Prior expectations influence the way incoming stimuli are processed. A standard, validated way of manipulating prior expectations is to bias participants to perceive a stimulus by instructing them to look out for this type of stimulus. Here, we investigated the influence of prior expectations on the processing of incoming stimuli (emotional faces) in adolescence. Using functional magnetic resonance imaging, we assessed activity and functional connectivity in 13 adolescents and 13 healthy adults (matched for gender and intelligence quotient), while they were presented with sequences of emotional faces (happy, fearful, or angry). A specific instruction at the start of each sequence instructed the participants to look out for fearful or angry faces in the subsequent sequence. Both groups responded more accurately and with shorter reaction times (RTs) to faces that were congruent with the instruction. For anger, this bias was lower in the adolescents (for RTs), and adults demonstrated greater activation than adolescents in the ventromedial prefrontal cortex (vMPFC) and greater functional connectivity between the vMPFC and the thalamus when the face was congruent with the instruction. Our results demonstrate that the influence of prior expectations (in the form of an instruction) on the subsequent processing of face stimuli is still developing in the adolescent brain.

Keywords: adolescence, emotion perception, functional connectivity, prior expectations, ventro-medial prefrontal cortex

Introduction

We are constantly bombarded with a multitude of sensory stimuli and it is necessary for the brain to prioritize the stimuli that are most relevant to our current activities and goals. It has been postulated that the neurocognitive processes responsible for fast and appropriate stimulus detection and selection are dependent on 2 mechanisms: attention and expectation (Summerfield and Egner 2009). "Attention" prioritizes the stimulus processing in 2 ways: on the basis of bottom-up, sensory-driven salience (e.g. a wide, bright and obvious stimulus), and by top-down, goal-directed selection (e.g. a stimulus that you are searching for). In addition, we are also able to make predictions about the nature of an incoming stimulus based on our "prior expectations". Prior expectations influence the stimulus processing on the basis of prior likelihood and can be biased simply by manipulating the instruction cues. For example, it has been shown that participants are more efficient (in terms of reaction times (RTs) and/or accuracy) at detecting face stimuli as compared with houses and cars when instructed to look out for faces (Summerfield et al. 2006).

There are many examples in everyday life in which emotion processing might be facilitated by our prior expectations. For example, one might anticipate encountering positive facial expressions at a wedding, and expressions of sorrow at a funeral. Facial expressions that are incongruent with our expectations in either case would surprise us. The first aim of this study was to investigate the influence of prior expectations on perception of emotional faces in the human brain. The second aim was to investigate how the influence of prior expectations on stimulus perception develops during the period of adolescence.

The Emotional Face Processing Network

An increasing number of studies have investigated the functional specialization and integration of brain regions involved in the widely distributed face processing network. Different brain regions are involved in different aspects of face processing. First, regions located in the inferior temporal lobe, including the occipital face area, the fusiform face area, the posterior superior temporal sulcus, and the temporal poles, are mainly involved in the visuo-perceptual aspects of face processing (Kanwisher et al. 1997; Gauthier et al. 2000; Hoffman and Haxby 2000). Secondly, these regions receive inputs from areas involved in the more social and emotional aspects of face processing, including the amygdala, the insula, the medial prefrontal cortex, the anterior paracingulate cortex, the basal ganglia, the thalamus, and the hypothalamus (Gobbini and Haxby 2007; Pessoa and Adolphs 2010). A third set of regions is involved in the top-down control of face processing, which uses existing knowledge and expectations to improve the efficiency at detecting facial characteristics. This system is primarily located on the prefrontal cortex, particularly the medial prefrontal cortex (Pessoa 2008). In the current study, we were interested in regions subserving the influence of prior expectations on the emotional characteristics of the face.

Prior Expectations in The Brain

A number of recent studies have investigated how prior expectations are represented in the brain, using paradigms investigating reward expectations (Kringelbach 2005), decision-making (Bechara et al. 1994; Wallis 2007), top-down visual perception (Bar et al. 2006; Summerfield et al. 2006; Kveraga et al. 2007), and perceptual matching (Summerfield and Koechlin 2008). For example, Summerfield and Koechlin (2008) have shown that the congruence between expected and observed orientations of Gabor patches activated the ventro-medial prefrontal cortex (vMPFC) (Summerfield and Koechlin 2008). Connectivity from the vMPFC to face-responsive regions in the fusiform gyrus and the amygdala is enhanced by expected detection of faces when compared with other types of stimulus such as houses and cars (Summerfield et al. 2006). In the current study, we investigated functional activations and interactions between brain...
regions (using psychophysiological interaction analysis) related to the influence of prior expectations on the processing of emotional face stimuli in the adult and the adolescent brain. When an individual is faced with a stimulus that matches their prior expectation, it is predicted that the vMPFC will play a role in confirming and reinforcing the validity of prior expectations (Daw et al. 2006; Hampton et al. 2006). In addition, the vMPFC is proposed to facilitate emotional responsiveness, offering an initial prediction as to the identity of the forthcoming emotion (Bar et al. 2006; Summerfield et al. 2006; Kveraga et al. 2007), via top-down control of regions involved in emotional processing and known to be anatomically and functionally connected to the vMPFC (i.e. the cingulate cortex, the orbito-frontal cortex, the insula, the amygdala, the hippocampus, and the thalamus). Finally, the vMPFC has been shown to be predominantly activated for faces versus houses (Summerfield et al. 2006), possibly reflecting an inclination to predict the more salient stimulus.

