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Negative affect is related to reduced differential neural responses to social and non-social stimuli in 5-to-8-month-old infants: A functional near-infrared spectroscopy-study

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ABSTRACT

Both social perception and temperament in young infants have been related to social functioning later in life. Previous functional Near-Infrared Spectroscopy (fNIRS) data (Lloyd-Fox et al., 2009) showed larger blood-oxygenation changes for social compared to non-social stimuli in the posterior temporal cortex of five-month-old infants. We sought to replicate and extend these findings by using fNIRS to study the neural basis of social perception in relation to infant temperament (*Negative Affect*) in 37 five-to-eight-month-old infants.

Infants watched short videos displaying either hand and facial movements of female actors (social dynamic condition) or moving toys and machinery (non-social dynamic condition), while fNIRS data were collected over temporal brain regions. *Negative Affect* was measured using the *Infant Behavior Questionnaire*.

Results showed significantly larger blood-oxygenation changes in the right posterior-temporal region in the social compared to the non-social condition. Furthermore, this differential activation was smaller in infants showing higher *Negative Affect*.

Our results replicate those of Lloyd-Fox et al. and confirmed that five-to-eight-month-old infants show cortical specialization for social perception. Furthermore, the decreased cortical sensitivity to social stimuli in infants showing high *Negative Affect* may be an early biomarker for later difficulties in social interaction.

1. Introduction

Recent research using electroencephalography and functional near-infrared spectroscopy (fNIRS) has greatly advanced our knowledge of the development and specialization of the “social brain” in infancy (for review see Grossmann, 2015; Grossmann and Johnson, 2007). The sensitivity of the neural correlates of social perception to genetic and environmental factors however is less explored (Grossmann et al., 2011). In the present study, we investigated the impact of infant temperament on the early cortical specialization for processing social stimuli.

Temperament may be defined as a set of biologically-based psychological tendencies (McCrae et al., 2000; Rothbart and Bates, 1998, 2006). It comprises individual differences in reactivity (i.e., latency, intensity and duration of emotional, attentional and motor responses to changes in the internal and external environments) and regulation (i.e., processes of effortful control and orienting that modulate reactivity) (Rothbart and Bates, 2006; Salley et al., 2013). Temperamental features have regularly been shown to be continuous from infancy into childhood and even into adulthood (Caspi, 2000; Kandler et al., 2013). Moreover, individual differences in temperament predict individual differences in social functioning, family functioning, academic achievement, and internalizing and externalizing behavior later in life (Sanson et al., 2004). The strongest developmental continuity has been found for the temperamental dimension *Negative Affect,* which is also the first emerging form of reactivity (Putnam et al., 2001; Rothbart et al., 2000). During infancy, *Negative Affect* comprises behaviors such as anger, frustration, sadness, social fear/shyness, general distress-proneness and poor soothability (Rothbart et al., 2001). High levels of *Negative Affect* in infancy have been associated with several aspects of poorer social functioning later in life, including social competence (Sanson et al., 2004; Rothbart et al., 2001), social responsiveness, social

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awareness, social information processing, capacity for reciprocal social communication, social motivation, and repetitive/restricted interest (Salley et al., 2013). In addition, high *Negative Affect* has been associated with infants being less frequently involved in joint attention, which is considered to be a key factor in infants' social-cognitive development (Salley and Dixon, 2007; Todd and Dixon, 2010; Vaughan et al., 2003; Vaughan Van Hecke et al., 2007).

A considerable number of studies have linked temperament, including *Negative Affect,* to differential activation in, and connectivity between subcortical and cortical brain regions which are part of the "social brain network", including the amygdala, ACC, medial PFC and posterior STS/TPJ (Ball et al., 2012; Davey et al., 2015; Harnett et al., 2015; Perlman et al., 2015; Whittle et al., 2006; Vrticka et al., 2013). However, these studies almost exclusively involve school-age children, adolescents and adults. The neural correlates of social perception observed in infants have been shown to be largely similar to those observed in adults, and predominantly include bilateral temporal and (orbito-) frontal cortical regions (Blasi et al., 2007; Lloyd-Fox et al., 2009; Lloyd-Fox et al., 2013; Minagawa-Kawai et al., 2009; Nakato et al., 2011; Vanderwert and Nelson, 2014; Grossmann, 2015). There are only two infant studies linking individual differences in *Negative Affect* to differential brain activation for social perception, one EEG-study (Martinos et al., 2012) and one fNIRS-study (Ravicz et al., 2015); both studies found a relation between processing of social information, specifically facial emotion, in fronto-central brain regions and infants' level of *Negative Affect*.

