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Research Paper

Facial expressions perceived by the adolescent brain: Towards the proficient use of low spatial frequency information

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A R T I C L E I N F O

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A B S T R A C T

Rapid decoding of emotional expressions is essential for social communication. Fast processing of facial expressions depends on the adequate (subcortical) processing of important global face cues in the low spatial frequency (LSF) ranges. However, children below 9 years of age extract fearful expression information from local details represented by high SF (HSF) image content. Our ERP study investigated at which developmental stage this ineffective HSF-driven processing is replaced by the proficient and rapid LSF-driven perception of fearful faces, in which adults are highly skilled. We examined behavioral and neural responses to high- and low-pass filtered faces with a fearful or neutral expression in groups of children on the verge of pre-adolescence (9–10 years), adolescents (14–15 years), and young adults (20–28 years). Our results suggest that the neural emotional face processing network has a protracted maturational course into adolescence, which is related to changes in SF processing. In mid-adolescence, increased sensitivity to emotional LSF cues is developed, which aids the fast and adequate processing of fearful expressions that might signal impending danger.

1. Introduction

Fast and adequate identification of emotional expression is essential for daily functioning as it helps to evaluate the state and intentions of others. Especially fearful or angry facial expressions, which may signal impending danger requiring an immediate response, should be recognized as fast as possible. Fearful expressions are primarily extracted from information in the low spatial frequency (LSF) content of faces (e.g., Méndez-Bértolo et al., 2016; Vlamings, Goffaux, & Kemner, 2009). However, the proficient use of LSF cues for configural face processing (i.e., relational processing of facial features) shows a slow development, reaching only full maturation in young adulthood (Peters, Vlamings, & Kemner, 2013). The present study investigates whether an equally protracted development occurs for LSF processing of emotional expressions.

In adult face perception, information carried by different SF bands is combined following a coarse-to-fine sequence (Goffaux et al., 2011; see Ruiz-Soler & Beltran 2006 for review). LSF conveys highly important coarse information on emotional and configural aspects that is extracted first, before more fine-grained high SF (HSF) information is examined for further facial cues (related to for example facial age; cf. LSF- and HSF-filtered faces in Fig. 1). LSF and HSF information is primarily processed via different visual channels (e.g., Shoham, Hubener, Schulze, Grinvald, & Bonhoeffer, 1997; De Valois & De Valois, 1988). LSF information is mainly relayed through the magnocellular pathway. This relatively fast pathway makes coarse information rapidly available to not only the visual cortex, but also to the prefrontal cortex (Bar et al., 2006) and amygdala (Vuilleumier, Armony, Driver, & Dolan, 2003) for immediate responses to threats. The amygdala initiates instant reactions to emotional events (LeDoux, 2000; Morris, Ohman & Dolan, 1999), such as when a fearful facial expression is detected in the visual scene. However, the amygdala can only decode fearful expressions adequately when LSF information is present (M & ndez-B & rtolo et al., 2016; Vuilleumier et al., 2003). In contrast to LSF input, HSF information is conveyed by the parvocellular pathway, projecting solely to visual cortex (Merigan & Maunsell, 1993). In visual cortex, LSF and HSF appear to remain partly segregated: LSF information mainly travels via the middle occipital gyrus to an area in the fusiform gyrus

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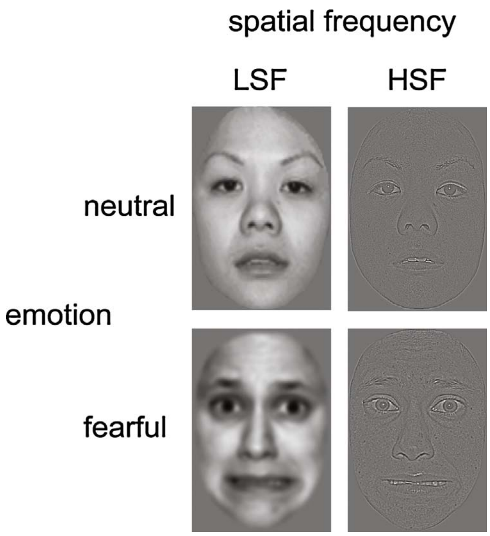

Fig. 1. Example of low-pass (LSF), and high-pass filtered (HSF) face with a fearful or neutral expression.

specialized in face processing (the so-called fusiform face area, Kanwisher, Mc Dermott, & Chun, 1997), where it converges with HSF information primarily coming from inferior occipital and temporal areas (Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007; Vuilleumier et al., 2003; Winston, Vuilleumier & Dolan, 2003). Recent neuroimaging studies have shown that these structures mature at a much slower speed than previously assumed, and are not fully matured till adulthood. Throughout adolescence, there is progressive neural proliferation (Gomez et al., 2017; Golarai et al. 2007; Golarai, Liberman, Yoon, & Grill-Spector, 2010) and functional tuning (Passarotti, Smith, DeLano, & Huang, 2007) of the neural face network (see Cohen-Kadosh & Johnson, 2007; Grill-Spector, Golarai, & Gabrieli, 2008 for reviews), including the amygdala (Guyer et al., 2008; Thomas et al., 2001).

It is unclear how this adolescent neural reorganization affects the spatial frequency pathways running through the face network. Previous studies provide some indications that the LSF- and HSF pathways mature at different speeds. Visual processing in newborns is solely based on LSF information (De Heering et al., 2008; Slater & Sykes, 1977), due to immaturity of the visual system at several levels (Hammarrenger, Lepor & , Lipp & , Labrosse, Guillemot & Roy, 2003; Johnson, 2005). However, although LSF processing is present in newborns, sensitivity for LSF is only fully matured in preadolescence (12/13-year-olds; Madrid & Crognale, 2000). This is much later than the maturation of HSF processing at 3–4 years (Adams & Courage, 2002). Further research suggests that it takes even longer time to proficiently use LSF information for the fast, holistic processing of faces, in which we humans are so uniquely skilled. For example, adolescents show an immature neural processing of the LSF information needed for configural face perception (Peters et al., 2013). It is yet unknown whether adolescents also have a suboptimal LSF processing for emotional expressions.