Development of Prior Expectations in Adolescence

In addition to studying the influence of prior expectations on the processing of emotional stimuli in the healthy adult brain, the second aim of the current study was to investigate the development of this influence in adolescence. The influence of prior expectations on stimulus perception might be expected to change in adolescence for a number of reasons. First, a key brain region involved in the processing of prior expectations, the vMPFC, develops structurally during adolescence, both in the terms of the gray matter and white matter (Sowell et al. 2002; Giedd 2004). A second argument as to why the influence of prior expectations on stimulus perception might develop in adolescence comes from developmental studies investigating the reward system. Adolescents tend to perform less well than adults on gambling tasks in which participants must use their expectations (implicitly learnt from the beginning of the task) to predict the occurrence of the reward and punishment outcomes (Cron and van der Molen 2004; Hooper et al. 2004). These tasks, designed to approximate real-life decision-making under conditions of uncertainty, typically show hypoactivation of the vMPFC in the adolescents when they have to anticipate risky rewards (Bjork et al. 2007). Thirdly, a study in which participants were exposed to pro-social versus non-social words—which acted as primes—demonstrated that RTs to imitate others\' actions decreased after participants were primed with pro-social words, but not non-social words. This effect of pro-social primes facilitating the imitation of others\' actions was found in the adults, but not found in the adolescents. This study suggests a reduced effect of prior expectations (in this case, priming) on social behavior (imitation) in adolescence.

Emotional face recognition continues to develop during adolescence (Herba and Phillips 2004; Herba et al. 2006; Thomas et al. 2007). However, while some neuroimaging studies suggest that “hyperactivation” in regions involved in emotion processing, in particular the amygdala, contribute to higher emotional reactivity in adolescence (Monk et al. 2003; Killgore and Yurgelun-Todd 2007; Guyer et al. 2008; Hare et al. 2008; Passarotti et al. 2009; Pfeifer et al. 2011), other studies (Pine et al. 2001; Nelson et al. 2003; McClure et al. 2004; Aylward et al. 2005) showed adult-like or decreased activation to emotional faces in the same regions. To explain these discrepant findings, it could be postulated that brain regions that typically respond to emotional faces are differentially activated depending on the cognitive resources available to process emotional faces (Pessoa 2008). For example, Monk et al. (2003) have demonstrated that, when attention was unconstrained, adolescents showed higher levels of activations in the orbito-frontal cortex (OFC), the anterior cingulate, and right amygdala, in response to emotional faces. However, the OFC was hypoactivated in adolescents compared with adults when attention was focused on the emotion in a fearful face as opposed to a non-emotional aspect of the face (e.g. the nose). This finding was interpreted as showing that attention influences the processing of emotional faces differentially in adolescents and adults. Whether the same applies to the influence of prior expectations on emotional face perception during development is unknown, and is the focus of the current study.

The Current Study

In healthy adult participants, a standard, validated way of manipulating prior expectations is to bias participants to perceive a stimulus by instructing them to look out for this type of stimulus. Indeed, it has previously been shown that a simple instruction asking for a presence/absence (or “yes/no” judgment) creates an internal “template” against which to match incoming sensory information (Dayan et al. 1995; Dosh 1999). Thus, the signal conveyed by the instruction favors the anticipation of one perceptual alternative and, as such, can be considered a prior expectation. In turn, these prior expectations improve the ability to discriminate incoming stimuli that match the instruction (Summerfield et al. 2006; Summerfield and Koechlin 2008). In the current study, we adapted this paradigm to investigate the influence of prior expectations in the adolescent brain.

We presented short sequences of photographs of faces displaying 1 of 3 emotional expressions—happy, fear or angry—to 13 adolescents and 13 adults in an functional magnetic resonance imaging (fMRI) study. At the beginning of each sequence, participants were instructed to look out for faces with a particular “target” expression. Participants were asked to respond to each face stimulus by pressing 1 of 2 response buttons: 1 corresponding to the target emotion, the other to all non-target emotions.

Our first hypothesis was that this manipulation of the instruction cue would provide a prior expectation bias towards the corresponding emotion, which would result in reduced RTs and increased accuracy on the trials in which the emotional face stimulus matched the emotion targeted in the instruction (Summerfield and Koechlin 2008). Secondly, we predicted that activation in the vMPFC would be higher when perceptual matching occurs (i.e. when the expression displayed on the face was congruent with the emotion targeted in the instruction) compared with when there was a mismatch between prior expectations and facial expression (Summerfield et al. 2006; Summerfield and Koechlin 2008). Thirdly, we predicted that functional connectivity between the vMPFC and regions involved in emotional processing and known to be anatomically and functionally connected to the vMPFC (i.e. the cingulate cortex, the orbito-frontal cortex, the insula, the amygdala, the hippocampus, and the thalamus) would be greater during facial expressions that were congruent with the
Materials and Methods

Participants

Thirteen healthy, right-handed adolescents (6 males; age range = 11–17; mean [standard deviation, SD] age = 14.1 [2.2]) and 13 healthy, right-handed adults (8 males; age range = 25–38; mean [SD] age = 28.6 [3.9]) took part in the current study. Intelligence quotient (IQ) of the participants was measured using 2 subsets (vocabulary and matrix reasoning) of the Wechsler abbreviated scale of intelligence (Wechsler, 1999). There was no significant difference in IQ between adolescents (mean [SD] = 125.2 [6.6]) and adults (mean [SD] = 126.2 [3.9]) (t(24) = 0.8, P = 0.8).

