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Frontal theta activation associated with error detection in toddlers: influence of familial socioeconomic status

Ángela Conejero | Sonia Guerra | Alicia Abundis-Gutiérrez | M. Rosario Rueda

Department of Experimental Psychology & Center for Research on Mind, Brain, and Behavior (CIMCYC), University of Granada, Granada, Spain

Correspondence
M. Rosario Rueda, Dpto. Psicología Experimental, Facultad de Psicología, Campus de Cartuja s/n 18071 Granada, Spain.
Email: rorueda@ugr.es

Abstract

Error detection is one of the functions of the executive attention network, a brain system involved in executive control that includes the anterior cingulate cortex and other prefrontal regions. Despite the key role of this function in a wide range of life outcomes, very limited research has examined the early development of the network and whether its functional efficacy is related to environmental factors. Electrophysiological studies with adults have shown oscillatory activity in theta (4–7 Hz) range arising from medial frontal cortex that follows the detection of self-committed or observed errors. In the current study, we designed a novel experimental procedure that involved a familiarization phase with simple three-pieces puzzles followed by an experimental phase in which toddlers observed the puzzles being formed either correctly or incorrectly. Observation of incorrect configurations produced increased potentials in midline channels and greater power theta activity for both toddlers (n = 56) and adults (n = 14). In addition, socioeconomic status of the family in general, and parental education in particular, contributed to individual differences in the amplitude of the error-related signal and associated theta power in toddlers, indicating that children raised in lower SES families show poorer activation of the executive attention network. These data demonstrate the influence of environmental factors at the earliest stages of development of the executive attention network. Importantly, the results show that error-detection EEG signals can be used as neural markers of the initial development of executive attention, which can be of great help for the early detection of risk for developmental disorders involving deficits in this function.

RESEARCH HIGHLIGHTS

- This paper presents a novel experimental protocol to study error detection in pre-verbal subjects.
- Electrophysiological responses to errors (i.e., evoked potentials and oscillatory neural activity in the theta range) are neural markers of the executive attention network in the adult brain.
- Results show frontal theta activation associated with error detection in toddlers, and reveal that familial SES contributes to individual differences in activation of the system.
- Data from this study contribute to the understanding of individual differences in the early development of the neural system supporting the emergence of self-regulation.

1 | INTRODUCTION

Executive attention (EA) refers to the effortful and voluntary control of attention, a function that involves processes of conflict resolution, inhibitory control, and error detection (Rueda, Posner, & Rothbart, 2005). This function is related to a network of brain structures including the anterior cingulate (ACC) and lateral prefrontal cortices, and their connections with parietal regions (Petersen & Posner, 2012). EA underlies both perceptual and conceptual learning as well as the ability to self-regulate behavior (Posner & Rothbart, 2007, 2014). Individual differences in EA and self-regulation are reliable predictors of schooling achievement and socio-emotional competence during childhood and early adolescence (Checa, Rodríguez-Bailón, & Rueda, 2008; Rueda, Checa, & Rothbart, 2010), as well as life outcomes including health and professional success (Moffitt et al., 2011).

First signs of EA development can be observed as early as around 6 months of postnatal life, when babies begin to show rudimentary forms of attention control (Holmboe, Pasco Fearon, Csibra, Tucker, & Johnson, 2008; Johnson, 1995). Later, during the second half of the first year of life, infants show increased control of attention and display increased behavioral flexibility. During this period, infants become able to overcome the tendency to look for interesting objects in locations previously reinforced but that are not correct anymore (A not B task) or the tendency to reach for an object in the line of sight when inappropriate, both being conflict tasks that demand the activation of prefrontal structures (Diamond & Doar, 1989). Then, by the end of the second year of life, toddlers are able to perform a somewhat more difficult version of the reaching task that requires an arbitrary means-action (e.g., pressing a lever) in order to reach a toy (McGuigan & Núñez, 2006). Likewise, they can resolve a more complex version of the A not B task that requires searching for a hidden toy in one of five possible locations (Miller & Marcovitch, 2015).

Developmental changes in the prefrontal cortex are thought to underlie increases in EA skills (Diamond & Goldman-Rakic, 1989). During the first years of life, there are substantial structural changes in prefrontal regions, including myelination of white matter fibers (Dean et al., 2014; Deoni, Dean, Remer, Dirks, & O'Muircheartaigh, 2015), large increases in grey matter volume and cortical thickness (Gilmore et al., 2012; Li, Lin, Gilmore, & Shen, 2015) and growth of thalamo-cortical connections (Alcauter et al., 2014).