Previous ERP studies of our lab investigated the influence of SF content on the processing of facial expressions in children between 3 and 8 years old (Vlamings, Jonkman, Kemner, 2010) and young adults (Vlamings et al., 2009), and observed an interesting developmental change in the use of SF information. In children, the detection of fearful expressions affected the earliest stages of cortical processing: the P1, an ERP component generated in occipital cortex around 100 ms after stimulus onset, was higher for faces with a fearful compared to neutral expression. Importantly, this effect was only present when faces contained HSF information. In contrast, adults showed a higher N170 response for fearful than neutral expressions, but only for faces with LSF content. The N170 is generated in fusiform and temporal gyri (Henson et al., 2003) around 170 ms after stimulus onset. Unlike the early and rather unselective P1, the N170 is face-selective and associated with in-depth configural face processing (Itier & Taylor, 2004). In sum, children showed a *HSF*-driven, superficial processing of facial expressions, whereas adults showed advanced configural processing driven by *LSF* content. This suggests that in (pre-) adolescence, a qualitative developmental change in SF use takes place. The present ERP study examined this developmental shift by measuring P1 and N170 responses to emotional expressions in 1) children on the verge of pre-adolescence (9–10-year-olds) 2) adolescents (14–15-year-olds), and 3) young adults (20–28-year-olds). We compared neural responses to faces with fearful and neutral expressions, in which only LSF or HSF information was available (Fig. 1). To facilitate direct comparisons between our results and findings in 3–8-year-olds and adults, we used an identical experimental paradigm (same stimuli, stimulus paradigm, EEG electrodes, and EEG setup) as, respectively, Vlamings, Jonkman, Kemner, 2010 and Vlamings et al. (2009). Furthermore, our adult dataset largely overlapped with Vlamings, Jonkman, and Kemner (2010). Finally, we could track behavioral development of expression identification from childhood to adulthood, by measuring children's and adolescent's behavioral responses in an additional emotional categorization task, employing the same paradigm as our previous studies.

Our ERP and psychophysical results suggest that the neural network involved in perception of fearful expressions has a protracted maturational course into early adolescence. In adolescence, sensitivity to the important facial expressions conveyed by LSF content is developed, which aids the fast and adequate processing of fearful expressions essential for the detection of impending danger.

2. Methods

2.1. Participants

Sixty-one healthy participants with (self-reported) normal or corrected-to-normal visual acuity were divided in three groups according to their age: children between 9 and 10-year-olds (n = 20; 10 males; median age = 10.2-year-olds; range 9.0–10.9-year-olds), adolescents between 14 and 15-year-olds (n = 20; 7 males; median 15.0-year-olds; range 14.0–15.8-year-olds), and young adults (university students) between 20 and 28-year-olds (n = 21; 10 males; median age = 22.2-year-olds). Note that originally 21 adolescents were included, but data of 1 adolescent was eliminated due to technical problems with EEG recording. Furthermore, the data of 20 adults in our dataset were previously obtained and published by Vlamings et al. (2009). We reanalyzed this adult dataset using the same EEG analysis procedure as applied to the set of children and adolescents to achieve a fair comparison between age groups. Participants in these three groups were recruited from a primary school, high school, and university in Zuid-Limburg (The Netherlands), respectively.

Each child and adolescent was in the normal cognitive range (i.e., IQ > 90) for its age, as assessed by the block design and vocabulary test of the WISC-III (Wechsler, 1991). Note that the estimated total IQ score derived from these subtests has a mean reliability of 0.94 and a mean validity of 0.91 compared to the complete WISC-III (Spreen & Strauss, 1998). In addition, none of the children or adolescents had emotional or behavioral problems as indicated by scores on the Child Behaviour Checklist (Achenbach, 1991). Participants (adolescents, and adults) and parents (children and adolescents) gave their written informed consent to participate. All procedures were approved by the ethics committee of the Faculty of Psychology and Neuroscience of Maastricht University.

2.2. Stimuli and task design

Sixteen grayscale front-view photographs of Caucasian faces with a fearful (n = 8; 4 males) or neutral (n = 8; 4 males) expression served as stimuli. Stimuli were selected from the NimStim Face Set (Tottenham et al., 2009) and trimmed to remove neck and hairline. These stimuli have shown to evoke emotional effects at the level of N170 (Blau, Maurer, Tottenham, & McCandliss, 2007). The spatial frequency content of each face was filtered with a high-pass (HSF; ≥ 6 cycles/deg of visual angle = 27 cpfw) or low-pass (LSF; ≤ 2 cycles/deg of visual angle = 9 cpfw) cut-off. These cut-offs were chosen to exclude most of the intermediate frequencies (8–16 cpfw) pivotal for adequate face recognition (e.g., Gold, Bennett, & Sekuler, 1999), in line with our previous studies (e.g., Peters et al., 2013; Boeschoten, Kenemans, van Engeland, & Kemner, 2007; Vlamings et al., 2009; Vlamings, Jonkman, & Kemner, 2010; Vlamings, Jonkman, van Daalen, van der Gaag, & Kemner, 2010)

Thus, there were four stimulus conditions in total as defined by spatial frequency content (LSF, HSF) and emotional expression (fearful, neutral; Fig. 1). In addition, a fifth stimulus condition consisting of nine different animation figures was included in the experiment to ensure subjects paid attention to the presented faces throughout the measurement. During the task, subjects were instructed to press a button as soon as an animation was shown on the screen. Stimuli from different conditions were randomly presented for 500 ms (except for animation figures, which were presented until response), with an interstimulus interval of 1600–1800 ms.

Subjects were comfortably seated in front of a 21 inch LCD monitor (60 Hz refresh rate) in a dimly lit room. They were instructed to maintain a fixed viewing distance from the monitor and experimenters monitored this throughout the measurements. They received 64 randomized trials of each face stimulus condition (8 repetitions of each stimulus). In addition, 36 trials of the animation stimulus condition were presented (four repetitions of each stimulus), resulting in 292 trials in total. These trials were divided in four runs, in between which subjects could shortly rest. Participants were instructed to fixate on the middle of the screen and to press the button of a buttonbox as fast and accurately as possible, when they detected a colored animation.