Exclusion criteria for all participants were the presence of any neurological or psychiatric disorder (including developmental disorders) for the participant or first-degree relatives. After the procedure was fully explained, written consent was obtained from adult participants, and from parents of adolescent participants who also gave their written assent to take part in the study. Participants were paid £15. The study was approved by the local ethics committee.

The Emotion Task

The emotion task had a 3 × 2 factorial design, with factors facial emotion (fearful, angry, and happy) and instruction (anger vs. fear). Note that we included happy faces to increase the difficulty of the task by increasing the variety of stimulus types. Including happy faces produced an additional cognitive constraint as participants had to choose among 3 (and not only 2) alternatives. We reasoned that including happy faces would increase the congruency effect because participants would rely more on their expectations to make their choice than without such an additional cognitive constraint.

The emotion discrimination task consisted of 80 sequences, divided into 4 experimental blocks of ~9 min each. The order of sequences was counterbalanced between participants. Each sequence began with an instruction cue, presented for 5 s on a uniform black background screen. This was followed by a fixation cross in the center of the screen presented for a mean duration of 1.5 s (jittered with a uniform distribution of 100 ms intervals between 1 and 2 s). This was followed by presentation of 8 faces expressing 3 emotions (angry, fearful, and happy), each with duration of 0.5 s. Presentation of each face was followed by a black screen (as the inter-stimulus interval) for a mean duration of 1.5 s (jittered with a uniform distribution of 100 ms intervals between 1 and 2 s). Each sequence ended with a rest period in which a blank screen was presented for mean 4.5 s (jittered with a uniform distribution of 100 ms intervals between 3 and 6 s).

The instruction at the beginning of each sequence that informed participants about the nature of the target facial expression (i.e. fear or anger) changed on a sequence-by-sequence basis (Fig. 1). In each sequence, participants were told to press the target button if the emotion face stimulus was congruent with the instruction and the non-target button if it was not. The instruction at the beginning of each sequence pertained to either fear or anger. For example, in the sequences in which fear was the emotion targeted in the instruction (fear instruction), participants were instructed to press the target button if the stimulus was a fearful face and the non-target button if the face displayed angry or happy expressions. For each stimulus, participants were asked to use their right index finger and middle finger for the 2 response buttons (target/non-target). The order of fear and anger instruction sequences, as well as the response keys used for target/non-target emotions, was counterbalanced between participants. Participants were instructed to respond as quickly and accurately as possible. No feedback was given throughout the experiment.

Of the 8 faces that comprised each sequence, 4 were target and 4 non-target stimuli. Because each sequence was comprised of 3 different stimuli (angry, fearful, and happy faces), there were 2 types of non-target stimuli in each sequence. This followed the methods used by Summerfield and Koechlin (2008). For example, in anger

Figure 1. Experimental paradigm. In this figure, anger is the target expression and red is the target response button. According to the instruction, participants had to press the red button for every angry facial expression displayed and the green button for any other expression displayed (non-target expressions).
instruction sequences, there were 4 angry faces (target), 2 fearful faces (non-target), and 2 happy faces (non-target). Likewise, in fear instruction sequences, there were 4 fearful faces (target), 2 angry faces (non-target), and 2 happy faces (non-target). In other words, there were twice as many congruent stimuli as each type of incongruent stimulus within each sequence. Therefore, the probability of a specific stimulus appearing in a sequence differed according to which emotion was targeted in the instruction. Note that this is different from response selection, which was maintained constant throughout each sequence. Indeed, only half the motor responses in each sequence were driven by each of the 2 response fingers. This prevented the participants from being biased by a motor response choice (i.e. right index finger/right middle finger) in each sequence. Finally, in each sequence, the non-target stimuli were equally distributed over the whole experiment.

Face stimuli were selected from the NimStim database, validated in healthy participants, and consisted of 34 identities of 17 Caucasian, 7 Hispanic, 7 Asian, and 7 Black ethnicities with the highest degrees of emotion identification accuracy (Tottenham et al. 2009). Each single image was presented on average 7 times per participant for angry and fearful expressions, and 5 times per participant for happy expressions. All faces presented a direct gaze and an open mouth. We used Adobe Photoshop CS3 to remove extra-facial elements and to adjust pixel intensity and size of the presented picture (13.97 mm in width and 20.66 mm in height). The order of the stimuli within a sequence was pseudo-randomized so that no more than two consecutive pictures displayed the same expression or the same gender, and the 8 pictures represented 8 different identities. The task was presented on a laptop using the Cogent Software Package (http://www.cogentsoftware.net/). Accuracy and RT were recorded for each trial.