An important function related to EA is error detection. In adults, a negative ERP component arises at about 100 ms following the commission of an error (Gehring, Goss, Coles, Meyer, & Donchin, 1993). The so-called error-related negativity (ERN) can be observed after self-committing errors or in response to perceived errors (Bates, Patel, & Liddle, 2005; Mesika, Tzur, & Berger, 2014). Also, source localization of the ERN shows that this potential originates in the ACC (Luu, Tucker, Derryberry, Reed, & Poulsen, 2003; Perry, Swingler, Calkins, & Bell, 2016) and is related to neural activation in the theta frequency range.

Berger, Tzur, and Posner (2006) studied error-related brain activity in infants and found that, similarly to adults, 7- to 9-month-olds show a fronto-central negative component around 330–560 ms following the presentation of an incorrect arithmetic operation performed with puppets. Also, Reid and colleagues (2009) observed that 9-month-olds (but not 7-month-olds) show a similar burst of activation over fronto-central leads at about 350–650 ms after seeing simple action sequences completed in an unexpected way (for example, the action of eating finished in the ear instead of in the mouth).

Increased frontal midline theta power following an error has been observed in different studies with adults (Luu, Tucker, & Makeig, 2004; Trujillo & Allen, 2007; Tzur & Berger, 2009). Changes in theta-band oscillations generated in the ACC and medial prefrontal cortex are thought to reflect EA processes (Tsujimoto, Shimizu, & Isómera, 2006). During infancy, age-related increases in theta rhythm have been reported and are associated with the development of the cortical pathways supporting EA (Orekhova, Stroganova, & Posikera, 1999; Stroganova, Orekhova, & Posikera, 1998). However, in the previously mentioned error-related studies with infants, results regarding theta power were not conclusive. In the Berger et al. study, the difference in theta power between correct and incorrect conditions was not statistically significant, and no differences in theta power were obtained for expected and unexpected movements in the Reid et al. study.

On the other hand, a growing body of literature shows the impact of familial socioeconomic status (SES) on the development of cognitive skills, including EA. Studies indicate that low SES is related to poorer academic outcomes and lower performance in cognitive tasks, particularly when executive control is required (Duncan, Yeung, Brooks-Gunn, & Smith, 1998; Noble, McCandliss, & Farah, 2007). Moreover, parental education is associated with differences in cortical thickness of frontal structures within the EA network (Lawson, Duda, Avants, Wu, & Farah, 2013). However, most research examining the effect of SES on cognitive development has been conducted with children and adolescents, and only a few studies have focused in infancy and early childhood. Some studies have shown that home environment and experience impact the development of executive skills from very early on (Clearfield & Jedd, 2013; Lipina, Martelli, Vuelta, & Colombo, 2005; Noble et al., 2015), and very few have examined the extent to which SES influences the development of brain function at an early age. In a longitudinal study including 5-month-old infants who were followed until the age of 3 years, Hanson et al. (2013) found that familial income is associated with the rate of gray matter growth in frontal and parietal lobes. Also, Tomalski et al. (2013) found that 6–9-month-old infants raised in low-SES families show lower EEG activity in the gamma range frequency, a measure thought to support sustained attention processes. All this literature suggests that functions of the frontal lobe are susceptible to the influence of environmental factors from very early on. Given the central role of frontal regions in EA in general, and error detection in particular, it can be expected to find significant individual differences in this function in different SES groups. Yet, no prior studies have examined changes occurring at the brain functional level during early development associated with EA skills, and no other studies have tested SES-related variability in error detection skills in early childhood.

In the present study, we aimed at investigating brain mechanisms involved in error detection as a neural marker of EA function in toddlers in the second year of life, as well as examining whether individual differences in error detection at this age are related to familial socioeconomic status. For that purpose, we designed an experimental paradigm in which toddlers first played with three-piece puzzles of cartoon animals, which were subsequently presented on a computer monitor being either correctly (as learned previously) or incorrectly completed while EEG was recorded. Based on the previous work, we expected to find an ERN-like potential associated with the perception of the erroneous completion of the puzzles over mid frontal channels. Also, we anticipated that increased theta-band power would be found in incorrect compared to correct completions of the puzzles. Finally, parents were asked to report on a number of different aspects of the home environment including parental education, parental occupation and family income, which were used to calculate an index of familial socioeconomic status. Based on previous work showing the impact of environmental factors on the structural growth of frontal regions of the brain, we hypothesized that toddlers from low-SES families would show decreased efficacy of EA skills revealed by reduced brain responses to errors compared to toddlers being raised in high-SES families.

