; Uhlhaas, Roux, Singer, Haenschel, Sireteanu & Rodriguez, 2009), have also been reported. Behavioural and functional changes are often interpreted as being a consequence of the structural changes (Horská, Kaufmann, Brant, Naidu, Harris & Barker, 2002; Lewis 1997; Tseng & O'Donnell, 2005, 2007; see Spear 2000 for review). However, very few studies to date have attempted to combine behavioural, functional and structural data to better understand non-linear developmental changes. This multi-method approach is the one we took in the current study. We first carried out a large-scale behavioural study to evaluate development in performance on a specific cognitive control task, and then a functional magnetic resonance imaging (fMRI) study to investigate the relationship between functional and structural neural changes with age in this task.

The rostrolateral prefrontal cortex (RLPFC), corresponding to the lateral portion Brodmann area 10 (BA10), undergoes substantial structural changes during adolescence (see Dumontheil, Blakemore & Burgess, 2008 for review). RLPFC is involved in the elaboration, evaluation and maintenance of abstract rules and information (Burgess, Dumontheil & Gilbert, 2007; Christoff & Gabrieli, 2000; Christoff, Keramatian, Gordon, Smith & Mädler, 2009; Koechlin, Ody & Kouneiher, 2003; Ramnani & Owen, 2004) and has been particularly implicated in relational reasoning (Christoff *et al.*, 2001; Kroger, Sabb, Fales, Bookheimer, Cohen & Holyoak, 2002). The relational reasoning demands of a problem can be defined in terms of the number of dimensions, or sources of variation, that need to be considered simultaneously to reach a correct solution; impaired relational reasoning has been specifically associated to frontal dementia (Waltz *et al.*, 1999). Children under 5 years can solve 0- and 1-relational problems, but fail to solve 2-relational problems (Halford, Wilson & Phillips, 1998). Early improvements in relational reasoning may reflect a shift from a focus on object similarity to relational similarity (Rattermann & Gentner, 1998). Further improvements during childhood and adolescence may relate to increased relational knowledge or increased working memory capacity (Crone, Wendelken, van Leijenhorst, Honomichl, Christoff & Bunge, 2009; Sternberg & Rifkin, 1979: see Richland,

Morrison & Holyoak, 2006 for discussion). In a neuroimaging study, Crone *et al.* (2009) found that children aged 8-12 made more errors in 2-relational Ravens Progressive Matrices problems than did adults, and that the activation profiles in RLPFC and parietal cortex varied with age during this task.

We employed a relational reasoning task (Christoff, Ream, Geddes & Gabrieli, 2003; Bunge, Helskog & Wendelken, 2009), which has been shown to reliably activate RLPFC at the single subject level in adults (Smith, Keramatian & Christoff, 2007). The task requires participants to assess similarities between items that vary along two dimensions, shape and texture. In the Control condition participants judge whether items have the same shape or texture (1-relational problem); in the Relational condition participants evaluate whether two pairs of items change along the same dimension (2-relational problem) (**Figure 1**). Here, we employed this task first in a behavioural study (N=178, age 7-27) and then in an fMRI study (N=37, age 11-30). We predicted age-related changes in performance and in the recruitment of the RLPFC and associated network of brain regions during the resolution of Relational trials compared to Control trials. In both cases, we investigated possible non-linear developmental changes. Finally, by using individual structural scans, we investigated whether neural activity changes with age could be accounted for by structural maturation.

Experiment 1

Methods

Participants

179 female volunteers between the ages of 7.3 and 27.5 years were recruited for this study. Child and adolescent participants were divided according to age into four groups of similar N to the adult group (**Table 1**).

Insert Table 1 here

Design

The behavioural task had a 2x5 factorial design with one within-subjects factor (Condition: Control or Relational) and one between-subjects factor (Age group: Child I, Child II, Adolescent I, Adolescent II, Adult). The task was computer-based and adapted from the study in adults by Smith *et al.* (2007) and administered in a single 15 min session. Stimuli consisted of six different geometric shapes filled with one of six different textures (**Figure 1**). In the Control condition participants were presented with three items and judged whether the bottom item matched either one of the top two items along a specified dimension (shape or texture). In the Relational condition participants were presented with four items. Participants were asked to infer the changing dimension between the top two objects (shape or texture), and then to determine whether the bottom two objects differed along the same dimension. Participants responded 'yes' or 'no' by pressing the index or middle finger of their right hand on keys of a computer keyboard. (see Supplementary Methods).