A recent series of fNIRS studies has shed light on the cortical specialization for social information processing by robustly demonstrating the involvement of the posterior temporal lobe in the processing of social dynamic stimuli compared to non-social dynamic stimuli in young infants (Lloyd-Fox et al., 2009, 2011, 2013, 2014, 2016; Farroni et al., 2013). Within the posterior temporal lobe, activation in the pSTS is associated with processing of gaze shifts, gestures and biological motion in adults (e.g. Burnett et al., 2011; Lotze et al., 2006; Pelphrey et al., 2005); thus, it is likely that infant hemodynamic responses to social dynamic stimuli underlie pSTS activation. Relevant for our study, infants at risk for autism (who often score high on *Negative Affect*) showed less differential activation in temporal regions in response to social dynamic stimuli than their typically developing peers (Lloyd-Fox et al., 2013).

In the present study, we aim to replicate the results of Lloyd-Fox et al. (2009) and investigate the impact of infant *Negative Affect* (as measured by parental questionnaire) on the early cortical specialization for processing social dynamic stimuli. To this end, we used a similar fNIRS paradigm and the same stimuli as used previously by Lloyd-Fox et al. (2009, Experiment 2). Functional Near-Infrared Spectroscopy makes use of differences in light absorption by Oxygenated and Deoxygenated hemoglobin to measure blood oxygenation changes in the cortex, an indicator of neural activity (see Gervain et al., 2011 for an introduction to the basic methodology of fNIRS). We studied typically-developing children aged 5–8 months to a) determine whether cortical specialization for social dynamic stimuli remains stable over these ages and b) assess the influence of *Negative Affect* on the processing of social stimuli. The paradigm used in this study compares the perception of dynamic social stimuli to the perception of dynamic non-social stimuli. Since no explicit emotional valence is present, this allows us to assess the association between temperament and social processing independent of emotional processing. In line with earlier findings (Lloyd-Fox et al., 2009), we focused our data analysis on the posterior temporal region, i.e. the posterior channels of the optode layout. We hypothesized that infants with higher scores on *Negative Affect* would show weaker hemodynamic response to social compared to non-social stimuli in the posterior-temporal cortex, based on three findings discussed above: 1) the observed relation between Negative Affect and joint attention in infancy, 2) the overlap between brain regions associated with *Negative Affect* and social information processing, and 3) the observed reduced sensitivity in posterior temporal regions to social dynamic stimuli in infants at risk for autism.

2. Methods

2.1. Participants

Thirty-seven healthy infants between 5 and 8 months of age participated in the study (mean age = 185.1 days, SD = 29.0 days, range: 142–275 days; 16 females and 21 males). An additional 32 infants were tested but excluded from the NIRS data analysis because they failed to look at the stimuli for the minimum number of trials (n = 17) or because they did not have usable data in at least one of the relevant channels (n = 15). See the data pre-processing section for further explanation. Infants were recruited though direct mail after birth and invited to participate in the study over telephone when they reached the appropriate age. Addresses were provided by the Leiden city council. The study protocol was approved by the Leiden University Cognitive Psychology Ethics Committee. The mean average education level of the parents was 4.42 (SD = 0.61, range: 3–5) on a 5-point scale (1: primary school, 2: vocational school, 3: secondary school, 4: post-secondary applied education, 5: university degree). Infants who were excluded from the NIRS analysis did not differ from the included infants in gender, age, mean parental education level, or *Negative Affect* ($p_s > 0.18$).

2.2. Procedure

The participating infant's parent was first fully informed about the procedure and asked to sign the consent form. The head circumference of the infant was measured, and a cap of the appropriate size was chosen and prepared for the experiment (Easycap infant caps for head sizes 42–48 cm). During fNIRS recording, the infant sat on the parent's lap in a sound-proof booth facing a 42-inch screen at approximately 70 cm distance. The NIRS cap was placed on the infant's head, positioning it relative to the ears and the midline. Optode cables were supported by a cable arm and cable trees at the back of the head to reduce optode movement. During the session infants were recorded by a video camera placed under the screen. Stimulus presentation lasted a maximum of 13 min, but was stopped earlier if the infants became bored or fussy.

Our experiment used identical stimuli to those in Experiment 2 from Lloyd-Fox et al. (2009) and closely followed its procedure. It included a social dynamic and a non-social dynamic experimental condition, in addition to a static baseline condition. The social dynamic condition consisted of video clips displaying a female actor performing different combinations of eye movements, silent vowel mouth-movements or playing "peek-a-boo" and "incy-wincy spider" games with her hands. The non-social dynamic condition consisted of video clips showing different combinations of moving machine cogs, pistons and spinning toys. The baseline condition consisted of still images of different types of transport (i.e., cars and helicopters) presented randomly for a pseudorandom duration (1–3 s). The video clips and still images were each presented for 16 s. They were displayed at a size of 30 × 20 cm, where the female actors' face was approximately life-size. None of the stimulus videos contained sound, but continuous instrumental music was played softly during stimulus presentation.