2 | MATERIALS AND METHODS

2.1 | Participants

Participants were initially informed about the study by means of advertisements in nurseries located in different socio-demographic areas (from wealthy to socioeconomically deprived neighborhoods) of the city of Granada (Spain), local newspapers, local radio programs and the university website. Parents who expressed a willingness to participate were contacted by phone and informed of the general purpose of the study. Only children whose parents/legal guardians gave informed written consent to participate were included in the study. A total of 88 toddlers aged 16 to 18 months were initially recruited. Toddlers born prematurely (n = 3), who did not have quality data because of fussiness before or during the experiment (n = 9), or did not reach the minimum of computable trials per condition (n = 24; see procedure section below) were excluded from data processing. The final sample consisted of 52 toddlers (26 males, 26 females, mean age = 16.75 months; SD = 0.67). Children received a 10€ gift card to use in a local educational toys store in appreciation for their participation in the study, and parents received a report of the general results and data of their child at completion of the study.

In addition, 14 adults (13 females) between 18 and 25 years of age (mean = 21.93; SD = 2.34), recruited through the website of the Experimental Psychology Department of the university, who gave written consent to be involved in the study, participated in exchange for course credits.

2.2 | Procedure

Upon arrival at the laboratory, children and caregivers were received and given a few minutes to become comfortable with the experimenter as well as the lab setting. Once toddlers were ready, we carried out a familiarization phase in order to acquaint them with the correct configuration of three-piece puzzles of different animal cartoons (sheep, monkey and chicken), similar to the stimuli to be used in the experimental phase (see Figure 1, and Figure S1). The familiarization phase consisted of two parts. During part I, toddlers were encouraged to handle the pieces and complete the puzzles with the help of the experimenter. The experimenter guided the child to always start by placing the feet, then the body, and finally the head of each puzzle. After correctly completing each puzzle, the experimenter indicated the name of the animal that was represented, a process that was repeated three times with each puzzle. This procedure was run with all participants and intended to help the child to create a representation of the process of building each puzzle correctly. This part of the familiarization phase took less than 5 minutes altogether. During part II, toddlers were seated on their caregiver's lap facing a computer screen at a distance of approximately 60 cm. Parents were instructed to remain silent and not interact with their children during the entire experiment. The experimenter moved to a contiguous room and monitored children's behavior with a web cam facing the child. Real photos of each puzzle in color were presented on the screen next to schematic black and white line drawings of the same puzzles. This intended to familiarize children with line drawing pictures of the previously hand-held objects. Line drawings of the puzzles were to be used as stimuli in the subsequent experimental phase in order to avoid the effect of color mismatch in the EEG signal in conditions in which pieces corresponding to different animals would be mixed. Toddlers were shown the completion of each puzzle in the