Insert Figure 1 here

Data analysis

Mean accuracy and mean of individuals' median response times (RT) in correctly responded trials were analysed using mixed model repeated measures ANOVA. Effect sizes (η_p^2) are also provided and range from values of 0 to 1, with 1 indicating the strongest effect.

Results

Percentage accuracy was on average >80%. The main effects of Condition ($F(1, 173) = 87.15$, $p < .001$, $\eta_p^2 = .34$), and Age group ($F(4, 173) = 6.04$, $p < .001$, $\eta_p^2 = .12$), as well as their interaction ($F(4, 173) = 4.58$, $p =$

.002, η_p^2 = .10), were significant for accuracy (**Figure 2a and Supplementary Figure 1**). Accuracy was lower in the Relational (Mean ± SD: 88.3% ± 10.0) than in the Control condition (94.7% ± 4.7). Child I and Adolescent I participants made more errors than did Adult participants ($p \leq .001$). None of the other pairwise comparisons reached significance. Additional 2x2 repeated measures ANOVAs compared performance in each condition between the Adult group and each of the younger groups. There was a significant interaction between the adults and all younger groups (all $F(1, 69 \text{ or } 70) > 7.1$, $p < .01$, $\eta_p^2 > .09$) indicating more errors in Relational than Control trials in the younger groups than in the Adult group, with the exception of the Child II group ($F(1, 70) = .20$, $p = .66$).

Further comparisons were performed to test whether performance of the Child II group was different from the other Child and Adolescent groups. There was a significant (or marginal) interaction between Task and Age group between the Child II and the three other young groups (Child I: $F(1, 69) = 8.37$, $p = .005$, $\eta_p^2 = .11$; Adolescent I: $F(1, 70) = 5.58$, $p = .021$, $\eta_p^2 = .07$; Adolescent II: $F(1, 69) = 3.71$, $p = .058$, $\eta_p^2 = .05$), indicating that the Child II group made fewer errors in Relational compared to Control condition than the other young groups.

Insert Figure 2 here

For the RT data (**Figure 2a**), the main effects of Condition ($F(1, 173) = 475.58$, $p < .001$, $\eta_p^2 = .73$) and Age group were significant ($F(4, 173) = 10.44$, $p < .001$, $\eta_p^2 = .19$). The interaction was not significant ($F(4, 173) = 1.71$, $p = .5$). Participants responded more slowly in the Relational condition (2790 ms ± 1000) than in the Control condition (1385 ms ± 348). Child I participants were slower than all other age groups (all *p*s < .01). Results of Experiment 1 thus show non-linear accuracy, but not RT, changes with age in relational reasoning between late childhood and adulthood.

Experiment 2

Methods

Participants

37 right-handed female participants aged between 11.0 and 30.4 years, with no history of psychiatric or neurological disorder, took part in the study. Participants were divided into three age groups: Early Adolescent, Mid Adolescent and Adult (**Table 1**).

Experimental Design

The fMRI task followed a block design and was a further adaptation of the relational reasoning task (Christoff *et al.*, 2003; Smith *et al.*, 2007). To match the demands of the Control and Relational conditions in terms of visual processing, an additional identical item was added to the bottom row in Control stimuli (**Figure 1**) (see Supplementary Methods).

MRI Data Acquisition

A 1.5 Telsa Siemens Avanto MRI scanner was used to acquire both 3D T_1-weighted fast-field echo structural images and multi-slice T_2*-weighted echo-planar volumes with blood-oxygen level dependant (BOLD) contrast (TR= 3s; TE= 50ms; TA= 2.9143s). 140 volumes comprising 35 axial slices with a resolution of 3 x 3 x 3 mm were acquired in two 7 min functional scanning sessions.

Statistical analysis

Median RTs and mean accuracy were analysed using mixed model repeated measures ANOVAs with Age group as the between-subject factor and Condition as the within-subjects factor. One subject showed poor performance (< 50% accuracy) in the second scanning session, which was excluded from the analyses.

fMRI data were analysed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm) and modelled for each subject using boxcar regressors for the three block types (Fixation, Relational and Control blocks) (see Supplementary Methods). Parameter estimates calculated from the least mean squares fit of the model to the data were used in pair-wise contrasts (Control > Fixation and Relational > Fixation) at the individual subject level. These contrasts were entered into a 2 (Condition) x 3 (Age group) second level analysis, where ‘subject’ was treated as a random effect. Main effects, simple effects and interactions between factors were then specified

by weighted linear contrasts and determined using the *t*-statistic on a voxel by voxel basis, correcting for family wise errors (FWE) across the whole brain ($p < .05$).