Each recording session started with a resting period (30s) during which the infant was shown small animal pictures in randomly varying positions on the screen to familiarize the infant with the setup and to allow time for calibration. During calibration, the signal for each source-detector combination (channel) is optimized. Following calibration, the presentation of the stimulus trials started. The two experimental conditions were presented in pseudo-random order with a baseline trial following each experimental trial (see Lloyd-Fox et al., 2009 for a graphical representation of the paradigm). Randomization was restricted to a maximum of three consecutive social or non-social dynamic trials, and a maximum of four social or non-social dynamic trials in every 6 consecutive experimental trials. A maximum of 24 baseline and 24 experimental (12 social and 12 non-social) trials were presented. No differences were found between the experimental conditions regarding the number of trials infants were exposed to (social dynamic: mean/SD = 9.8/2.6; non-social dynamic: mean/SD = 9.9/2.7, $p > .1$) or the number of included trials in statistical analyses (social dynamic: mean/SD = 8.7/2.8; non-social dynamic: mean/SD = 8.2/2.9, $p > .1$). Following the experiment, information about temperament, health and general development of the infant was obtained through parental questionnaires.

2.3. Data acquisition and array placement

fNIRS data were recorded using a NIRx NIRScout 8 × 16 apparatus with NIRStar acquisition software (NIRx Medical Technologies, Berlin, Germany). The NIRScout apparatus performs dual-wavelength continuous-wave near infrared diffuse tomographic measurements using LED emitters at two wavelengths (760 and 850 nm). Our placement of the optodes was equivalent to that in Experiment 2 from Lloyd-Fox et al. (2009). Four sources and four detectors were inserted in the cap on each hemisphere with a source-detector separation of 20 mm defining 10 channels over the left, and 10 channels over the right frontal and temporal cortices (Fig. 1), resulting in a sampling rate of 6.25 Hz.

2.4. Data analysis

Valid trials were selected based on the looking behavior of each infant. The video recording of each measurement session was coded for looking behavior using ELAN (ELAN Linguistic annotator v.4.8.1, Max-Planck-Institute for Psycholinguistics, Nijmegen, The Netherlands). Following Lloyd-Fox et al.'s (2009) procedure, only those experimental and baseline trials were included in the analysis during which the infant looked at the screen for a minimum of 80% of the trial duration. Trials that did not meet this criterion were excluded from the analysis. A minimum of three valid trials for each condition (social dynamic, non-social dynamic and baseline) were required to include an infant in the study.

Data-preprocessing was performed in NIRSlab v. 2016.01 (NIRx Medical Technologies, Berlin, Germany). The quality of the raw attenuation data was assessed per channel for each infant. Channels in which the coefficient of variation (CV: SD/mean*100) was larger than 10%, the gain was larger than 8, or where no heartbeat was visible in the signal spectrum were excluded from the analyses. In the majority of cases, channels were excluded based on CV's > 10%, which were driven by subject movement. It should be noted that, in the future, the use of advanced data correction algorithms may help to correct rather than exclude such data, leading to lower attrition rates.

Remaining artifacts were removed from the attenuation data using the NIRSlab built-in algorithm for the removal of step artifacts, applying a five-SD threshold on the difference between each set of two consecutive data points. Any large spikes remaining in the data after this procedure were identified and removed, replacing them with the nearest signal.

Following artifact rejection, data were filtered using a low-pass filter with a cut-off frequency of 1.8 Hz and a roll-off width of 15%. HbO (Oxygenated hemoglobin) and HbR (De-oxygenated hemoglobin) concentration changes were then computed from the attenuation data using the modified Beer-Lambert law. Differential path length factors for the two wavelengths were adapted to infant values according to the equation published by Scholkmann and Wolf (2013).

To compute block averages, individual stimulation blocks were first corrected for baseline by subtracting the mean of the signal during the five seconds preceding stimulation. Following baseline correction, individual subject block averages for each experimental condition (social dynamic and non-social dynamic) and channel were computed in NIRSlab by averaging HbO and HbR concentration time courses over valid trials. Subsequently, peak HbO and HbR changes in the time window between 10 and 25 s past stimulus onset were extracted for each infant and channel to be used in further statistical analysis. This time window was selected based on the timing of the HbO peaks in our sample.