Following a short break after the EEG recordings, each child and adolescent participated in a psychophysical emotion discrimination experiment. Experimental design was identical to the EEG session, except that no animation figures were presented and that participants had to decide as fast and accurate as possible whether each of the faces had a fearful or a neutral expressing by pressing the appropriate response button (left/right). Furthermore, they performed 4 − 6 runs (instead of the 4 runs in the EEG setting) of 64 trials. One male (child) and three females (one child, two adolescents) did not finish at least 4 runs and were therefore eliminated from further analyses. Button assignments of the button box were counterbalanced across subjects. Preceding the experiment, participants trained the task in two steps: First, participants were presented with a colored animation face of a lion with a fearful or neutral expression and had to decide whether the face of the lion looked “fearful” or “usual/neutral” by pressing the appropriate response button. In each of the 32 practice trials, the stimulus was shown until response. Subsequently, subjects performed the same task but with stimulus duration and ISI similar to the EEG session. The participant received auditory feedback after each response (the exclamation “Yoohoo!” for correct or “Boing!” for incorrect responses) in the training, but not in the main task.

2.3. Electrophysiological recording and data analysis

The electroencephalogram (EEG) was recorded (sampling rate 500 Hz; band-pass filter of 0.01–200 Hz; Brain Products amplifier, Munich, Germany) from 35 AgCl scalp electrodes (extended International 10/20 system) with reference electrodes placed at the mastoids. Signals were collected using the left mastoid as reference and re-referenced off-line to the average activity of all electrodes. Horizontal and vertical electrooculograms (EOG) were recorded with bipolar electrodes placed at the external canthii and above and below the left eye. Electrode impedance was kept below 20 kOhm for all electrodes.

EEG data were epoched (−100–500 ms, relative to stimulus onset), filtered (0.01–30 Hz band-pass and 50 Hz notch filters) and baseline corrected (100 ms pre-stimulus interval) using Vision Analyser (Brain Products, Munich, Germany). Artefacts from horizontal eye movements and blinks were reduced with the algorithm of Gratton, Coles, and Donchin (1983). Trials with artifacts (samples exceeding ± 75 μV, steep gradients [50.00 μV per sampling point] or low activity [1.00 μV over 100 ms interval]) were excluded from subsequent analyses. For each subject-specific averaged EEG epoch of a condition, latencies and amplitudes were automatically extracted at global peak-maximum at each tempero-occipital (PO7, PO8) electrodes in the P1 interval (100–190 ms for children and 70–160 ms for adolescents & adults, respectively) and N170 interval (140–240 ms for children and 130–240 ms for adolescents & adults). Electrode PO7 of 1 adolescent was not properly recorded and peak values of this participant were therefore replaced by condition-specific means of the adolescent group. Peak amplitudes and latencies of the P1 and N170 were submitted to separate repeated-measures ANOVAs with SF (LSF, HSF), Emotional Expression (fearful, neutral), and Hemisphere (left, right) as within-subject factors and Age Group (children, adolescents, and adults) as between-subject factor. Puberty has a later onset in boys than girls (Tanner and Whitehouse, 1976). This variability in pubertal status might contribute to gender-related differences in emotional expression recognition in early adolescence (e.g., Lawrence, Campbell, & Skuse, 2015), which can disappear again in late adolescence (McGivern, Andersen, Byrd, Mutter, & Reilly, 2002). To investigate whether gender contributed to any of the within-groups effects in the present study, Gender (male, female) was included as an additional between-subject factor to compare potential gender-related developmental changes in children and adolescents. All ANOVA results were Greenhouse-Geisser corrected (but uncorrected degrees of freedom are reported). Finally, correct reaction times and accuracy of the psychophysical task were subjected to separate repeated-measures ANOVAs with Spatial Frequency (LSF, HSF) and Emotional Expression (fearful, neutral) as within-subject factors and Age Group (children, adolescents) and Gender (male, female) as between-subject factors. Furthermore, bias-free sensitivity indexes (d’; Stanislaw & Todorov, 1999) were computed for each subject in the psychophysical task and entered in a repeated-measures ANOVAs with SF (LSF, HSF) as within-subject factors and Age Group (children, adolescents) and Gender (male, female) as between-subject factors.

Effect sizes of reported effects were estimated using partial eta squared (η^2). This is a standard metric in repeated-measure designs that estimates the magnitude of a given effect by quantifying the percentage of variance explained by a given factor when excluding the contribution of inter-subject variance. Note that main effects are not discussed when they interact with other factors. Instead, subsequently performed posthoc, Bonferroni-corrected paired were performed (but uncorrected degrees of freedom and p-values are reported). Main effects (of non-interacting factors) and interactions that are not reported did not reach significance. All statistical analyses were performed in SPSS 22 (SPSS INC, Chicago, IL).

3. Results

3.1. Behavioral data

Participants performed the detection task in the EEG session at ceiling level (accuracy children = 99.7%, adolescents and adults 100%). Furthermore, there were no performance differences between age groups ($p > 0.3$).

The separate psychophysical task (Fig. 2) was performed fast (mean RT of 705.9 ms; s.e. 20.1 ms) and accurately (mean accuracy of 74.8%; s.e. 3.2%; mean d’ = 1.6; s.e. 0.21). Gender did not influence RT (i.e.,

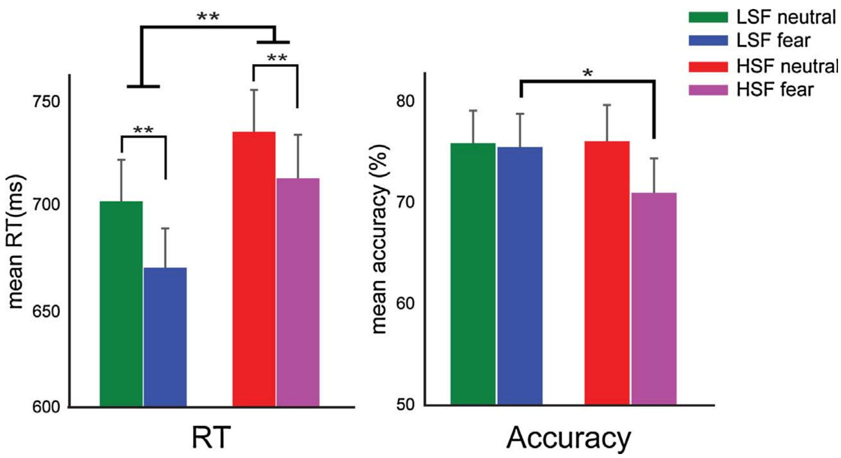

Fig. 2. Mean reaction times (RT; left) and accuracy (right) across children and adolescents for all stimulus conditions. * $p < 0.01$; ** $p \leq 0.005$.

all main and interaction effects: p's > 0.1). In contrast, a main RT effect of Age group ($F(1,34) = 18.3$, $p = 0.0002$; $\eta^2 = 0.35$) revealed that adolescents had a faster RT than children. However, age group did not interact with any of the within-subject factors (p's > 0.3). Both SF ($F(1,34) = 82.0$, $p < 0.00001$; $\eta^2 = 0.71$) and emotional expression ($F(1,34) = 11.6$, $p = 0.002$; $\eta^2 = 0.25$) were highly significant: Responses to LSF faces were 39 ms faster than to HSF faces. In addition, fearful faces were 28 ms faster recognized than neutral faces.