Parameter estimates of the peak voxels of clusters showing a main effect of experimental condition were extracted and analysed for effects of age using independent *t*-tests between age groups. This is an unbiased method as the voxels of interest were defined from a fully balanced orthogonal contrast to the effect of age (Kriegeskorte, Simmons, Bellgowan & Baker, 2009). Significant effects were further explored and univariate ANOVAs with 2 age group levels were performed covarying RT and accuracy differences between the Relational and Control conditions, and individual structural differences.

Voxel based morphometry

Voxel based morphometry (VBM) (Ashburner & Friston, 2000) investigating grey and white matter tissue volumes was carried out on all participants using SPM5 VBM5 toolbox (v1.15 http://dbm.neuro.uni-jena.de/vbm/) (see Supplementary Methods). The MarsBaR toolbox for SPM5 (http://marsbar.sourceforge.net/) was used to calculate mean grey and white matter adjusted volumes within spheres of 5 mm in radius, centred around the peak voxels of the main contrasts that exhibited significant age effects. Grey and white matter adjusted volumes were investigated for effects of age using independent *t*-tests between age groups.

Results

Behavioural results

2 (Condition) x 3 (Age group) mixed model repeated measures ANOVAs were performed on accuracy and RT data. Analysis of accuracy revealed a main effect of Condition ($F(1, 34) = 35.2$, $p < .001$, $\eta_p^2 = 0.5$), with lower accuracy in Relational (88.4% ± 8.1) than in Control trials (96.2% ± 3.4) (**Figure 2c**). The main effect of Age group ($F(2, 34) = 1.3$, $p = .29$) and Condition x Age group interaction ($F(2, 34) = 2.0$, $p = .15$) were not significant. Analysis of the RT data revealed a main effect of Condition ($F(1, 34) = 209.5$, $p < .001$, $\eta_p^2 = .86$), with slower responses in Relational (2011 ms ± 390) than Control trials (1250 ms ± 213), and an interaction between Condition and Age group ($F(2, 34) = 3.7$, $p = .035$, $\eta_p^2 = .18$), but no main effect of Age group ($F(2, 34) = 1.6$, $p = .22$). Follow-up 2 x 2 ANOVAs revealed the Condition x Age group interaction was significant between the two adolescent groups only ($F(1, 22) = 10.9$, $p = .003$, $\eta_p^2 = .33$); the Mid Adolescent group responded to Relational trials faster than did the Early Adolescent group ($t(22) = 2.7$, $p = .013$) (**Figure 2d**).

Neuroimaging results

Main effect of condition

The main effect of experimental condition (Relational – Control) across the three age groups revealed large bilateral activations in the RLPFC, inferior frontal sulcus (BA46/44/45), anterior insula/frontal operculum (AI/FO), lateral premotor cortex (BA6), across the inferior and superior parietal lobules (BA7/40), and along the medial part of the frontal cortex (medial frontal gyrus and cingulate gyrus (BA8/32)) (**Table 2, Figure 3a**).

Insert Table 2 and Figure 3 here

Comparison of the Relational and Control conditions was also performed separately for each group (**Figure 3b, Supplementary Table 1**). Overall there was a consistent network of regions activated in each of the three age groups, including in the left RLPFC, right middle frontal gyrus (BA46), medial superior frontal gyrus (BA8) and superior parietal lobule and supramarginal gyrus (BA7 and BA40).

Effect of age group on the Relational – Control contrast

To investigate non-linear changes in activity with age, parameter estimates were extracted from single peak voxels from the main effect analyses and evaluated using orthogonal contrasts. Independent samples *t*-tests performed between the age groups revealed different patterns of changes with age in the contrast Relational – Control.

In the left RLPFC (posterior peak at [-48 45 -3]), there was a decrease in activation between Mid Adolescent and Adult groups ($t(23) = 2.1$, $p = .044$), and a marginally significant increase between Early and Mid Adolescent groups ($t(23) = 2.0$, $p = .061$). The left AI/FO ([-30 27 0]) also exhibited decreased activation between the Mid Adolescent and Adult groups ($t(23) = 2.1$, $p = .042$). The medial superior frontal gyrus (mSFG, [3 27 42]) exhibited a decrease in activation between Early Adolescent and Adult groups ($t(23) = 2.3$, $p = .031$) (**Figure 4a,b**). (See Supplementary Material for separate analyses of the Control and Relational conditions vs. Fixation). No main effect of age or interaction between age group and condition were observed in the whole brain analysis (FWE, $p < .05$).