Statistical analysis of fNIRS data was restricted to channels lying over the bilateral posterior temporal and parietal regions (channels 7, 8, 9, 10, 17, 18, 19 and 20; marked green in Fig. 1). In this region, Lloyd-Fox et al. (2009, 2011, 2013, 2014, 2016) repeatedly demonstrated significant differences between HbO changes elicited by social versus non-social dynamic stimuli in an identical paradigm.

2.5. Negative affect

To assess *Negative Affect* in infants, parents were asked to complete the Infant Behavior Questionnaire – Revised – Short form (Gartstein and Rothbart, 2003; Putnam et al., 2014). This questionnaire consists of 91 questions regarding the behavior of the infant in a multitude of possible situations over previous week(s). Questions are rated on a 7-point Likert-scale (1 = never; 7 = always). Four scales are used to measure *Negative Affect* (25 questions): fear, distress to limitations, rate of recovery from distress, and sadness (Cronbach's α in our sample was 0.75). *Negative Affect* thus gives an indication of how frustrated or negative infants react to situations, people and their general environment with a minimum score of 1 and a maximum of 7, with higher scores indicating higher level of *Negative Affect*. Mean score on *Negative Affect* was 2.5 (range: 1.33–4.07; SD = 0.66) for the infants included in the analysis.

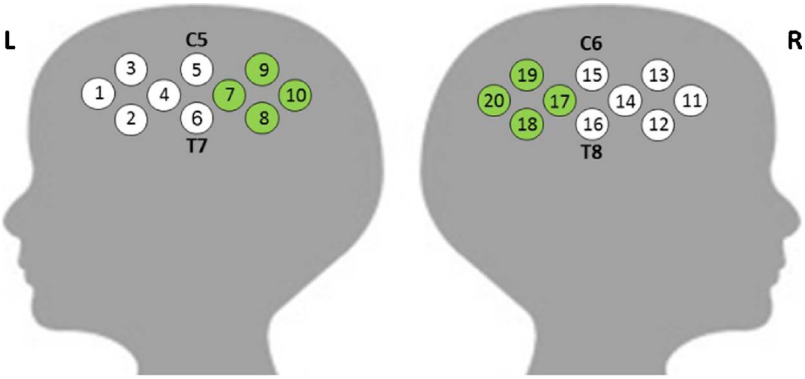

Fig. 1. Location of the NIRS channels over the left and right hemisphere, relative to 10–20 positions T7 and T8. Channels within the Region of Interest are marked green.

3. Results

3.1. Preliminary analysis – looking behavior

Each infant's interest in the stimuli was assessed by calculating the percentage of looking in each condition. There was no difference in the average of looking percentages between the two experimental conditions (social dynamic: mean = 91%; non-social dynamic: mean = 88%), suggesting that potential differences in the activation of temporal cortical areas are not due to general attention differences between the two types of experimental stimuli. However, infants did look more at the stimuli in both experimental conditions than at the stimuli in the baseline condition (baseline: mean = 75%; social dynamic versus baseline: $t = 6.3$, df = 32, $p < 0.001$; non-social dynamic versus baseline: $t = 6.5$, df = 32, $p < 0.001$) which can be explained by the fact that the baseline stimuli were static. There were no significant correlations between age or *Negative Affect* and the percentage of looking time differences, total looking times, number of valid channels or number of valid trials in any of the conditions, $p_s > 0.12$.

3.2. Main effect of social perception

Fig. 2 shows grand mean average time courses of HbO and HbR across infants for each of the experimental conditions in each channel of interest. One-sample *t*-tests were conducted to assess HbO and HbR concentration changes compared to baseline for the social dynamic and the non-social dynamic conditions, while paired *t*-tests were used to compare HbO and HbR concentration changes between the two experimental conditions. Table 1 gives a summary of the results. All *p*-values given in Table 1 survive correction for multiple comparisons according to the False Discovery Rate (Benjamini and Hochberg, 1995; see Gervain et al., 2016 for its use in infant fNIRS).

The social dynamic condition showed a significant increase in HbO compared to baseline in all channels of interest in the right hemisphere and the three most posterior channels in the left hemisphere ($p_s \leq 0.008$). Furthermore, social dynamic stimuli elicited a significant HbR concentration decrease compared to baseline in all channels of interest over the right hemisphere, and in channels 7 and 10 over the left hemisphere. The non-social dynamic stimuli elicited significant HbO increases in two channels over each hemisphere ($p_s \leq 0.017$), and significant HbR decreases were found in four channels over the left and in three channels over the right hemisphere ($p_s \leq 0.016$).