Similar to RT, gender did not influence accuracy (main and interaction effects: p's > 0.2). Furthermore, accuracy was not affected by age (main and interaction effects: p's > 0.4). However, emotional expression and SF did interact ($F(1,34) = 4.7$; $p = 0.04$; $\eta^2 = 0.12$). Posthoc tests revealed that fearful faces were more accurately detected when they contained LSF compared to HSF information ($t(36) = 2.8$; $p = 0.009$). In contrast, d' was not influenced by any of the factors (p's > 0.4).

3.2. Age effects

As can be seen in Fig. 3, the morphology of both the P1 as well as the N170 changes across development. Both the amplitude ($F(2,58) = 29.2$; $p < 0.00001$; $\eta2 = 0.50$) and latency ($F(2,58) = 35.1$; $p < 0.00001$; $\eta2 = 0.55$) of the P1 strongly decreased with increasing age. All age groups significantly differed for latency (all p's < 0.005) and amplitude (all p's < 0.00001, except for adolescents compared to adults), indicating a continuous modification of the P1 across development. Along the same line, the N170 amplitude became more negative with increasing age ($F(2,58) = 17.8$; $p < 0.00001$; $\eta2 = 0.38$), whereas its latency ($F(2,58) = 20.4$; $p < 0.00001$; $\eta2 = 0.41$) decreased. N170 peaks in children differed from both adolescents as well as adults in both amplitude (p's < 0.001) and latency (p's < 0.0001), indicating a modification of the N170 in adolescence.

3.3. P1

The P1 peak was faster ($F(1,58) = 74.1$; $p < 0.00001$; $\eta2 = 0.56$) and higher ($F(1,58) = 25.6$; $p = 0.000005$; $\eta2 = 0.31$) for LSF than HSF faces (Fig. 3). No other effects were observed.

3.4. N170

The N170 peak was faster ($F(1,58) = 101.2$; $p < 0.00001$; $\eta2 = 0.64$) for LSF than HSF faces (Fig. 3).

The effects on the N170 amplitude were more complex. Within-subject factors were tested per age group, since age group influenced the effect of SF ($F(1,58) = 12.0$; $p = 0.00005$; $\eta2 = 0.29$) and tended to interact with hemisphere ($F(1,58) = 3.0$; $p = 0.06$; $\eta^2 = 0.09$) as well as with the interaction between SF and emotional expression ($F(2,58) = 2.7$; $p = 0.085$; $\eta^2 = 0.82$). Children showed larger N170 amplitudes for LSF than HSF faces ($F(1,18) = 19.3$; $p = 0.0004$;

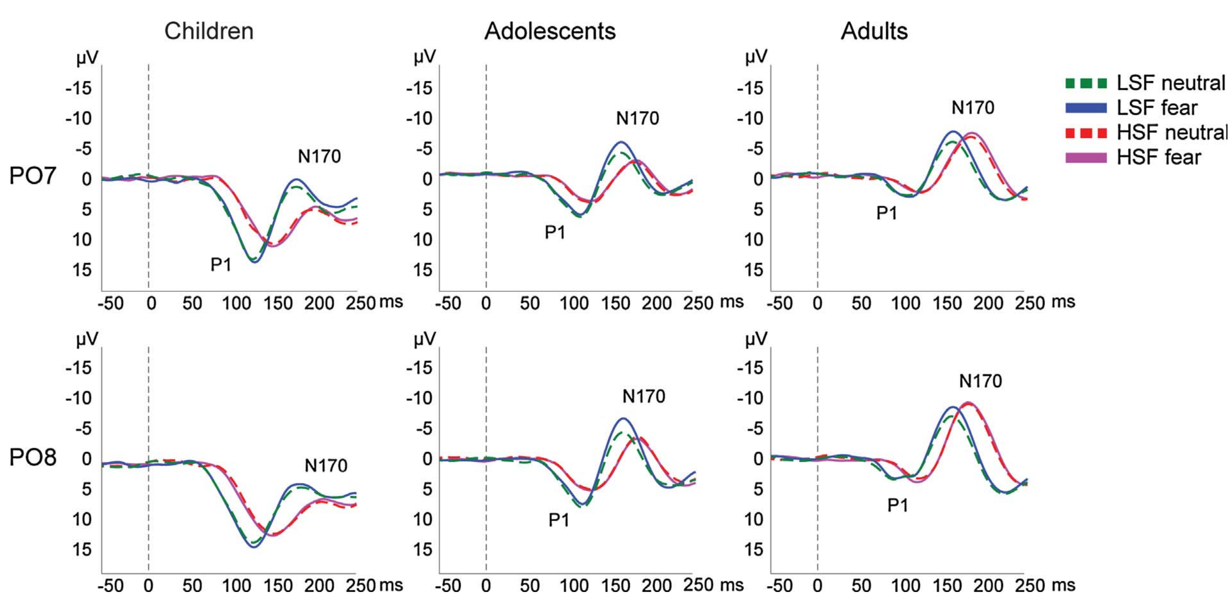

Fig. 3. Grand-averages for children (left), adolescents (middle), and adults (right) at electrodes PO7 (top) and PO8 (bottom).

$\eta 2 = 0.52$), but SF was not influenced by emotional expression, gender, or hemisphere (p's > 0.2). In stark contrast, emotional expression did influence SF in the group of adolescents ($F(1,18) = 17.4$; $p = 0.001$; $\eta 2 = 0.49$), and adults ($F(1,20) = 12.6$; $p = 0.002$; $\eta 2 = 0.39$). In adolescents, the interaction between SF and emotion was influenced by gender ($F(1,18) = 7.2$; $p = 0.02$; $\eta 2 = 0.29$). However, further tests per gender group did not reveal additional effects (p's > 0.1), which might be due to the relatively small sample size per gender group. For both adolescents as well as adults, N170 amplitudes were higher for fearful than neutral faces, but only when faces contained *LSF* information (adolescents: $t(19) = 4.9$; $p = 0.0001$; adults: $t(20) = 6.4$; $p < 0.00001$). In adults, SF was additionally influenced by hemisphere ($F(1,20) = 7.3$; $p = 0.014$; $\eta 2 = 0.27$). Posthoc tests revealed lower N170 responses to LSF than HSF faces in PO8 ($t(20) = 3.1$; $p = 0.05$), but not in PO7 ($p > 0.1$).