Insert Figure 4 here

Effect of age on brain structure

Grey and white matter volumes adjusted for head size were evaluated in 5 mm spheres around the left RLPFC, left AI/FO and mSFG peaks showing significant age effects. Grey matter volumes were smaller in the Adult than in the Early (all $t(23) > 4.4$, $p < .001$) and Mid Adolescent groups (all $t(23) > 3.3$, $p < .005$) in all three regions (**Figure 4c**). White matter volumes did not differ between age groups in the left RLPFC or mSFG (all *p*s > .11). However, in the left AI/FO white matter volume was larger in the Adult than in the Mid Adolescent group ($t(23)=2.2$, $p = .036$), and the Early Adolescent group (trend: $t(23) = 3.4$, $p = .083$) (**Figure 4d**).

Relationship between functional, structural and behavioural development

The age differences in brain activation were differently related to performance and structure in the three brain regions. The decrease in brain activation between Mid Adolescent and Adult groups in left RLPFC remained when covarying performance ($p = .037$), although the difference in Accuracy between Relational and Control trials accounted for some variance in BOLD response ($p = .024$), but not when covarying local structural measures ($p > .7$). The marginal increase in activation between Early Adolescent and Adult groups in this region did not remain when covarying out performance ($p > .4$). The decrease in brain activation between Early Adolescent and Adult groups in the mSFG did not remain when covarying performance or structure ($p > .18$, $p > .6$ respectively); there was a trend for the effect to be accounted for by differences in Relational – Control RT ($p = .075$). Finally, the difference between Mid Adolescent and Adult groups in the left AI/FO remained both when covarying performance ($p = .023$) and when covarying structure ($p = .01$), although there was a trend for the effect to be accounted for by grey matter volume ($p = .089$).

Discussion

This is the first study to combine a large scale behavioural study, and structural and functional imaging, to investigate the development of relational reasoning. The first aim of the study was to investigate the timecourse of performance changes from late childhood to adulthood. Our behavioural study (Experiment 1) revealed non-linear changes in performance with a temporary reduction in accuracy during mid-adolescence. The second aim was to investigate changes in the neural basis of relational reasoning during adolescence. Our fMRI study (Experiment 2) demonstrated a mixture of linear and non-linear changes in activity in the prefrontal cortex with age. Our third aim was to evaluate the relationship between brain structure and function. Only linear changes in brain structure were observed. The results further demonstrated that some changes in brain activation with age could in part be accounted for by performance and structural changes with age, while others did not and may reflect the maturation of cognitive strategies.

In the behavioural study, we tested 178 participants ranging in age from 7.3 to 27.5 years and divided into five groups. The youngest group's overall RTs were slower than the older age groups, however there was no age effect on the difference in RT between the Relational and Control conditions (see Crone *et al.*, 2009 for similar results). There were non-linear developmental changes in the Relational condition in terms of accuracy. Accuracy increased and reached adult levels at age 9-11, before decreasing and remaining lower than adult levels at ages 11-13 and 14-17. This decline in performance was specific to Relational trials. Dips in cognitive performance at around this age have been reported in a variety of tasks including face recognition tasks (Carey *et al.*, 1980; Diamond *et al.*, 1983) and a match to sample task (McGivern et al. 2002). McGivern and colleagues proposed that the dip in performance may be related to the peak in grey matter that occurs in early adolescence (Giedd et al. 1999). However, this has not previously been explored.

In the fMRI study, we explored the relationship between performance, brain activity and brain structure. The pattern of performance changes between adolescence and adulthood was qualitatively similar to that observed in Experiment 1. However, only a decrease in RT between the Early and Mid Adolescent groups reached significance. The fMRI task was not self-paced, and this may have affected the speed-accuracy trade-off. The lack of a significant interaction between condition and age group in accuracy may have been a consequence of the increased practice of the fMRI task, the simplification of the textures of the stimuli, and the smaller sample size. Activations in the RLPFC for Relational relative to Control conditions were accompanied across subjects by bilateral activations in dorsolateral prefrontal cortex and AI/FO, as well as

activations in the lateral premotor cortex, the medial part of the frontal cortex and the inferior and superior parietal lobules. The frontal and parietal activations were observed in all three age groups separately. Three frontal cortex regions exhibited changes in activation with age. Analyses of the peak activations from the main effect of condition revealed that local grey matter volumes around these three peaks were reduced in the Adult compared to the Early and Mid Adolescent groups, while local white matter volumes exhibited an increase between the Mid Adolescent and Adult groups in the left AI/FO only. These structural findings are consistent with previous findings (Barnea-Goraly *et al.,* 2005; Giedd *et al.*, 1999; Shaw *et al.*, 2008; Sowell *et al.*, 1999; Tamnes *et al.*, 2010).