Paired *t*-tests revealed a significant difference in HbO concentration between the conditions in channel 18 over the right posterior temporal region ($t = 3.15$, $df = 17$, $p = 0.006$), with a larger increase in HbO concentration in the social dynamic compared to the non-social dynamic condition (see Table 1). When testing for lateralization, direct comparison with the corresponding channel in the left hemisphere revealed a trend, indicating a larger difference in the right hemisphere (one-tailed paired-sample *t*-test: Mean difference = 0.0012, $t = 1.773$, $df = 13$, $p = 0.05$). Age was not significantly related to differential responses in the right posterior temporal region (Pearson's $r = -0.06$, $p > 0.8$).

3.3. Temperament and social vs non-social differences in HbO

Associations between HbO or HbR concentration changes and *Negative Affect* were assessed using Pearson's correlations. *Negative Affect* correlated negatively with HbO differences between the social dynamic and non-social dynamic conditions in channel 20 in the right hemisphere (Pearson $r = -0.58$, $p = 0.007$, N = 20, FDR-corrected for multiple comparisons). Trends in the same direction were observed in two additional channels in the right posterior region (channel 17: Pearson $r = -0.41$, $p = 0.051$, N = 23; channel 18: Pearson $r = -0.44$, $p = 0.07$, N = 18), see Fig. 3 for plots. Moreover, differences in HbR concentration changes between the two conditions correlated positively with *Negative Affect* in channel 19, which can be interpreted as a decreased negative or positive HbR response in infants with high *Negative Affect* (Pearson $r = 0.48$, $p = 0.019$, N = 24, FDR-corrected for multiple comparisons). Infants with lower levels of *Negative Affect* thus seem to show a larger difference in right posterior temporal activation between the experimental conditions. Including the infants' age or the difference between looking percentages for social and non-social stimuli in the analyses (partial correlations) did not affect the (significant) correlations between *Negative Affect* and HbO or HbR differences for the social dynamic and non-social dynamic conditions.

4. Discussion

The first objective of this study was to investigate whether differential activation in response to social dynamic versus non-social dynamic stimuli could be observed in the posterior temporal cortex of infants aged five to eight months. The differential activation in the posterior region most likely reflects processing in the superior temporal sulcus (STS), a brain region consistently activated by processing faces and different forms of biological motion in adults (Burnett et al., 2011; Lotze et al., 2006). In the present study, we indeed found more activation in the social dynamic compared to the non-social dynamic condition, indicated by significantly larger HbO increase in the posterior temporal region in the social dynamic condition. We thus replicated the findings of Lloyd-Fox et al.'s study (2009). However, while Lloyd-Fox et al. (2009) reported bilateral activation in five-month olds, the HbO increase we observed for social-dynamic compared to non-social dynamic stimuli was only significant in the right hemisphere. Since our lateralization analysis only proved marginally significant, we cannot draw strong conclusions on the lateralization of social perception in infants. However, previous studies did show right lateralized responses to similar stimuli. In adults, perception of eye and mouth movements (Pelphrey et al., 2005) and gaze shifts (Pelphrey et al., 2003) has been shown to evoke right-lateralized STS activation as well. Furthermore, in five-month-old infants, mouth movements were also shown to specifically activate the right middle temporal cortex (Lloyd-Fox et al., 2011). Further studies are needed to determine whether processing of social information becomes increasingly lateralized in older infants.

Age of the infants was not related to posterior temporal activation in response to social-dynamic compared to non-social dynamic stimuli, which indicates that selective processing of dynamic social stimuli remains stable between the ages of five and eight months, and that the brain regions supporting this selective processing do not change in this period. This result corroborates a recent fNIRS finding by Farroni et al. (2013), showing that this area's specialization for biological motion might already be present in newborns, and aligns with behavioral studies that have shown infants' ability to discriminate between biological and non-biological motion from birth onwards (Simion et al., 2008; Bardi et al., 2011).

The second objective of this study was to investigate the relation between temperament and neural correlates of social perception in infants. We found that *Negative Affect* was negatively correlated with differential activation between social dynamic and non-social dynamic stimuli in the right posterior temporal region. That is, infants with higher *Negative Affect* scores showed a reduced hemodynamic response in the social dynamic compared to the non-social dynamic condition. This result confirmed our hypothesis that high *Negative Affect* is negatively related to cortical specialization for social dynamic stimuli. It is important to point out that this finding cannot be explained by an attention bias associated with *Negative Affect*, since there was no relation between *Negative Affect* scores and infants' interest in the social dynamic or non-social dynamic stimuli. Furthermore, the smaller differential posterior temporal activation in infants with higher *Negative Affect* could not simply be attributed to poorer fNIRS data quality in

