Neuroscience Letters 650 (2017) 118–125

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

Research article

Infants and adults have similar regional functional brain organization for the perception of emotions

N. Rotem-Kohavi [a], T.F. Oberlander [b,c], N. Virji-Babul [c,d,*]

[a] Graduate Program in Neuroscience, University of British Columbia, Vancouver, BC, Canada
[b] University of British Columbia, Pediatrics, Canada
[c] Child and Family Research Institute, Vancouver, BC, Canada
[d] Department of Physical Therapy, Faculty of Medicine, Djavad Mowafaghian Centre for Brain Health, University of British Columbia, Vancouver, Canada

HIGHLIGHTS

- Graph analysis was applied during emotional faces observation in infants and adults.
- Parietal and temporal nodes are most influential in the network in both groups.
- Global network density was higher in infants compared to adults.
- Functional organization of frontal and parietal nodes was similar between groups.
- Infants exhibit basic regional organization while global organization still develops.

ARTICLE INFO

Article history:
Received 20 February 2017
Received in revised form 10 April 2017
Accepted 18 April 2017
Available online 21 April 2017

Keywords:
Emotion
Perception
Infant
EEG
Functional connectivity
Graph theory
Development

ABSTRACT

An infant's ability to perceive emotional facial expressions is critical for developing social skills. Infants are tuned to faces from early in life, however the functional organization of the brain that supports the processing of emotional faces in infants is still not well understood. We recorded electroencephalography (EEG) brain responses in 8–10 month old infants and adults and applied graph theory analysis on the functional connections to compare the network organization at the global and the regional levels underlying the perception of negative and positive dynamic facial expressions (happiness and sadness). We first show that processing of dynamic emotional faces occurs across multiple brain regions in both infants and adults. Across all brain regions, at the global level, network density was higher in the infant group in comparison with adults suggesting that the overall brain organization in relation to emotion perception is still immature in infancy. In contrast, at the regional levels, the functional characteristics of the frontal and parietal nodes were similar between infants and adults, suggesting that functional regional specialization for emotion perception is already established at this age. In addition, in both groups the occipital, parietal and temporal nodes appear to have the strongest influence on information flow within the network. These results suggest that while the global organization for the emotion perception of sad and happy emotions is still under development, the basic functional network organization at the regional level is already in place early in infancy.

1. Introduction

Recognizing and understanding the actions and emotions of others is an essential prerequisite for learning, social cognition and social interactions. Adults make critical inferences about the emotional state of others by observing facial expressions and use emotional cues to respond under different social contexts [1]. For non-verbal infants, perception of emotional faces is of great importance as it may provide valuable information for interpreting the immediate environment, and offer clues on how they should act on different objects and in different social contexts [2]. How these abilities develop from early infancy is still unclear. It is well established that infants are attracted to and selectively respond to faces early in life. [3]. Young infants are sensitive to emotional information and are able to discriminate between facial expressions of different emotions including happiness, anger, fear, sadness, and surprise [4–6]. A fundamental question in developmental cognitive neuro-

* Corresponding author at: Department of Physical Therapy, University of British Columbia, 212-2177 Wesbrook Mall, Vancouver, British Columbia, V6T 1Z3, Canada.
E-mail address: naznin.virji-babul@ubc.ca (N. Virji-Babul).

http://dx.doi.org/10.1016/j.neulet.2017.04.031
0304-3940/

science is how the neural networks underlying the perception of emotional facial expressions emerge and how the characteristics of these networks develop over time.

From a behavioral perspective, there are clear developmental changes in response to the processing of emotional facial expression during the first year of life [7]. At three month of age, infants are able to discriminate between happy and angry faces [8]. By 7 months of age, infants are able to discriminate fearful faces in comparison with happy/neutral faces [9]. By the end of the first year of life, infants are able to use the facial expressions of others for guiding them in ambiguous situations [2].