Participants were trained outside the scanner prior to the start of the experiment using a short practice session of ~10 sequences for about 5–10 min. This was done to ensure that they fully understood the task and to minimize learning effects while they were in the scanner.

Functional Imaging Preprocessing
Pre-processing was carried out using SPM5 (Wellcome Department of Imaging Neuroscience, UCL, UK, http://www.fil.ion.ucl.ac.uk/spm/spm5.html). In each block for each participant, 219 functional volumes were obtained following 5 dummy scans. These initial dummy volumes were excluded from further analysis to prevent the non-equilibrium effects of magnetization. Next, the functional volumes were slice-time corrected and were realigned to the first volume to correct for inter-scan motion. No participant was excluded for excessive movement (defined as >3 mm translation, >2 degrees rotation). All the acquired images (EPI functional and structural T1) were then co-registered and transformed into a standardized, stereotaxic space (according to the Montreal Neurological Institute template). Subsequently, the transformation parameters were used to normalize the functional volumes. The functional images were then spatially smoothed with an 8-mm full-width-at-half-maximum isotropic Gaussian kernel and temporally processed in a high-pass filter with a frequency cut-off of 128 s. Subsequently, a first order autoregressive model was used to account for the serial correlations. Finally, image volumes and slices with significant artifacts were identified, and repaired, using the ArtRepair toolbox (http://cibs.stanford.edu/tools/ArtRepair/ArtRepair.htm) based on scan-to-scan motion (1 SD change in the head position) and outliers relative to the global mean signal (3 SD from the global mean).

Functional Imaging Statistical Analysis
fMRI data were analyzed using SPM5. The volumes acquired during the 4 blocks were treated as separate time series. For each series, variance in the blood-oxygen-level-dependent signal was decomposed with a set of regressors in a general linear model.

The regressors were constructed by convolving dirac functions (time locked to the onset of each stimulus or motor response) with the canonical hemodynamic response function.

We defined 4 categories of regressor:
1. Two regressors were related to the instructions (one for each targeted emotion).
2. Six regressors were related to the face stimuli: fearful faces in a face instruction sequence, fearful faces in an anger instruction sequence, angry faces in a face instruction sequence, angry faces in an anger instruction sequence, happy faces in a face instruction sequence, and happy faces in an anger instruction sequence.
3. Two regressors were related to the motor responses (one for each response button).
4. In each block, 6 regressors representing residual movement-related artifacts and the mean over scans were added in the design matrix.

In a first level analysis we contrasted, for each subject separately, emotion face stimuli that were congruent with the targeted emotion (the emotion specified by the instruction) with emotion face stimuli that were incongruent. We performed an analysis of each target emotion separately (fear vs. anger), instead of performing an overall analysis that included all faces. The rationale behind this is that the behavioral analyses demonstrated a differential congruency effect on face perception depending on the emotion being processed (emotion x congruency interaction on RT; see the Behavioral Results section). We refer to this as the “perceptual matching” contrast. As in the behavioral analyses, happy faces were not included and we performed our analyses on 4 different conditions (fearful and angry faces with congruent instructions, and fearful and angry faces with incongruent instructions).

In a second level analysis, each of the first level contrasts (one for fearful face stimuli and one for angry face stimuli) was entered into separate independent-samples (adolescents vs. adults) t-test models, where “subject” was treated as a random effect. Then, to identify
regions showing a congruency effect in either group for each emotion, we generated 2 whole-brain omnibus F contrast (one for fearful face stimuli and one for angry face stimuli). Both contrasts were thresholded at \( P < 0.001 \) uncorrected at the voxel level and \( P < 0.05 \) FWE (family-wise error) corrected at the cluster level (Friston et al. 1996).

For fearful and angry face stimuli, we then conducted regions of interest (ROI) analyses in the regions identified using the above analysis (see Results section). A percent signal change from a sphere of 5 mm around the peak voxel in each of these regions was separately entered into 2 univariate repeated-measure ANOVAs (one for fear and one for angry face stimuli), with congruency (congruent—i.e. fearful faces in the fear instruction sequence and angry faces in the anger instruction sequence—vs. incongruent) as a within-subject factor and group (adults vs. adolescents) as between-subject factor. In these regions, we specifically tested the group \times congruency interaction effect.

ROI analysis is usually considered less stringent than whole-brain voxel-wise SPM analysis because the latter approach is unbiased in that it requires no a priori information about the location of possible differences in activation. However, in the regions showing a congruency effect in either group (see Results section), we specifically tested the group \times congruency interaction effect—an effect that is orthogonal to the initial congruency contrast (Kriegeskorte et al. 2009). Thus, our ROI analyses were not biased by possible pre-existing differences in activations in these regions. In addition, those ROI analyses were FWE-corrected for multiple comparisons, taking into account the number of ROIs in which these factorial analyses were carried out.

Note that we also performed an analysis on emotion valence (positive vs. negative valence), as well as the congruency \times emotion interaction on the fMRI data (reported in Supplementary File 2).