4. Discussion

The present study investigated developmental changes in the use of spatial frequency (SF) content of facial expressions, by comparing ERP responses in children, adolescents and young adults. Results showed that sensitivity to the important emotional LSF cues is only developed in mid-adolescence, suggesting a slower maturation of emotional processing than previously assumed.

4.1. LSF availability in faces improves emotion categorization performance

The behavioral emotion categorization task revealed faster reaction times for fearful compared to neutral expressions. Such fast responses to fearful expressions are essential, as fearful expressions can signal impending danger necessitating immediate action. The pivotal facial expression cues needed for a speeded detection of fear are conveyed by LSF. Indeed, the amygdala is not directly activated when fearful faces lack LSF content (Méndez-Bértolo et al., 2016, Vuilleumier et al., 2003). This important role of LSF content was reflected in our behavioral results: Facial expressions could be faster discriminated when faces contained LSF rather than HSF information. Moreover, fearful faces were more accurately detected when LSF rather than HSF information was available.. The present results of 9–10-year-old children and adolescents, showed a similar behavioral pattern as the adult subjects in Vlamings et al. (2009), who performed an identical task. However, our results do differ from results obtained with younger children (Vlamings, Jonkman, & Kemner, 2010): Children below 9 only showed a marginally ($p = 0.053$) faster response to fearful compared to neutral expressions, regardless of SF content. The fast and adequate recognition of fearful expressions from 9 years of age on, compared to the flawed performance of younger children, is in line with other behavioral studies showing a progressive maturation of emotional face processing around this age (De Sonneville et al., 2002; Vicari et al., 2000).

4.2. LSF cues drive neural processing of fearful expressions

The ERP results revealed that the neural processing of fearful expressions continued to develop after the age of ten. There was a clear change in ERP morphology across age groups, showing a smaller P1 and more pronounced N170 with increasing age (see also Itier & Taylor, 2004; Peters et al., 2013). Importantly, an adolescent developmental shift was observed in the role of SF content in processing facial expressions. We used an identical experimental paradigm as a previous ERP study (Vlamings, Jonkman, Kemner, 2010), which revealed that children below 9 show enhanced P1 responses to fearful compared to neutral expressions, but only when *HSF cues* are present. Such HSF-driven effect was not observed for the slightly older children in the current study, which were on the verge of pre-adolescence (9–10-year-olds). Moreover, our pre-adolescents did not show any processing advantage for fearful over neutral expressions, irrespective of SF content. Only in 14–15-year-olds the adult pattern started to emerge: Both adolescents and adults showed higher N170 amplitudes for fearful than neutral faces, but only when faces contained *LSF* information. Together, these data suggest that whereas children below 9 extract fearful expressions from *HSF* cues at an early processing stage (i.e., P1, around 100 ms after stimulus onset), adolescents show *LSF*-driven perception of facial expressions at a later processing stage (i.e., N170, around 170 ms after stimulus onset).

The shift from P1- to N170-dependent processing of facial expressions likely relates to the observed shift from a bias towards a superficial, holistic level of face processing (associated with P1 activity) to a deeper level of comprehensive, configural processing (linked to N170 activity; Itier & Taylor, 2004; Boutsen, Humphreys, Praamstra, & Warbrick, 2006). That is, although infants already show a sensitivity to holistic face cues (e.g., Simion et al., 2002), proficient configural face processing skills develop relatively slowly and continue to mature until adulthood (e.g., Maurer, Le Grand, & Mondloch, 2002; Mondloch, Le Grand, & Maurer, 2002; Cohen-Kadosh, 2012). For example, a recognition advantage for upright compared to inverted faces (i.e., the Face Inversion Effect), a hallmark of configural face processing, is not reliably shown in children below 10 (e.g., Schwarzer, 2000). Moreover, we previously measured the neural counterpart of the Face Inversion Effect and observed a shift from modulation of P1-related to N170-related face processes during adolescence that resembles the shift for facial expressions: in 9–10-year-olds, face inversion affected P1 activity (irrespective of SF content), which was likely caused by a disruption in holistic processing of global face orientation. In contrast, adults showed altered N170 activity for inverted faces, suggesting a disruption of in-depth configural processing. Notably, the adult N170 was only modulated by inversion when faces contained LSF information. Remarkably, adolescents showed a hybrid pattern: Similar to children, face inversion affected their P1 activity, irrespective of SF content. However, adolescents also showed the adult pattern with face inversion affecting N170 activity for LSF faces (Peters et al., 2013).

The previous and present findings on SF perception of emotional expressions show similar changes as in Peters et al. (2013), but in slightly different developmental periods: P1 was only affected in children below 9, whereas adolescents solely showed an (LSF-driven) effect of facial expressions for N170 but not P1 activity. This suggests that the shift from P1- to N170- modulated processing occurs at an earlier stage in adolescence for perception of facial expressions, compared to the perception of more general configural face cues in neutral faces. The evolutionary importance of fast and adequate recognition of face cues signalling imminent danger might have advanced the maturational process of extracting emotional cues from LSF face content over LSF information of less paramount significance. The relatively early emergence of LSF-driven processing of emotional expressions in 14–15-year-olds might, speculatively, be facilitated by the increased importance of social interactions as children enter adolescence. The importance of social acceptance and the corollary sensitivity to peer evaluation increases in early adolescence (e.g., Scherf, Behrmann, & Dahl, 2011). Therefore, correct interpretations of subtle emotional face cues become more and more important in peer interactions, and an increasing number of opportunities emerges to practice LSF-guided emotional face recognition skills. For example, moving from a small primary school to a large high school requires encoding of many new face identities and their emotional status (see also Carey, 1981). A psychophysical study indeed revealed a relation between experience and effective use of LSF cues in objects of expertise (Viggiano, Righi & Galli, 2006): Compared to novices, tool-experts needed less additional information in the middle and high SF spectrum of pictures for correct tool identification. Likewise, increased facial expression expertise might aid the adequate use of LSF information for emotional face processing. Although adolescents are able to use emotional face cues in LSF, the qualitative differences in the ERP waves between adolescents and adults suggest that neural processesing of facial expressions is not yet fully matured in

14–15-year-olds. Indeed, although the recognition of fearful expressions is matured around 7 years of age (Durand et al., 2007), neuroimaging findings suggest that until late adolescence, neurodevelopmental changes in fear perception occur throughout the brain (Monk et al., 2003; Thomas et al., 2007).