Neuroimaging studies in adults suggest that emotional facial processing does not occur only in a specific brain region, but involves different brain regions (including the amygdala, temporal gyrus, frontal, parietal and occipital cortices [10]) that are associated with different aspects of facial and emotional processing [11]. These brain circuits use processing strategies by which faces are viewed more holistically (rather than focusing on the features of the face) in comparison to objects [12]. Electroencephalography (EEG) studies are commonly used to study developmental changes of facial processing in infancy. Studies of the event related responses (ERP) to emotional faces have shown that between 3 and 12 months of age there is an increased specificity of the evoked components (N290 and P400 similar to the adults N170 – the face sensitive component) for upright human faces in comparison to non-human faces. This suggests that infant's cortical response to human faces exhibit adult-like specificity toward the end of the first year of life [13]. For example, 7-month-old infants show a larger amplitude of the negative central (Nc) ERP component (an indicator for allocation of attention towards salient stimulations) over the fronto-central scalp regions in response to fearful expressions compared with happy expressions, similar to adults [14]. 7 month old infants also show a distinct evoked response to different categories of emotions (happy and sad) such that the Nc component is similar when infant observed faces from the same category (happy expressions) while they exhibit a differentiated response when they observed faces from different categories (different happy and sad emotions [15]). Together, the results from ERP studies suggest that infants in the second half of their first year of life have the basic ERP components for processing human emotional faces. However, processing emotional faces involves several brain regions that are connected with each other and it is becoming increasingly clear that a network perspective is needed to better understand how the brain processes emotional faces [16].

One approach that uses a network perspective analysis is graph theory, which has emerged in recent years as a promising tool for understanding both anatomical and functional brain networks [17,18]. Brain networks consist of spatially distributed brain regions that are functionally connected. The functional interactions between local and distant brain regions can be evaluated using functional connectivity which refers to the statistical interdependencies between time series recorded from different brain regions [19]. In this approach, the brain is characterized as a network that contains nodes and edges. Nodes represent different brain regions and edges represent the connecting pathways between those regions [20]. When describing functional connectivity, the edges represent functional connections between different brain regions (nodes) rather than structural (anatomical) connections. The relationship between nodes and edges provides information about the functional organization and efficiency of the network [20]. Information processing is proposed to be optimal in "small-world" networks that balance local specialization and global integration [21].

Fransson et al. [22] were the first to investigate the functional architecture in sleeping infants and showed that a small-world topology exists at birth with cortical hubs primarily in the sensory and motor regions of the brain. More recently, De Asis-Cruz reported that the neonatal brain has highly-connected hubs [23] suggesting that infants exhibit hub organization that is more similar to the adult configuration than previously suggested. While there are a number of researchers that have used a network perspective to understand network organization in sleeping infants, to our knowledge, there has been only one study that has used this approach to study task based responses in infants [24]. In particular, there have been no studies using this network perspective to understand facial emotion processing in infants. Since infants between 8 and 10 months of age typically show selective responses to happy and sad expressions [15,25], we used these basic expressions to compare the network organization underlying emotion processing in infants and adults. We ask: (1) Do infants and adults share common network properties for processing emotional facial expressions at the global level and regional levels? And 2) does the network organization differ between positive and negative emotions in both infants and adults? Based on recent results showing similarities in network organization between adults and infants in the resting state and in specific tasks related to action perception, we hypothesized that the global and regional network characteristics underlying the perception of emotional facial expressions would be similar in infants and adults. In addition, based on the literature showing emotion specific responses in both infants and adults [14,15], we hypothesize that each emotional expression would be characterized by a distinct network organization.

2. Methods

2.1. Participants

The Human Ethics Review Board at the University of British Columbia approved all experiments. All adults and parents provided written consent according to the guidelines of the Human Ethics Review Board at the University of British Columbia.

A total of 43 infants participated in this study. Data from 19 infants was excluded from the analysis due to excessive motion or insufficient artifact-free trials for each emotional expression. These exclusion rates are similar to exclusion rates reported previously for similar studies with infants in this age range [9,26]. A total of 24 infants between the ages of 8 and 10 months (mean age: 8.95 months, SD = 0.87, 13 males, 11 females) were included in the final analysis. Parents completed a developmental and social-emotional questionnaire (Ages & Stages) to confirm each infant's developmental stage [27].

Twenty adults between the ages of 21 and 37 years (mean age: 28.4 years, SD = 6.02, ten females, ten males) were also included in the analysis. All adult subjects reported normal or corrected-to-normal vision.

2.2. Stimuli

Given the importance of keeping infants engaged during the task, we used short video clips depicting dynamic facial expressions as opposed to static photographs. Previous work in adults has shown that dynamic displays are associated with more accurate performance in recognizing emotions in comparison with static photographs [28]. Dynamic facial expressions are more realistic and attractive and infants are more attentive to such stimuli in comparison with static photographs [29].

We used stimuli developed and validated by Simon et al. These stimuli have recently been used to study infant responses [29]. The stimuli consisted of color video clips of two different facial expressions (happy and sad) displayed by two different models [30]. Each emotional expression began with a neutral face and