**Functional Connectivity Analyses (PPIs)**

Psycho-physiological interaction (PPI) analysis is a statistical technique based on linear regression and provides insights that are independent and fundamentally different from those gained by conventional fMRI analysis. PPI analysis is based on the principle that if activity in 1 region (area A) predicts activity in another region (area B), then the strength of the prediction reflects the influence area A could be exerting on area B. If the strength of the prediction varies with the psychological context in which the physiological activity is measured (i.e. experimental condition), then this is evidence for a "psychophysiological interaction" (Friston et al. 1997). In PPI analysis, a brain ROI is defined as the physiological source. Note, however, that although PPI reflects a source and finds target regions, it cannot determine the directionality of connectivity. This is because the regression equations are reversible (the slope of A \rightarrow B is approximately the reciprocal of B \rightarrow A).

Here, we tested whether brain regions demonstrating a perceptual matching effect (i.e. when the facial expression was congruent with the instruction vs. when it was incongruent) in accordance with our initial hypothesis (i.e. the vMPFC) influenced activity in other brain regions when the incoming sensory evidence (facial expression) was congruent with the instruction versus when it was not.

The individual time series for the vMPFC were obtained by extracting the first principal component from all raw voxel time series in a sphere (5-mm radius) centered on the coordinates of the group-level activations (obtained from the omnibus F contrast). Using standard analysis techniques, these "physiological" time series were corrected for variance associated with parameters of no interest, deconvolved with the hemodynamic responses function (Gitelman et al. 2003), multiplied by a parameter encoding the relevant "psychological" contrast (1 for emotions that were congruent with the emotion targeted in the instruction, -1 for emotions that were incongruent with the emotion targeted in the instruction; 0 elsewhere), and reconvolved to form a PPI regressor. The PPI regressor was mean-corrected and orthogonalized with regard to the main effect of task (i.e. perceptual matching: psychological regressor) and the corresponding time series (i.e. vMPFC influences: physiological regressor). This PPI analysis was therefore used to investigate context-dependent vMPFC influences that occurred over and above any perceptual matching effects and context-independent vMPFC influences.

Brain regions receiving contextual vMPFC influences during perceptual matching were determined by testing for positive slopes of the PPI regressor, that is, by applying a t-test that was 1 for the PPI regressor and 0 elsewhere. Subject-specific contrast images were then entered into random effects group analyses for within- and between-group (i.e. adults vs. adolescents) analyses.

The significance of the results was assessed with a mask that comprised regions involved in emotion perception that are connected anatomically and functionally with the vMPFC. Specifically, these were the orbito-frontal cortex, cingulate cortex, insula, amygdala, hippocampus, and thalamus (Musil and Olson 1988). We used a significance threshold of \( P < 0.001 \) uncorrected at the voxel level and \( P < 0.05 \) FWE-corrected at the cluster level (Friston et al. 1996).

**Results**

Satisfactory sequences were defined as those completed with accuracy of at least 50% (i.e. fewer than 5 incorrect responses in each sequence). Using this criterion, on average, 1.9 (SD 3.5) sequences per participant in the adult group and 3.4 (SD 4.2) sequences per participant in the adolescent group were considered to be completed at the near-chance level and were excluded from subsequent analyses (no difference between groups: \( F(24) = 1.0, P = \text{ns} \)). In addition, we verified that the session order did not affect task performance by running an ANOVA on accuracy and RT, with group as a between-subjects factor and the session order as a within-subjects factor. This analysis yielded no significant main effect or interaction (all F < 2.1, \( P = \text{ns} \)).

**Behavioral Results**

To investigate the differential effects of congruency on accuracy and RT for fear and anger, we performed 2 (fearful vs. angry faces) \times 2(congruent vs. incongruent with the instruction) \times 2(adults vs. adolescents) repeated-measures ANOVA. There was a significant main effect of congruency for RT (\( F(1,24) = 154.6, P < 0.001 \)) and accuracy (\( F(1,24) = 32.9, P < 0.001 \)). These results indicated higher accuracy and reduced RT for the stimuli that were congruent with the target emotion when compared with the incongruent stimuli (Fig. 2). For accuracy, none of the main effects or interactions was significant (Fs (1, 24) < 4.2, \( P = \text{ns} \)). For RTs, we found an emotion (anger vs. fear) by congruency (congruent vs. incongruent) interaction (\( F(1,24) = 7.0, P < 0.05 \)), indicating that the congruency effect was different for the different emotions. Post hoc t-tests revealed that the congruency effect was greater for angry facial expressions (post hoc paired t-test: \( t(25) = 2.3, P < 0.05 \), Fig. 2). Finally, this emotion \times congruency interaction was qualified by a 3-way emotion \times congruency \times group interaction for RT (\( F(1,24) = 8.4, P < 0.01 \)) showing a stronger congruency effect in adults than in adolescents (post hoc 2-sample t-test: \( t(24) = 2.3, P < 0.05 \), Fig. 2).

**Functional Imaging Results**

**Angry Faces**

For anger, assessing congruency between instructions and emotional face stimuli in either group (omnibus F contrast) revealed activations in the vMPFC, and also the mid-cingulate cortex, the pre-supplementary motor area (SMA), the ventrolateral prefrontal cortex (vLPFC), the insula, and the premotor
cortex (Fig. 3A; Table 1). More specifically, the vMPFC displayed a main effect of congruency in favor of face stimuli that were congruent with the instruction (Fig. 3A lower right part of the figure), while the other regions displayed a main effect of congruency in favor of face stimuli that were incongruent with the instruction (Supplementary File 3).