In line with previous observations (Batty & Taylor, 2006), facial expressions did not influence P1 and N170 activity in 9–10-year-olds. This undetermined emotional face processing might be related to the general dip in face perception skills at the onset of puberty (Carey, Diamond, & Woods, 1980; Carey, 1992; Diamond, Carey, & Back, 1983; Flin, 1980; Lawrence et al., 2008; for review, see Chung & Thomson, 1995). Around 10 years of age a reorganization of face perception appears to take place, as suggested by psychophysical results (Schwarzer, 2000) and qualitative changes in N170 activity (Itier & Taylor, 2004; Taylor, Batty, & Itier, 2014). Before the age of 10, the N170 has a bifid morphology (and the peak amplitude is not negative yet) which reflects two different functional sources in temporo-occipital and lateral temporal cortices (Itier & Taylor, 2004). From 10 years on, the bifid N170 components starts to merge into a single component, resulting in a sharper and negative peak (cf. children and adolescents in Fig. 3) of which the neural sources continue to be fine-tuned for facial expressions (Wong, Fung, McAlonan, & Chua, 2009). Children on the verge of pre-adolescence, in the present and previous studies (Batty & Taylor, 2006), might be in slightly different transition phases of this neural reorganization process of N170 sources, which might have contributed to increased within-group variations. Moreover, the neural organization might have temporarily hampered processing of facial expressions. Gender-related differences might have also affected within-group variability in our study, especially in the adolescent group: Puberty has a later onset in boys than girls (Tanner and Whitehouse, 1976), which likely contributes to gender-related differences in recognition (Lawrence, Campbell, & Skuse, 2015; McGivern et al., 2002) and neural processing (McClure, 2000) of emotional expressions in early adolescence. In the present study however, gender did neither influence behavior nor ERP results. This might be due to the relatively small sample size per gender group. Future research can focus on early adolescence and estimate the influence of pubertal status and gender on SF-related processing of emotional expressions in larger subject samples.

4.3. LSF content in faces is faster processed than HSF content

In all age groups, LSF faces elicited faster P1 and N170 peaks than HSF faces, irrespective of facial expression. This is consistent with other ERP studies in adults (e.g., Hsiao, Hsieh, Lin & Chang, 2005; Vlamings et al., 2009) and reflects faster cortical processing of information that was conveyed by the magnocellular compared to parvocellular pathway (e.g., Maunsell et al., 1999; Schroeder et al., 1989). The peak latency difference between LSF and HSF for the P1 (mean 15 ms) and N170 (mean 17 ms) nicely concurred with the measured V1 input latency differences of 10–20 ms between the two pathways (Schmolesky et al., 1998) due to different axonal conduction velocities (Hess, 2004).

4.4. Future research

Taken together, these results suggest that LSF and HSF information in fearful faces differentially affect the speed and strength of neural processes underlying emotional face perception, and that the distinctive use of SF information changes during adolescence. Future research could investigate whether these findings generalize to other emotional expressions than fearful faces and/or investigate neurophysiological changes in emotion perception in 11–13-year-olds. Moreover, this research could be extended to explore SF-dependent emotional expression processes in neurodevelopmental disorders. For example, one could investigate how impaired configural face perception following early visual deprivation (Le Grand et al., 2001) affects the role of SF in emotional face recognition. Likewise, it would be interesting to examine whether the inadequate, LSF-based face perception mechanisms observed in individuals with Autism Spectrum Disorder (that contribute to their impaired face perception skills) might also contribute to their atypical perception of emotional expressions (Deruelle, Rondan, Salle-Collemiche, Bastard-Rosset, & Da Fons & ca, 2008; Deruelle, Rondan, Gepner, & Tardif, 2004; Johnson, 2005; Vlamings, Jonkman, van Daalen et al., 2010). If inefficient processing of LSF content indeed hampers LSF-guidance of emotional expression processing in such disorders, it might be worthwhile to investigate whether emotion recognition skills can be improved by training-induced increases in LSF sensitivity (Peters, van den Boomen, & Kemner, 2017).

5. Conclusion

The present study shows that perception of fearful expressions still undergoes important changes during early adolescence. Previous work showed that whereas children below 9 years of age extract fearful expressions from *HSF* cues at an early processing stage (around 100 ms, P1), adults show *LSF*-driven perception of facial expressions at a later processing stage (around 170 ms, N170), suggesting a qualitatively different mode of facial analysis. The present ERP findings suggest that this adult pattern starts to emerge in mid-adolescence, whereas children on the verge of pre-adolescence (9–10-year-olds) do not show any indications of such processing yet. Thus, in mid-adolescence, typically developing individuals improve their sensitivity to the important emotional expression cues available in LSF content. Further research on the potentially suboptimal development of LSF-related processing of facial expressions in children and adolescents with Autism Spectrum Disorder might provide further insights in developmental challenges in the acquisition of emotional perception skills during these dynamic neurodevelopmental phases.

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References

Achenbach, T. M. (1991). *Manual for the child behavior checklist 4–18*. VT: University of Vermont, Department of Psychiatry Burlington.
Adams, J. A., & Courage, M. L. (2002). Using a single test to measure human contrast sensitivity from early childhood to maturity. *Vision Research*, *42*, 1205–1210.
Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmidt, A. M., Dale, A. M., et al. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 449–454.
Batty, M., & Taylor, M. J. (2006). The development of emotional face processing during childhood. *Developmental Science*, *9*, 207–220.
Blau, V. C., Maurer, U., Tottenham, N., & McCandliss, B. D. (2007). The face-specific N170 component is modulated by emotional facial expression. *Behavioral and Brain Functions*, *3*, 7.
Boeschoten, M. A., Kenemans, J. L., van Engeland, H., & Kemner, C. (2007). Face processing in Pervasive Developmental Disorder (PDD): the roles of expertise and spatial frequency. *Journal of Neural Transmission*, *114*, 1619–1629.
Boutsen, L., Humphreys, G. W., Praamstra, P., & Warbrick, T. (2006). Comparing neural correlates of configural processing in faces and objects: an ERP study of the Thatcher illusion. *Neuroimage*, *32*, 352–367.
Carey, S., Diamond, R., & Woods, B. (1980). Development of face recognition: a maturational component? *Developmental Psychology*, *16*, 257–269.
Carey, S. (1981). The development of face recognition. In G. M. Davies, H. D. Ellis, & J. W. Shepherd (Eds.), *Perceiving and remembering faces.*. London: Academic Press.
Carey, S. (1992). Becoming a face expert. *Philosophical Transcripts of the Royal Society London*, 95–103.
Chung, M. S., & Thomson, D. M. (1995). Development of face recognition. *British Journal of Psychology*, *86*, 55–87.
Cohen-Kadosh, K., & Johnson, M. H. (2007). Developing a cortex specialized for face perception. *Trends in Cognitive Sciences*, *11*, 267–269.
Cohen-Kadosh, K. (2012). Differing processing abilities for specific face properties in mid-childhood and adulthood. *Frontiers in Psychology*, *2*, 400. http://dx.doi.org/10.3389/