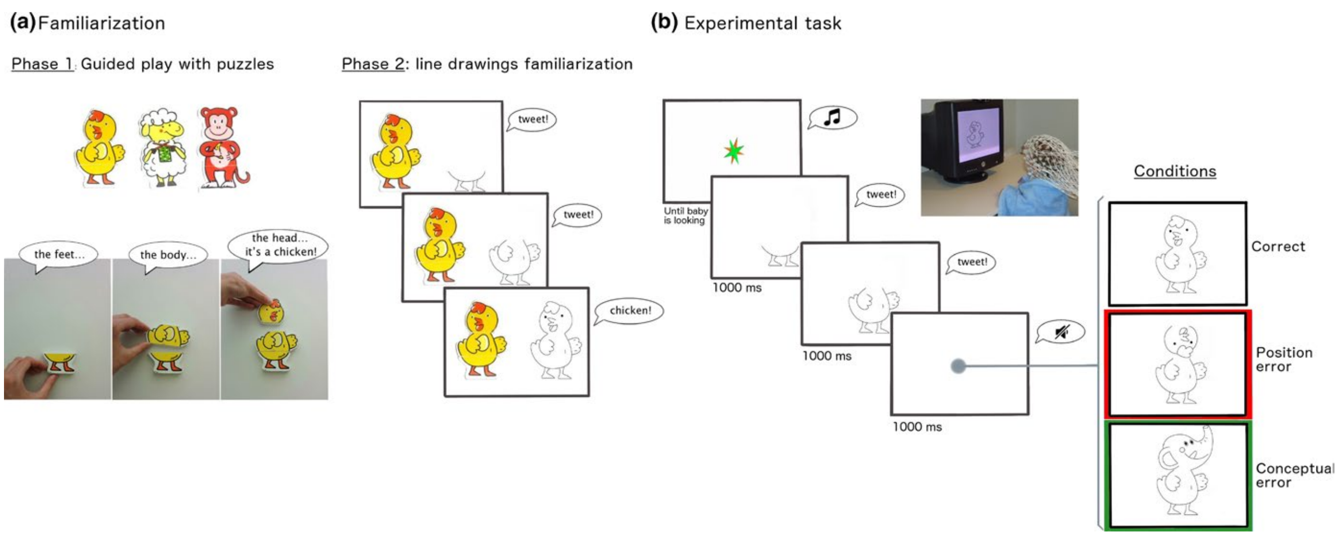

FIGURE 1 Experimental procedure. (a) Familiarization was divided into two phases: (1) toddlers manipulated puzzles with the help of the experimenter; (2) toddlers observed pictures of the real puzzles associated to their corresponding line drawing in black and white. (b) Experimental procedure: toddlers sat on the caregiver's lap while observing the progressive completion of puzzles on the computer screen. Three conditions were presented: correct completion, incorrect completion related to the last piece position (upside-down), incorrect completion related to a conceptual mistake (head of a different animal)

computer screen three times. Pieces of the puzzles were presented sequentially from feet to head, as in the previous familiarization phase. The presentation of the first two pieces of the puzzle was accompanied with a characteristic sound of the represented animal (e.g., the tweet sound for the chicken), whereas at the time of the presentation of the third piece toddlers heard the name of the animal (see Figure 1). The experimenter ensured that the child was looking at the computer screen before initiating the presentation of stimuli.

The experimental phase began following the familiarization procedure. In order to record toddlers' electrical brain activity, we used a pediatric high-density 128 sensor net (EGI Geodesic Sensor Net, Eugene, OR) suitable for 1- to 2-year-old children with a head circumference between 47 and 51 cm, which was the case for all participants in our study. This net was fitted on the head of each child just before part II of the familiarization procedure. However, brain activity was only recorded during the experimental phase. Toddlers remained in front of the computer monitor sitting on the caregiver's lap while the experimenter controlled stimuli presentation from an adjacent room. Stimuli were presented in E-Prime 2.0 software (Psychology Software Tools, Inc.) and synchronized with NetStation software for EEG recording (EGI, Eugene, OR) with E-Prime extension. Each trial started with a centrally located colorful rotating star presented with music, intended to attract toddlers' attention. Once the child looked at the screen, the experimenter initiated the trial. In each trial, the puzzle of an animal was formed progressively from feet to head. All puzzles were matched in size, subtending a visual angle of 12.5° × 5°. Each piece was presented for 1 second. Presentation of the first two pieces was accompanied by the sound of the corresponding animal, whereas no sound was played when displaying the third piece. Twelve trials of a particular animal puzzle (sheep, monkey or chicken) were presented in each block of trials. In one-third of trials the puzzle was formed correctly (correct condition), while in the remaining trials it was formed incorrectly by either presenting the head of the corresponding animal upside down (position error condition) or presenting the head of a different animal (conceptual error condition; see Figure 1). Block presentation order was randomized and the type of trial was randomly selected within each block. There were a total of 36 trials, with 12 trials per condition (correct, position error or conceptual error).

For adult participants, the procedure was exactly the same, excluding the familiarization phase. They were asked to look at the stimuli with no further instructions and were blind to the aim of the study. Ethical approval was obtained from the ethics in human research committee of the university.

2.3 | Stimuli selection

To build stimuli of the conceptual error condition, sheep, monkey and chicken bodies were mixed with the heads of different animals (crocodile, dog, cow, elephant, horse, lion, zebra, pig and giraffe) to form a total of 27 different combinations (see Figure S1). In order to determine which of the resulting animals' combinations are more clearly perceived as erroneous, we presented the different combinations to a group of 32 voluntary participants, all second-year students of psychology that were blind to the purpose of the study. Participants had to identify whether the drawings of animals represented a real animal (head and body corresponded to the same animal) or an unreal animal (incorrect combination of head and body). All newly created animals' head-body combinations as well as the correct combination for all the animals used were randomly presented to all participants. They had 1 second to observe each combination and to decide whether it was either correct or incorrect by pressing the corresponding key. The proportion of participants that judged a combination as incorrect was calculated for all the combinations presented (see Table S1). Only combinations perceived as erroneous by over 90% of participants were considered. Combinations with clear differences in the perceptual pattern of head and body (e.g., those having heads with black shapes) were also excluded. All included and excluded combinations are shown in Figure S1.