The 2 (congruent vs. incongruent) \times 2 (adults vs. adolescents) repeated-measures ANOVA in the regions activated by this omnibus \( F \) contrast (ROI analysis in the vMPFC, midcingulate cortex, the pre-SMA, the vLPFC, the insula, and the premotor cortex) revealed a group \times congruency interaction in the vMPFC (\( F(1,24) = 9.9; P < 0.001 \)), driven by a stronger congruency effect in adults than in adolescents (post hoc 2-sample \( t \)-test: \( t(24) = 2.7, P < 0.05 \), Fig. 3A lower right part of the figure). In contrast, we did not observe such an interaction in the other regions (all \( F_{\text{s}}(1,24) < 5.0; P = \text{ns} \), Supplementary File 3). The group \times congruency interaction in the vMPFC survived correction for multiple comparisons that took into account the 8 brain regions in which we carried out these factorial ROIs analyses (Bonferroni correction).

Note that activations in the vMPFC were correlated neither with RT nor with accuracy in either group (\( r < 0.26, P = \text{ns} \)). We performed another SPM analysis after having covaried out RTs (included as a parametric regressor in the design matrix) and errors. Limiting our analysis to that portion of the variance that did not vary with RTs or errors, we still found activations in the vMPFC (omnibus \( F \) contrast) with no major loss of statistical power (local maximum: \(-3, 60, -3; F = 13.13, P < 0.001 \), Ke = 17 voxels, false discovery rate corrected voxel level \( P = 0.08 \)). Thus, these activations are unlikely to be an artifact of a lower task demand on congruent trials (Gusnard et al. 2001).

Fearful Faces

For fear, assessing congruency in either group (omnibus \( F \) contrast), revealed activations in the motor cortex, pre-SMA, vlLPFC/insula, dorso-lateral prefrontal cortex (dLPFC), pre-motor cortex, and posterior parietal cortex (Fig. 3B; Table 2).

More specifically, the motor cortex displayed a main effect of congruency in favor of face stimuli that were congruent with the instruction, while the other regions displayed a main effect of congruency in favor of face stimuli that were incongruent with the instruction (Supplementary File 4).

The 2 (congruent vs. incongruent) \times 2 (adults vs. adolescents) repeated-measure ANOVA in the regions activated by this contrast (ROI analysis) revealed that the motor cortex demonstrated a group \times congruency interaction (\( F(1,24) = 21.1; P < 0.001 \)), driven by a congruency effect in adolescents but not in adults (post hoc 2-sample \( t \)-test: \( t(24) = 4.6, P < 0.001 \), Supplementary File 4). However, we did not observe such an interaction in the other regions (all \( F_{\text{s}}(1,24) < 4.3; P = \text{ns} \), Supplementary File 4).

Functional Connectivity (PPI Analysis)

To investigate in more detail the information-flow from regions related to perceptual matching (the vMPFC) to anatomically and functionally connected regions (orbito-frontal and cingulate cortex, insula, amygdala, hippocampus, and thalamus), we performed functional connectivity (PPI) analyses. In adults, PPI revealed a significant increase in functional connectivity between the vMPFC and left thalamus when prior expectations were congruent with the incoming angry faces. Activity in the vMPFC was significantly more highly correlated with activity in the left thalamus when the incoming angry face was congruent to the instruction relative to when it was incongruent (local maximum at \(-15, -15, 12; T = 5.58, P < 0.001 \), Ke = 30 voxels, FWE-corrected cluster level \( P = 0.04 \)) (Fig. 4).
No regions showed increased connectivity with the vMPFC in the adolescent group (even at a very liberal threshold of \( P < 0.1 \) uncorrected at the voxel level). In a direct comparison between the groups, the fronto-thalamic functional connectivity related to congruency between the incoming angry face and the instruction was significantly higher in adults than in adolescents (local maximum: \(-15, -15, 12\); \( T = 5.44, P < 0.001, Ke = 35 \) voxels, FWE-corrected cluster level \( P = 0.03 \)). No regions showed greater connectivity with the vMPFC in adolescents than in adults.

Discussion

In this study, we employed a facial emotion discrimination task where perception was biased by an instruction to investigate how prior expectations influenced emotional face perception in the adult and the adolescent brain. As expected, we found that both the adolescent and the adult groups responded more accurately and with shorter RTs to faces that were congruent with the instruction (Summerfield and Koechlin 2008). However, for angry faces, this bias was lower in the adolescents since they demonstrated a lower congruency effect than adults (for RTs). The fMRI results showed activations in both groups in the lateral prefrontal cortex and the pre-SMA when the threatening face was incongruent with the instruction. When the facial expression was congruent versus incongruent with the instruction (perceptual matching effect), activations were revealed in the vMPFC for anger and the motor cortex for fear. For angry faces, adults showed a