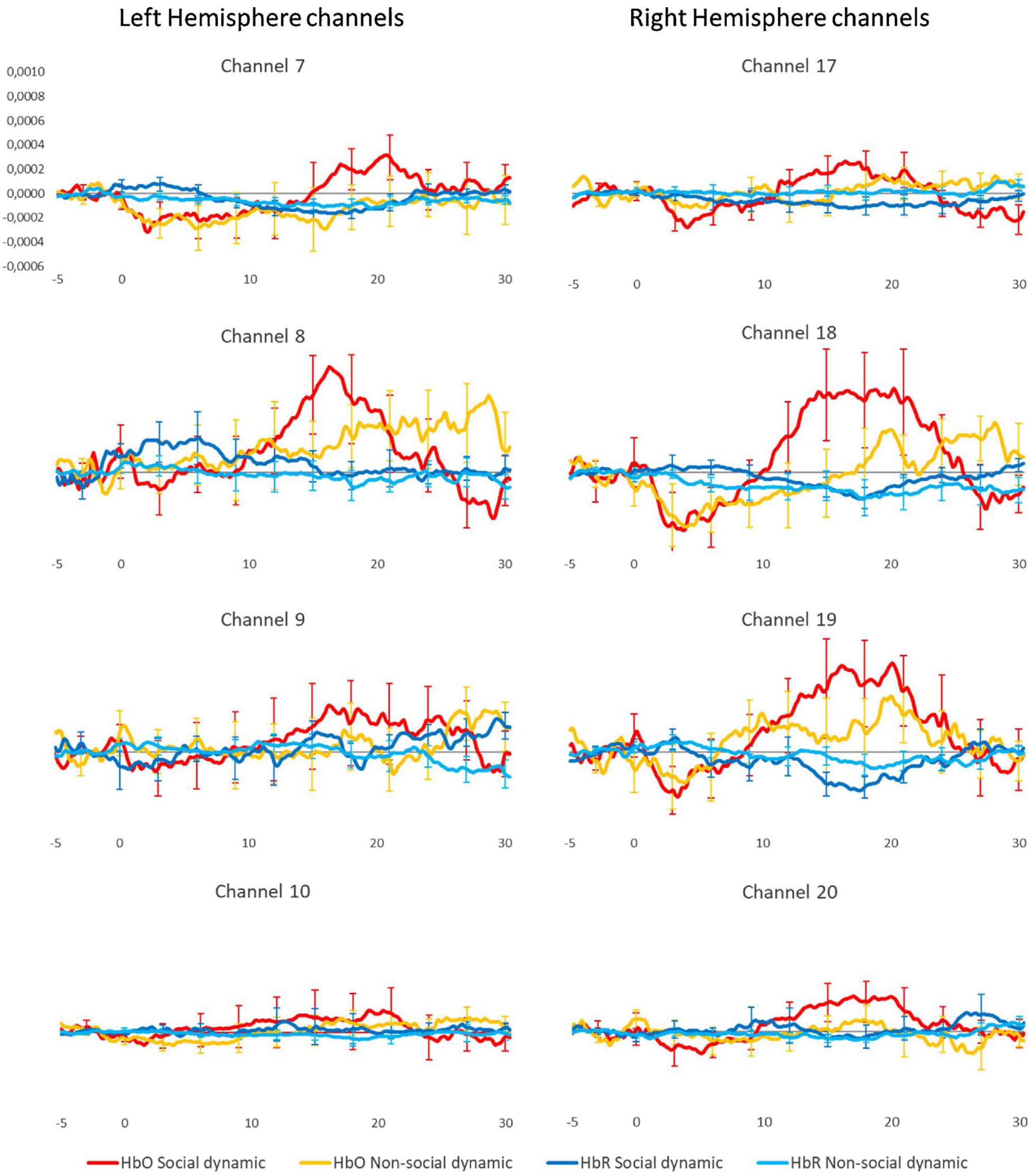

Fig. 2. Grand mean average time courses with Standard Error of HbO and HbR changes in millimolar (mM) as a function of time (stimulus block starts at 0) for each of the experimental conditions in the posterior temporal channels.

these children as there was no association between *Negative Affect* and either the number of excluded infants or the number of valid trials or channels within the included infants.