A decrease in activation was observed in the mSFG between the Early Adolescent and Adult groups, which did not remain after covarying performance and structure and appeared to be related to individual differences in RT. The mSFG supports the ability to inhibit a prepotent response (Chen, Muggleton, Tzeng, Hung & Juan, 2009). Increased activation in this region may thus reflect a longer period of response inhibition in the younger participants while the correct response was computed (see Richland et *al.*, 2006 for a discussion of the importance of inhibitory control in relational reasoning). A decrease in activation between the Mid Adolescent and Adult groups was observed in the left AI/FO, which was not accounted for by performance or structural changes with age. Functional changes in the left AI/FO may instead reflect the maturation of neurocognitive strategies (see Dumontheil, Hassan, Gilbert & Blakemore, 2010 for similar results), which may include changes in task specific connectivity between brain regions, supported for example by increased long range functional connectivity during development (Fair *et al.*, 2008), changes in the balance between mesocortical and mesolimbic systems (see Spear, 2000 for review), or else reflect the maturation of the neurotransmitter systems (Insel, Miller & Gelhard, 1990; Tseng & O'Donnell, 2005, 2007).

Finally, a posterior part of the left RLPFC showed a trend towards non-linear changes with age, with greater activation in the Mid Adolescent group than the Early Adolescent (p = .061) and Adult groups (p = .044). The early increase in activation did not remain when covarying task performance, while the later decrease in activation was party related to task performance, and did not remain significant when covarying structural measures. These results suggest that during relational reasoning, the observed trend for non-linear changes in activations in the RLPFC may be a consequence of a combination of performance and structural changes with age. In another study using a different relational reasoning paradigm, Crone *et al.* (2009) observed increase activation in RLPFC between 8 and 12 years when comparing 2-relational to 1-relational problems.

Although in the right hemisphere, this age effect was observed in a similarly posterior part of RLPFC (peak at [33 45 9]), and is consistent with the increase in activation observed during adolescence in our study. The developmental timecourse of the more anterior part of RLPFC typically recruited during relational reasoning remains to be identified, possibly through the use of 3-relational problems**.**

The non-linear trend of functional changes observed in the left RLPFC occurred later than the dip in accuracy observed in the behavioural task, but followed a similar developmental pattern to RT, both in the behavioural and the fMRI studies, over the 11 to adulthood age range. This suggests that brain activity in the present study may have been more sensitive to participants' speed of neural processing and responding than to their overall accuracy. Non-linear brain functional changes have been observed previously (Hare *et al.*, 2008; Uhlhaas *et al.*, 2009). The results suggest it is unlikely that these changes reflect a single developmental process, but rather a multitude of processes such as local changes in grey and white matter structure like in the left RLPFC in the present study, the maturation of complex balancing brain networks (e.g. the subcortical emotional processing and top-down prefrontal regulation systems (Hare *et al.*, 2008)) or the establishment of functional synchronisation across networks of brain regions (Uhlhaas *et al*., 2009).

Our results reinforce the importance of combining a variety of measures when studying cognitive development. Further work will be needed to better understand how dips in performance during adolescence relate to biological factors such as brain structure and neurotransmitter systems, or social and environmental factors such as motivation and a move to a new school (e.g. see West, Sweeting & Young, 2010; Whitby, Lord, O'Donnell & Grayson, 2006).

Conclusion

In this novel study, we used a multi-method approach to study the development during adolescence of performance and brain activation during relational reasoning. We observed non-linear changes in accuracy between late childhood and adulthood. Brain activity changes with age were observed in the mSFG, AI/FO and RLPFC, with a reduction in activity between mid-adolescence and adulthood. The age effect remained in the AI/FO after covarying individual performance and structural measures, suggesting it may instead reflect the maturation of neurocognitive strategies. These results provide evidence of a complex picture of linear and non-linear anatomical, functional and behavioural changes associated with subregions of the prefrontal cortex during adolescence.

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Figure legends

Figure 1: Examples of trials of the Control and Relational conditions in the Shapes task in Experiments 1 and 2. “Change”, “Shape” or “Texture” was written in the middle of the screen on each trial to ensure that the participants knew which task they were performing. In the Control condition, participants were asked whether one of the top items had the same Texture (or Shape) as the bottom item(s). Top left: in this Match Texture example, neither of the top items has the same texture as the bottom item, thus the answer is no. Bottom left: in this Match Shape example, the top left item has the same shape (circle) as the bottom items (which were identical in the Control condition of Experiment 2), thus the answer is yes. In the Relational condition, participants were asked whether the top and bottom pairs changed along the same dimension (shape or texture). Top right: in this example, the items of the top pair differ in the texture dimension, while the items of the bottom pair differ in the shape dimension, so the answer is no. Bottom right: in this example, both pairs of items differ along the shape dimension, so the answer is yes.