Table 1

<table>
<thead>
<tr>
<th>Regions</th>
<th>Coordinates (x, y, z)</th>
<th>Volume (mm³)</th>
<th>FWE cluster corrected P-value</th>
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<td>0.01</td>
<td>18.49</td>
<td>4.19</td>
</tr>
<tr>
<td>Left vLPFC</td>
<td>-45, 18, 27</td>
<td>441</td>
<td>0.005</td>
<td>17.81</td>
<td>4.13</td>
</tr>
<tr>
<td>Left pre-SMA</td>
<td>-6, 15, 48</td>
<td>261</td>
<td>0.005</td>
<td>17.32</td>
<td>4.08</td>
</tr>
<tr>
<td>Right pre-motor cortex</td>
<td>-27, -3, 51</td>
<td>198</td>
<td>0.01</td>
<td>16.07</td>
<td>3.96</td>
</tr>
<tr>
<td>vMPFC</td>
<td>-3, 57, -3</td>
<td>126</td>
<td>0.04</td>
<td>13.82</td>
<td>3.71</td>
</tr>
<tr>
<td>Left insula</td>
<td>-33, 24, 6</td>
<td>216</td>
<td>0.01</td>
<td>13.14</td>
<td>3.63</td>
</tr>
</tbody>
</table>

Figure 3. Activations in regions displaying a congruency effect for anger (A) and fear (B) in either the adult or the adolescent group (omnibus F contrast). Threshold: \( P < 0.001 \) uncorrected voxel-wise and \( P < 0.05 \) FWE-corrected cluster-wise. The red–white scale refers to \( F \) values. The graph in (A) showed a signal change in the vMPFC for the conditions in which angry faces were presented, when the instruction was congruent versus incongruent with the incoming emotional face stimulus (represented with dark and light colors, respectively). Data from the adolescents are in red and those from the adults are in blue. There was a group × congruency interaction driven by a greater difference in signal change for angry expressions that were congruent versus incongruent with the expression targeted in the instruction for adults relative to adolescents. The error bars represent the standard errors.

Table 2

<table>
<thead>
<tr>
<th>Regions</th>
<th>Coordinates (x, y, z)</th>
<th>Volume (mm³)</th>
<th>FWE cluster corrected P-value</th>
<th>F-score</th>
<th>Z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left motor cortex</td>
<td>-39, -21, 66</td>
<td>639</td>
<td>0.001</td>
<td>32.63</td>
<td>5.13</td>
</tr>
<tr>
<td>Right pre-SMA</td>
<td>9, 15, 54</td>
<td>2223</td>
<td>&lt;0.001</td>
<td>30.32</td>
<td>5.01</td>
</tr>
<tr>
<td>Right pre-motor cortex</td>
<td>21, 0, 45</td>
<td>1396</td>
<td>&lt;0.001</td>
<td>27.98</td>
<td>4.98</td>
</tr>
<tr>
<td>Left dlPFC</td>
<td>-39, 27, 30</td>
<td>513</td>
<td>0.002</td>
<td>23.11</td>
<td>4.56</td>
</tr>
<tr>
<td>Right vLPFC/insula</td>
<td>36, 21, 3</td>
<td>693</td>
<td>&lt;0.001</td>
<td>21.44</td>
<td>4.44</td>
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<tr>
<td>Left pre-motor cortex</td>
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<td>&lt;0.001</td>
<td>20.69</td>
<td>4.38</td>
</tr>
<tr>
<td>Left vLPFC/insula</td>
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<td>0.05</td>
<td>17.65</td>
<td>4.12</td>
</tr>
<tr>
<td>Right posterior parietal cortex</td>
<td>42, -39, 42</td>
<td>414</td>
<td>0.005</td>
<td>15.92</td>
<td>3.95</td>
</tr>
</tbody>
</table>

Figure 4. The region of the left thalamus that displayed increased functional connectivity with the vMPFC in Congruent Trials (relative to Incongruent Trials) for angry faces, for adults relative to adolescents. Threshold: \( P < 0.001 \) uncorrected voxel-wise and \( P < 0.05 \) FWE-corrected cluster-wise. The red-white scale refers to \( T \) values. Thal indicates thalamus.
greater activation than adolescents in the vMPFC, while they showed a lower activation in the motor cortex for fearful faces. Finally, for angry faces, adults demonstrated greater functional connectivity than adolescents from the vMPFC to the thalamus when the incoming face stimulus was congruent with the instruction.

Our behavioral results revealed a clear perceptual bias in favor of those emotions that were congruent with prior expectations (the instruction). Specifically, there was a higher accuracy and lowered RT for the stimuli congruent with the emotion targeted in the instruction. However, the effect of congruency was different between the negative emotions, with a stronger bias in RTs for angry stimuli. This facilitation for anger might be due to an increased need to predict the occurrence of an angry stimulus compared with a fearful stimulus. For angry faces, adolescents were less biased by the instruction than adults, suggesting a lower influence played by prior expectations on emotional perception in adolescence. This supports findings from a recent study that demonstrated a reduced effect of prior expectations on social decision in early adolescence (Cook and Bird 2011).