To date, only Ravicz et al. (2015) have related infant *Negative Affect* to fNIRS data. Their study showed that high *Negative Affect* is associated with decreased prefrontal responses to happy facial expression in seven-month-old infants. The two studies thus agree on the direction of temperamental influence, where weaker differential neural responses are related to higher levels of *Negative Affect*. Differences between our results and those of Ravicz et al., mainly lie in the brain regions where differential activity was observed, which can be attributed to the differences in stimulus material and to the type of contrast (emotional valence of facial expression vs. social vs non-social dynamic stimuli). Since our optode montage was not designed to capture oxygenation changes in prefrontal regions, we cannot exclude the possibility that prefrontal, *Negative Affect*-related differential activation might also be present using the current paradigm. The faces portrayed in our social dynamic stimuli were friendly but neutral, lacking explicit happy facial expressions. Therefore, the relation between *Negative Affect* and posterior-temporal differential activation in our current study is unlikely to be elicited solely by reduced sensitivity to positive facial expressions by infants with higher *Negative Affect*. Nonetheless, future studies are needed to tease apart both the neural correlates of processing dynamic facial/body movements vs. explicit facial expressions in infants, and their individual relations to *Negative Affect*.

Based on our current findings, we cannot draw firm conclusions on the causal direction of the association between *Negative Affect* and cortical specialization for social perception, nor on the cognitive mechanism underlying it. It has been proposed (Nabi, 1999; Salley et al., 2013) that temperamental negativity may impact infants' opportunities

Table 1
HbO and HbR changes in the social and non-social dynamic conditions relative to baseline and differences in HbO and HbR between social dynamic and non-social dynamic conditions. FDR-corrected *p*-values are shown.

Social condition HbO									
Left H	*t*	*df*	*p*	*Mean Difference*	**Right H**	*t*	*df*	*p*	*Mean Difference*
Ch 8	4.34	19	0.000	0.001457	Ch 17	3.79	22	0.002	0.000515
Ch 9	3.22	21	0.006	0.001023	Ch 18	3.23	17	0.007	0.001508
Ch 10	3.12	13	0.009	0.000711	Ch 19	3.75	23	0.002	0.001279
					Ch 20	4.20	19	0.000	0.000673
Non-social condition HbO									
Left H	*t*	*df*	*p*	*Mean Difference*	**Right H**	*t*	*df*	*p*	*Mean Difference*
Ch 8	3.70	19	0.005	0.001370	Ch 17	2.31	22	0.0496	0.000491
Ch 9	3.87	21	0.004	0.000978	Ch 19	4.36	23	0.000	0.001183
					Ch 20	2.63	19	0.034	0.000408
Social versus Non-social HbO									
Left H	*t*	*df*	*p*	*Mean Difference*	**Right H**	*t*	*df*	*p*	*Mean Difference*
					Ch 18	3.15	17	0.048	0.001038
Social condition HbR									
Left H	*t*	*df*	*p*	*Mean Difference*	**Right H**	*t*	*df*	*p*	*Mean Difference*
Ch 7	−3.47	26	0.004	−0.000305	Ch 17	−2.89	22	0.011	−0.000270
Ch 10	−3.74	13	0.004	−0.000246	Ch 18	−3.59	18	0.004	−0.000375
					Ch 19	−4.93	23	0.000	−0.000549
					Ch 20	−3.43	18	0.005	−0.000236
Non-social condition HbR									
Left H	*t*	*df*	*p*	*Mean Difference*	**Right H**	*t*	*df*	*p*	*Mean Difference*
Ch 7	−5.23	26	0.000	−0.000305	Ch 17	−2.39	22	0.026	−0.000187
Ch 8	−2.95	19	0.011	−0.000372	Ch 18	−3.59	17	0.003	−0.000508
Ch 9	−2.63	21	0.018	−0.000251	Ch 19	−4.11	23	0.000	−0.000305
Ch 10	−4.45	13	0.002	−0.000199	Ch 20	−5.64	19	0.000	−0.000215
Social versus Non-social HbR									
Left H	*t*	*df*	*p*	*Mean Difference*	**Right H**	*t*	*df*	*p*	*Mean Difference*