Figure 2: Behavioural results of Experiments 1 and 2. **(a)** Behavioural results of the behavioural study (Experiment 1)**.** Left: percentage accuracy, right: RTs (mean ±SE). Main effects of Age group and Condition were observed for both accuracy and RTs. In addition, a significant interaction between Condition and Age group was observed for accuracy, driven by significant interactions between Child I, Adolescent I and Adolescent II vs. Adults (represented by * on the graph). **(b)** Behavioural results of the fMRI study (Experiment 2). Left: percentage accuracy, right: RTs (mean ±SE). Main effects of Condition were observed for both accuracy and RTs. In addition, a significant main effect of Age group and a significant interaction between Condition and Age group were observed for RTs, driven by significant interactions between Early and Mid Adolescent groups (represented by * on the graph).

Figure 3: Neuroimaging results of the main contrast of interest (FWE $p < .05$, > 5 voxels) performed on the average of the three age groups and on each age group separately rendered on the left and right brain surfacea (left and right outer panels respectively) and shown on the sagittal slice ($x = 3$) (middle panel).

Figure 4: Age-related changes in brain activation and structure in peak coordinates obtained from the main effect analysis. **(a)** Loci of the three peak coordinates obtained from the analysis of the main effect of Relational – Control across the three age groups which show age effects. Left: horizontal slice at $z = -3$ showing the left RLPFC (L RLPFC) region; middle: saggital slice at $x = 3$ showing the medial superior frontal

gyrus activation (mSFG); right: horizontal slice at z = 0 showing the left anterior insula/frontal operculum (L AI/FO) activation. Grey and white matter volumes adjusted for head size were obtained in 5 mm spheres around these peaks, represented schematically by the white circles on the brain slices, while fMRI parameter estimates were extracted from the single peak voxels. **(b)** Parameter estimates for the contrast Relational – Control (mean ± standard error (SE)) plotted against age group (11-14: Early Adolescent, 14-18: Mid Adolescent, 22-30: Adult) in the left RLPFC, mSFG and left AI/FO. **(c)** Grey matter volumes in the left RLPFC, mSFG and left AI/FO plotted against age group (mean ± SE). **(d)** White matter volumes in the left RLPFC, mSFG and left AI/FO plotted against age group (mean ± SE). Significant differences between age groups are represented by * ($p < .05$).