Prior Expectations in The Adult Brain

Our fMRI analysis revealed activations in a set of regions (i.e. pre-SMA, dLPFC, vLPFC/insula, premotor cortex, posterior parietal cortex) that were specifically activated when incoming face stimuli were incongruent with prior expectations (the instruction). A similar pattern of activation has been found in previous fMRI studies from interference tasks in which participants have to select a specific action when there are conflicts between simultaneously active, competing representations, for example, the Stroop task (Carter and van Veen 2007). Indeed, those fMRI studies have revealed that the anterior cingulate cortex and the pre-SMA are involved in detecting conflicts between representations, while engaging regions in the lateral prefrontal cortex (including the dLPFC) to resolve such conflict (MacDonald et al. 2000; Kerns et al. 2004).

For anger, the vMPFC was the only region that was more strongly activated when the incoming face stimulus was congruent with prior expectations. This prior expectation effect in the vMPFC cannot be attributed to a specific face processing effect per se because activations associated with perceiving angry faces per se would have been subtracted out in the perceptual matching contrast. Previous studies using a similar paradigm with non-emotional faces versus cars and houses (Summerfield et al. 2006), and non-social stimuli such as Gabor patches (Summerfield and Koechlin 2008), have also found activations within the vMPFC in relation to the matching of incoming sensory stimuli with prior expectations. Likewise, this region was activated when participants had to process a likely outcome in an association task (Rushworth et al. 2007) and "old" over "new" items in a recognition memory task (Wagner et al. 2005). We suggest that vMPFC activations during a match between expectations and incoming sensory stimuli would confirm and reinforce the validity of the prior expectation (i.e. the emotion in the instruction). This interpretation is in line with previous studies that have demonstrated that this region is activated when the strength of a prior belief over another increases (Daw et al. 2006; Hampton et al. 2006). In turn, when the participant is faced with a perceptual match, vMPFC activation could guide action selection on the basis of prior expectations via the reinforcement of prior belief (Summerfield et al. 2006).

This interpretation is further corroborated by our functional connectivity analysis. We used PPI analysis to estimate functional connectivity between a source (vMPFC) and target ROI (regions involved in face processing that are connected with vMPFC), during trials in which the emotional face stimulus and the instruction were congruent versus trials in which they were incongruent. In adults, our PPI analyses revealed greater functional connectivity between the vMPFC and the thalamus when an incoming angry stimulus was congruent with the instruction, compared with when it was incongruent. It has previously been argued that the vMPFC is the source of backward top-down connections (Bar et al. 2006; Summerfield et al. 2006; Kveraga et al. 2007) for subsequent decision-making facilitation. According to the literature on emotion perception, the thalamus (and especially its pulvinar nucleus) acts as an intermediary between the retina and emotion-processing areas like the amygdala within the subcortical neural pathway, which then permits rapid and preconscious processing of potentially threatening stimuli (Pessoa and Adolphs 2010). Such functional connectivity between the vMPFC and the thalamus suggests a regulation of emotional responsiveness by top-down social expectations, that is, the likely forthcoming social events in the environment. Here, this translates as the appearance of an angry face when participants are instructed to look out for anger.

Prior Expectations in The Adolescent Brain

We found no differences in activation between adolescents and adults when there was a discrepancy between the incoming emotional face stimulus and the emotion targeted in the instruction. However, compared with adults, the adolescents showed hypoactivation in the vMPFC when faced with angry stimuli that were congruent with prior expectations. According to the role of the vMPFC described above, hypoactivation of the vMPFC in the adolescents might reflect a difference in the way this region is engaged in the development of expectations of probable future outcomes and the use of these to guide behavior (Wagner et al. 2005; Rushworth et al. 2007). Other studies have demonstrated developmental changes within the vMPFC in the adolescents in relation to their tendency to choose immediate, small rewards, rather than delayed but larger rewards (temporal discounting) (Olson et al. 2009; Christakou et al. 2011). This suggests a role played by vMPFC hypoactivation in the weak regulation of impulsive choices based on immediate rewards or new items in adolescence.

For anger, our PPI analysis further demonstrated lower functional connectivity between the vMPFC and the thalamus for congruent versus incongruent trials in the adolescents compared with adults. This result is in line with previous findings of developmental changes in functional or effective connectivity between areas involved in face processing, action observation, and mentalizing (Cohen-Kadosh et al. 2011; Shaw et al. 2011), thought to be related to the continued development of functional specialization of these regions (Cohen-Kadosh et al. 2011). Lower levels of connectivity between social brain regions in adolescence relative to adults...
might result in weaker resistance to the peer influence (Grosbras et al. 2007).

**Conclusion**

Our data support the finding that specific frontal regions are involved in integrating emotion perception and cognitive control (Pessoa 2008), and highlight the involvement of the vMPFC in the biased perception of emotional faces. While other studies have demonstrated the development of bottom-up and top-down attentional processes in the adolescent brain (e.g. Monk et al. 2003), here we investigated the neural development of another social decision-making bias: prior expectations (Summerfield and Egner 2009). Our results show functional development in vMPFC and changes in its functional connectivity with the thalamus during the period of adolescence. To our knowledge, this is the first study to demonstrate that the influence of prior expectations on emotional perception is still developing in the adolescent brain.

**Supplementary Material**

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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**References**