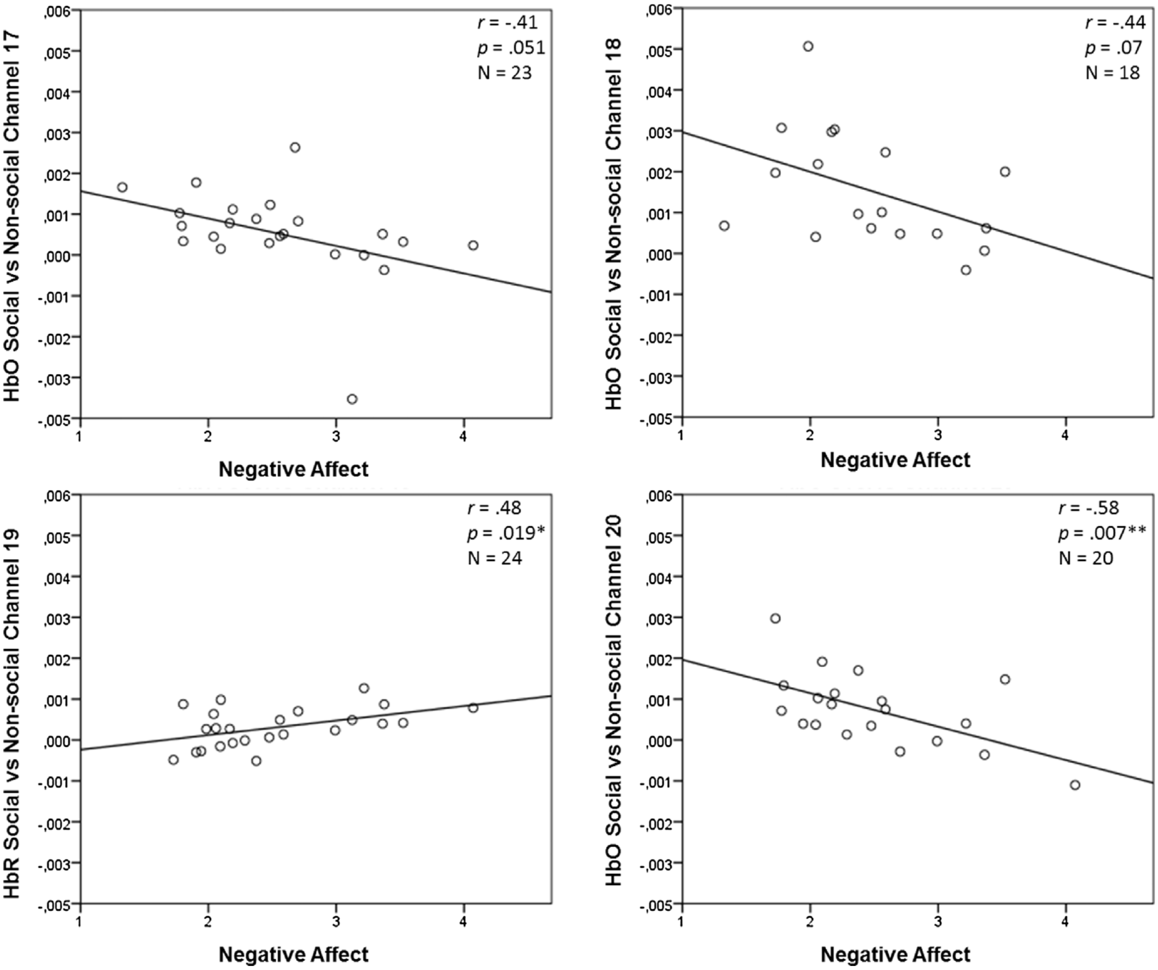

Fig. 3. Correlations between *Negative Affect* scores and differential HbO and HbR concentration changes (in mM) in the social dynamic compared to the non-social dynamic condition in the right posterior temporal region.

for processing social information since infants with higher *Negative Affect* may be less motivated to engage in social situations or they may react differently to their social environments. These differences could then lead to delays or differences in cortical specialization for social perception, and to difficulties in the social-cognitive development in infants. On a neural level, our finding of reduced differential activity in the posterior-temporal cortex in infants with higher *Negative Affect* may also be related to down-regulation of additional cortical and subcortical regions that are connected to the temporal cortex and are directly related to temperament (e.g. amygdala). One can also speculate that it is the weaker neural response of cortical regions related to social perception that (at least partly) leads to the emergence of temperament differences, that is, infants who show delays in or difficulties with processing social stimuli may become frustrated and stressed in social situations. Longitudinal studies following infants from younger than five months of age or even from birth onward are required for a better understanding of the emergence, and therefore of the direction of the association between social perception and temperament features.

5. Conclusion

We showed that blood oxygenation in the right posterior temporal cortex reflects the processing of social compared to non-social stimuli in five-to-eight-month-old infants. This supports the notion that the specialization of the posterior STS for the processing of faces and biological motion (Blakemore, 2008) is already in place at this early age.

We further demonstrated that *Negative Affect* was associated with hemodynamic responses to social compared to non-social stimuli in the right posterior-temporal cortex. Infants scoring high on *Negative Affect* showed a reduced differential response to social versus non-social stimuli, suggesting that temperament is related to the processing of social information at this age.

Earlier studies suggested that increased neural activity in response to social stimuli is present from birth onward (Farroni et al., 2013). However, the social brain will continue to develop and become more specialized with age, with shifts in both the location of activation and its intensity in response to social stimuli, in addition to changes in functional connectivity (Burnett et al., 2011). Although longitudinal studies will be needed to determine the continuity of the association between social perception and *Negative Affect*, social perception in infancy and its neural correlates might serve as early markers for behavioral outcomes later in life.

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