Figure 1

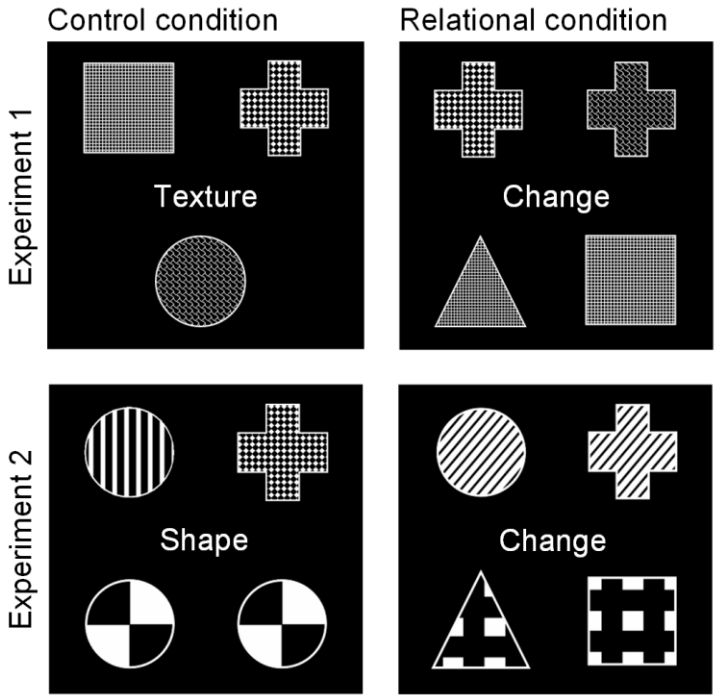

Figure 2

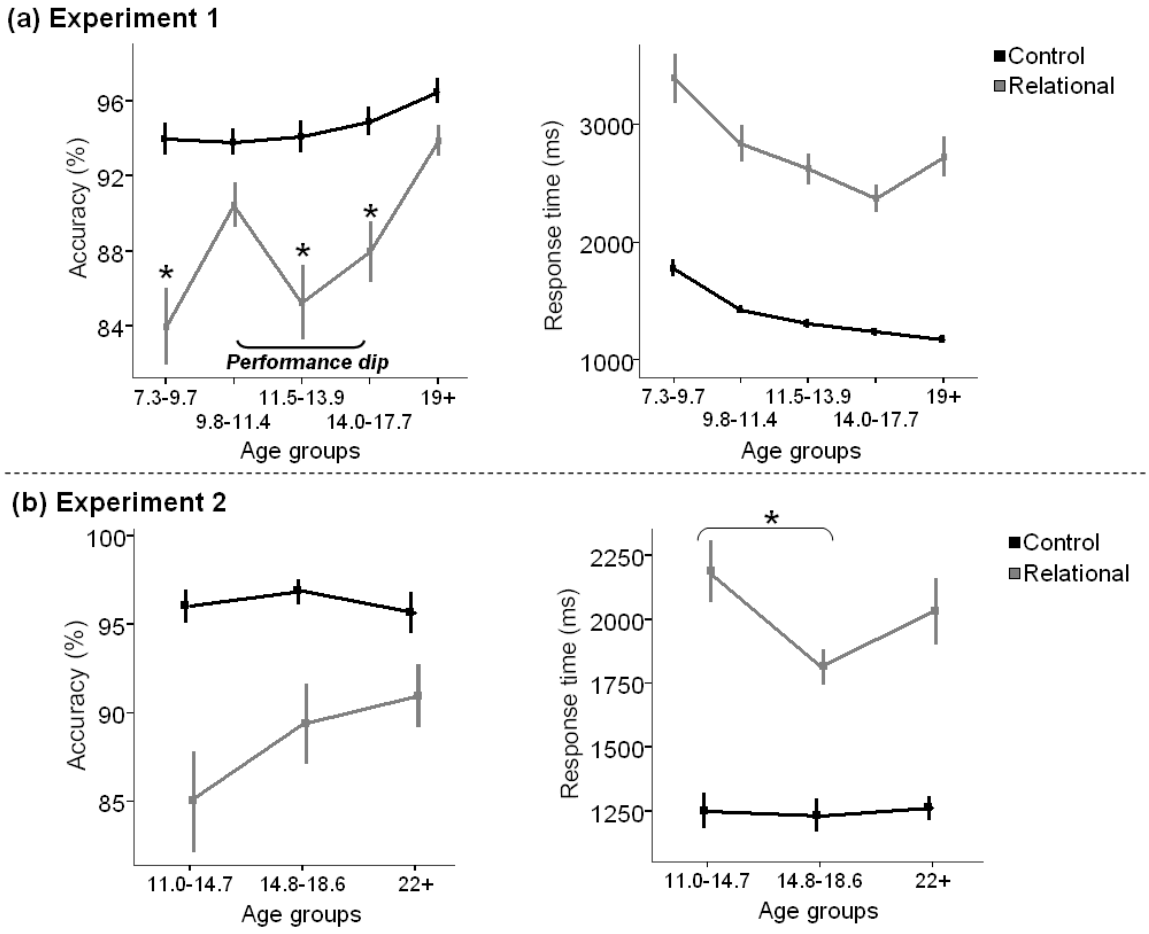