fpsyg.2011.00400.
De Heering, A., Turati, C., Rossion, B., Bulf, H., Goffaux, V., & Simion, F. (2008). Newborns' face recognition is based on spatial frequencies below 0.5 cycles per degree. *Cognition*, *106*, 444–454.
De Sonneville, L. M. J., Verschoor, C. A., Njiokiktjien, C., Op het Veld, V., Toorenaar, N., & Vranken, M. (2002). Facial identity and facial emotions: speed, accuracy, and processing strategies in children and adults. *Journal of Clinical and Experimental Neuropsychology*, *24*, 200–213.
De Valois, R. L., & De Valois, K. K. (1988). *Spatial vision*. New York: Oxford University Press.
Deruelle, C., Rondan, C., Gepner, B., & Tardif, C. (2004). Spatial frequency and face processing in children with autism and Asperger syndrome. *Journal of Autism and Developmental Disorders*, *34*, 199–210.
Deruelle, C., Rondan, C., Salle-Collemiche, X., Bastard-Rosset, D., & Da Fonséca, D. (2008). Attention to low- and high-spatial frequencies in categorizing facial identities: emotions and gender in children with autism. *Brain and Cognition*, *66*, 115–123.
Diamond, R., Carey, S., & Back, K. J. (1983). Genetic influences on the development of spatial skills during early adolescence. *Cognition*, *13*, 167–185.
Durand, K., Gallay, M., Seigneuric, A., Robichon, F., & Baudouin (2007). The development of facial emotion recognition: the role of configural information. *Journal of Experimental Child Psychology*, *97*, 14–27.
Flin, R. H. (1980). Age effects in children's memory for unfamiliar faces. *Developmental Psychology*, *16*, 373–374.
Goffaux, V., Peters, J., Haubrechts, J., Schiltz, C., Jansma, B., & Goebel, R. (2011). From coarse to fine?: Spatial and temporal dynamics of cortical face processing. *Cerebral Cortex*, *21*, 467–476.
Golarai, G., Ghahremani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., Gabrieli, J. D., et al. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience*, *10*, 512–522.
Golarai, G., Liberman, A., Yoon, J. M. D., & Grill-Spector, K. (2010). Differential development of the ventral visual cortex extends through adolescence. *Frontiers in Human Neuroscience*, *3*, 80.
Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Identification of band-pass filtered letters and faces by human and ideal observers. *Vision Research*, *39*, 3537–3560.
Gomez, J., Barnett, M. A., Natu, V., Mezer, A., Palomero-Gallagher, N., Weiner, K. S., et al. (2017). Microstructural proliferation in human cortex is coupled with the development of face processing. *Science*, *355*, 68–71.
Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for offline removal of ocular artefact. *Elektroencephalogram Clinical Neurophysiology*, *55*, 468–484.
Grill-Spector, K., Golarai, G., & Gabrieli, J. (2008). Developmental neuroimaging of the human ventral visual cortex. *Trends in Cognitive Sciences*, *12*, 152–162.
Guyer, A. E., Monk, C. S., McClure-Tone, E. B., Nelson, E. E., Roberson-Nay, R., Adler, A. D., et al. (2008). A developmental examination of amygdala response to facial expressions. *Journal of Cognitive Neuroscience*, *20*(9), 1565–1582.
Hammarrenger, B., Lepore, F., Lippe, S., Labrosse, M., Guillemot, J. P., & Roy, M.-S. (2003). Magnocellular and parvocellular developmental course in infants during the first year of life. *Documenta Ophthalmologica*, *107*, 225–233.
Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., & Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception: recognition and priming. *Cerebral Cortex*, *13*, 793–805.
Hess, R. F. (2004). Spatial scale in visual processing. In L. M. Chalupa, & J. S. Werner (Eds.), . *The Visual Neurosciences* (pp. 1043–1059). Cambridge, MA: MIT Press.
Hsiao, F. J., Hsieh, J. C., Lin, Y. Y., & Chang, Y. (2005). The effects of face spatial frequencies on cortical processing revealed by magnetoencephalography. *Neuroscience Letters*, *380*, 54–59.
Itier, R. J., & Taylor, M. J. (2004). Face recognition memory and configural processing: a developmental ERP study using upright, inverted, and contrast-reversed faces. *Journal of Cognitive Neuroscience*, *16*, 487–502.
Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, *6*, 766–774.
Kanwisher, N., Mc Dermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
Lawrence, K., Bernstein, D., Pearson, R., Mandy, W., Campbell, R., & Skuse, D. (2008). Changing abilities in recognition of unfamiliar face photographs through childhood and adolescence: performance on a test of non-verbal immediate memory (warrington RMF) from 6 to 16 years. *Journal of Neuropsychology*, *2*, 27–45.
Lawrence, K., Campbell, R., & Skuse, D. (2015). Age, gender, and puberty influence the development of facial emotion recognition. *Frontiers in Psychology*, *6*, 761. http://dx.doi.org/10.3389/fpsyg.2015.00761.
Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature*, *410*, 890.
LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184.
Madrid, M., & Crognale, M. A. (2000). Longterm maturation of visual pathways. *Visual Neuroscience*, *17*, 831–837.
Méndez-Bértolo, C., Moratti, S., Toledano, R., Lopez-Sosa, F., Martínez-Alvarez, R., Mah, Y. H., et al. (2016). A fast pathway for fear in human amygdala. *Nature Neuroscience*, *19*, 1041–1049.
Maunsell, J. H., Ghose, G. M., Assad, J. A., McAdams, C. J., Boudreau, C. E., & Noerager, B. D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience*, *16*, 1–14.
Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends Cognitive Science*, *6*, 255–260.
McClure, E. B. (2000). A meta-analytic review of sex differences in facial expression processing and their development in infants children, and adolescents. *Psychological Bulletin*, *126*, 424–453.
McGivern, R. F., Andersen, J., Byrd, D., Mutter, K. L., & Reilly, J. (2002). Cognitive efficiency on a match to sample task decreases at the onset of puberty in children. *Brain and Cognition*, *50*, 73–89.
Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.
Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception*, *31*, 553–566.
Monk, C. S., McClure, E. B., Nelson, E. E., Zarahn, E., Bilder, R. M., Leibenluft, E., et al. (2003). Adolescent immaturity in attention-related brain engagement to emotional facial expressions. *Neuroimage*, *20*, 420–428.
Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating unseen fear. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 1680–1685.
Passarotti, A. M., Smith, J., DeLano, M., & Huang, J. (2007). Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions to the upright orientation. *Neuroimage*, *34*, 1708–1722.
Peters, J. C., Vlamings, P., & Kemner, C. (2013). Neural processing of high and low spatial frequency information in faces changes across development: qualitative changes in face processing during adolescence. *European Journal of Neuroscience*, *37*, 1448–1457.
Peters, J. C., van den Boomen, C., & Kemner, C. (2017). Spatial frequency training modulates neural face processing: Learning transfers from low- to high-level visual features. *Front. Hum. Neurosci. 11*, 1. http://dx.doi.org/10.3389/fnhum.2017.00001.
Rotshtein, P., Vuilleumier, P., Winston, J., Driver, J., & Dolan, R. (2007). Distinct and convergent visual processing of high and low spatial frequency information in faces. *Cerebral Cortex*, *17*, 2713–2724.
Ruiz-Soler, M., & Beltran, F. S. (2006). Face perception: an integrative review of the role of spatial frequencies. *Psychological Research*, *70*, 273–292.
Scherf, K. S., Behrmann, M., & Dahl, R. (2011). Facing changes & changing faces in adolescence: Investigating the neural basis of key developmental shifts in social-information processing. *Developmental Cognitive Neuroscience. 2*, 199–219. http://dx.doi.org/10.1016/j.dcn.2011.07.016.
Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., & Shall, J. D. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology*, *79*, 3272–3278.
Schroeder, C. E., Tenke, C. E., Arezzo, J. C., & Vaughan, H. G., Jr. (1989). Timing and distribution of flashevoked activity in the lateral geniculate nucleus of the alert monkey. *Brain Research*, *477*, 183–195.
Schwarzer, G. (2000). Development of face processing: the effect of face inversion. *Child Development*, *712*, 391–401.
Shoham, D., Hubener, M., Schulze, S., Grinvald, A., & Bonhoeffer, T. (1997). Spatio-temporal frequency domains and their relation to cytochrome oxidase staining in cat visual cortex. *Nature*, *385*, 529–533.
Simion, F., Farroni, T., Cassia, V. M., Turati, C., & Barba, D. (2002). Newborns' local processing in schematic facelike configurations. *British Journal of Developmental Psychology*, *20*, 465–478.
Slater, A., & Sykes, M. (1977). Newborn infants' visual responses to square wave gratings. *Child Development*, *48*, 545–554.
Spreen, O., & Strauss, E. (1998). *A compendium of neuropsychological tests: administration, norms and commentary*. New York: Oxford University Press.
Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments & Computers*, *31*, 137–149.
Tanner, J. M., & Whitehouse, R. H. (1976). Clinical longitudinal standards for height weight, height velocity, weight velocity, and stages of puberty. *Archives of Disease of Childhood*, *51*, 170–179.
Taylor, M. J., Batty, M., & Itier, R. J. (2004). The faces of development: a review of early face processing over childhood. *Journal of Cognitive Neuroscience*, *16*, 1426–1442.
Thomas, K. M., Drevets, W. C., Whalen, P. J., Eccard, C. H., Dahl, R. E., Ryan, N. D., et al. (2001). Amygdala response to facial expressions in children and adults. *Biological Psychiatry*, *49*, 309–316.
Thomas, L. A., De Bellis, M. D., Graham, R., & LaBar, K. S. (2007). Development of emotional facial recognition in late childhood and adolescence. *Developmental Science*, *10*, 547–558.
Tottenham, N., Tanaka, J., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., et al. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research*, *168*, 242–249.
Vicari, S., Snitzer Reilly, J., Pasqualetti, P., Vizzotto, A., & Caltagirone, C. (2000). Recognition of facial expressions of emotions in school-age children: the intersection of perceptual and semantic categories. *Acta Pediatrica*, *89*, 836–845.
Viggiano, M. P., Righi, S., & Galli, G. (2006). Category-specific visual recognition as affected by aging and expertise. *Archives of Gerontology and Geriatrics*, *42*, 329–338.
Vlamings, P. H. J. M., Goffaux, V., & Kemner, C. (2009). Is the early modulation of brain activity by fearful facial expressions primarily mediated by coarse low spatial frequency information? *Journal of Vision*, *9*, 1–13.
Vlamings, P. H. J. M., Jonkman, L. M., & Kemner, C. (2010). An eye for detail: an event-related potential study of the rapid processing of fearful facial expressions in children. *Child Development*, *81*, 1304–1319.
Vlamings, P. H. J. M., Jonkman, L. M., van Daalen, E., van der Gaag, R. J., & Kemner, C. (2010). Basic abnormalities in visual processing affect face processing at an early age in autism spectrum disorder. *Biological Psychiatry*, *68*, 1107–1113.
Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*, 624–631.
Wechsler, D. (1991). *Wechsler intelligence scale for children* (3rd ed.). San Antonio, TX: Psychological Corporation.
Winston, J. S., Vuilleumier, P., & Dolan, R. J. (2003). Effects of low-spatial frequency components of fearful faces on fusiform cortex activity. *Current Biology*, *13*, 1824–1829.
Wong, T. K., Fung, P. C., McAlonan, G. M., & Chua, S. E. (2009). Spatiotemporal dipole source localization of face processing ERPs in adolescents: a preliminary study. *Behav Brain Funct*, *5*, 16.