Figure 3

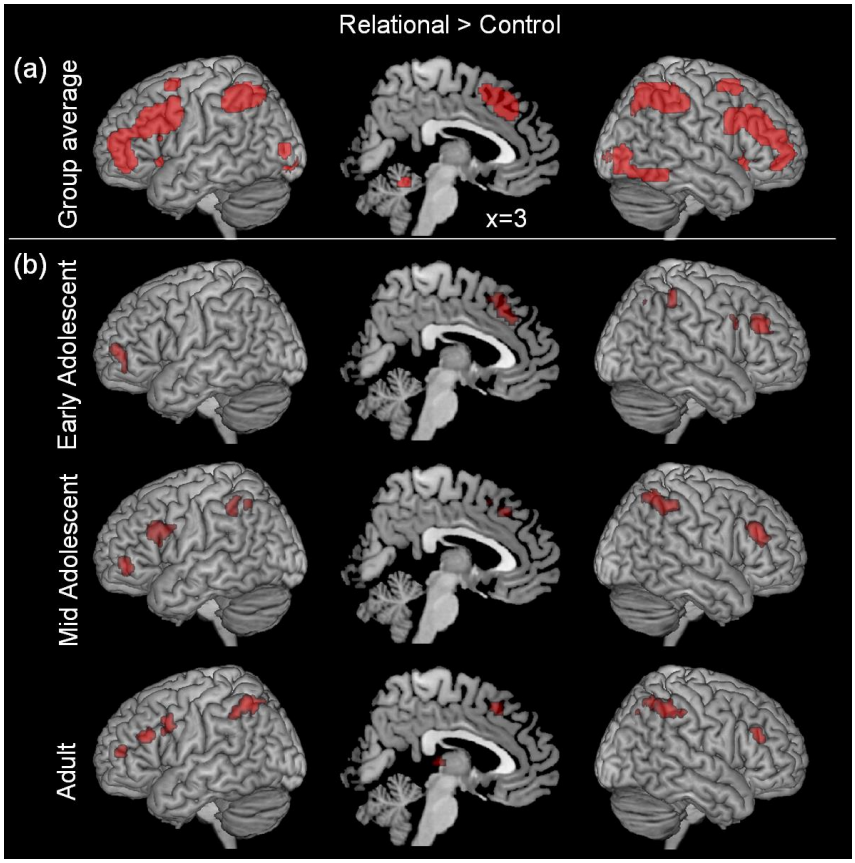
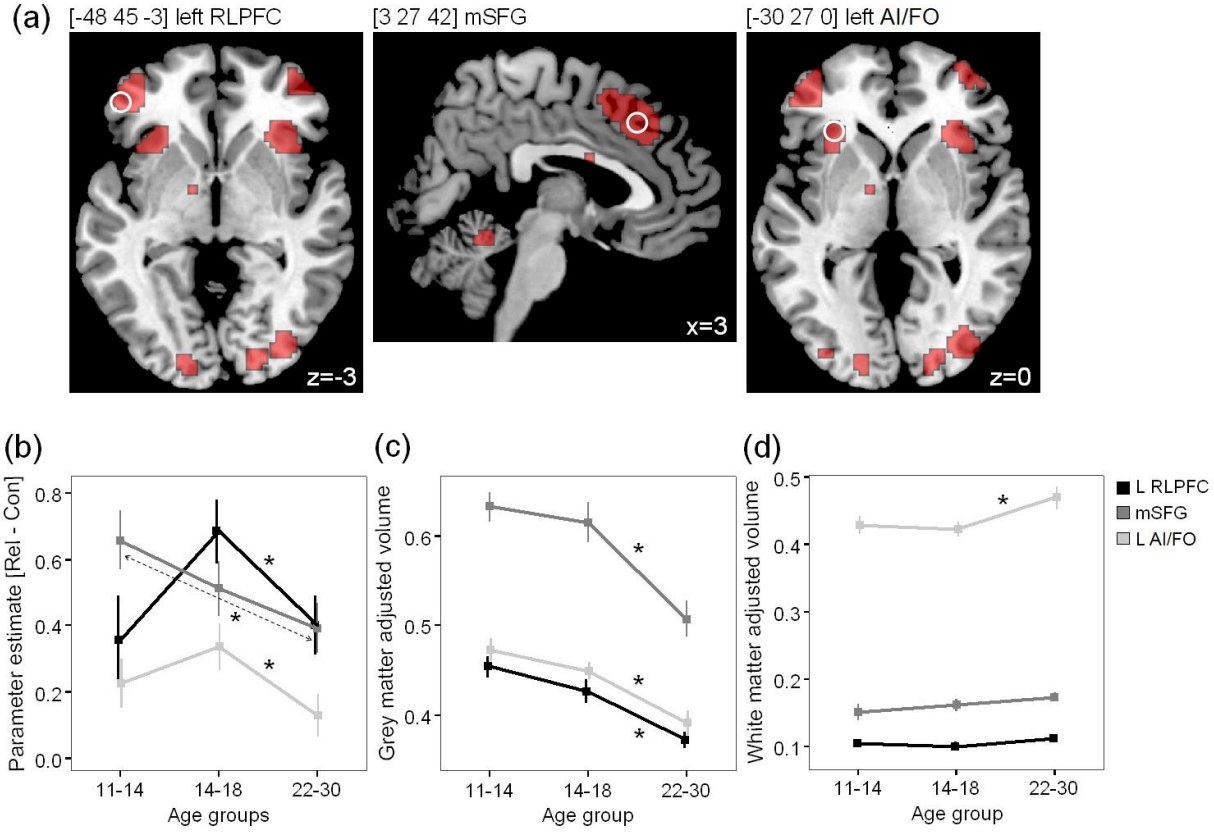
Figure 4