2.4 | SES

Information about family SES was obtained by means of a parent-reported questionnaire filled-up at the end of the experimental session. The questionnaire included information about parental education, parental occupation and family income (see Table 1). Parental education was rated from 1 to 7 as follows: (1) no studies; (2) elementary school; (3) secondary school; (4) high school; (5) technical college / university diploma; (6) university bachelor degree; and (7) postgraduate studies. Professional occupation was categorized according to the 9-point scale of the Spanish Occupation Classification (CNO-11) from the Spanish National Institute of Statistics (BOE, 2010) that ranged from 1 (unemployed) to 9 (manager). Finally, we calculated the family income-to-need ratio by dividing the total annual family income by the official poverty threshold provided by National Institute of Statistics of Spain (http://www.ine.es). The three components were positively correlated (Pearson's correlations: Parents Education – Parents Occupation: $r = 0.42$, $p < .01$; Parents Occupation – Family Income: $r = 0.53$, $p < .001$; Parents Education – Family Income: $r = 0.43$, $p < .01$). A general SES index was calculated averaging the z-transformed scores of the three measures for each participant.

2.5 | ERP analysis

We used EEGlab software (Delorme & Makeig, 2004) for preprocessing the continuous EEG recording. A 0.2 Hz high pass and 30 Hz low pass filter was applied. Bad channels were replaced by spherical interpolation provided that no more than 10 channels were identified as bad channels and were distributed over the scalp. Average re-reference was computed. Artifacts in the continuous EEG were

TABLE 1 Descriptive statistics of family SES indicators and general SES index

	Min.	Max.	Mean	*SD*
Parent's occupation (1–9)	1	7.5	5.05	1.25
Parents' education (1–7)	2.5	7	5.5	1.01
Family income-to-need ratio	.25	3.77	2.01	1.01
SES (*z*-score)	−2.06	1.29	.02	.78

identified by visual inspection and manually removed before running Independent Component Analysis (ICA) to detect and correct eye blink artifacts. Next, continuous EEG was segmented into 800 milliseconds long epochs time-locked to the presentation of the third piece of the puzzle (head). Only trials where toddlers were looking at the screen during the entire trial (according to the examination of the webcam recordings) were included in the analysis. Mean of trials excluded due to inattention were 0.76, 0.75, and 0.69, respectively, for correct, position error, and conceptual error conditions.

The subsequent analysis of the ERPs was made using ERPlab software (Lopez-Calderon & Luck, 2014). The average ERPs were calculated per condition and corrected by a 200 millisecond pre-stimuli baseline. Only children with a minimum of 7 computable trials per condition were included in the final analysis. Mean of valid trials were 8.15, 8.69, and 8.57 for correct, position error, and conceptual error conditions, respectively. No statistical differences were found between experimental conditions in the amount of valid trials ($F(2, 102) = 1.69$, $p > .05$). ERPs for each condition averaged across participants in each group (toddlers and adults) are presented in Figure 2.

As expected, the errors vs. correct contrast yielded a negative component with a mid frontal topographic distribution (Figure 2c). To analyze this error-related negativity (ERN) component, we selected a group of frontal midline electrodes around Fcz (electrodes 6, 7, 12, 13, 21, 24, 25, 30 and 31, and electrodes 4, 5, 11, 12, 20, 25 and 124 in the corresponding GSN lead locations, respectively, for toddlers and adults; see Figure S2). We calculated the mean amplitude of the evoked signal per condition in a time window from 450 to 750 post-target milliseconds for toddlers, and peak amplitude between 120 and 160 milliseconds for adults' potentials.

2.6 | Time-frequency analysis

A time-frequency analysis was conducted using Brainstorm software (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). We applied a Morlet wavelet transformed on the pre-processed and segmented EEG data. Wavelets family varied from 1 to 30 Hz, using 0.5 Hz steps. The f_0/σ_f ratio value was 7. The normalized change in power relative to a 200 millisecond pre-stimulus baseline was computed for each participant and condition for all the electrodes.

3 | RESULTS

3.1 | ERP results

A fronto-central negativity that was larger for incorrect compared to correct trials was observed in toddlers as well as in adults (see Figure 2). Mean amplitude data per condition (correct, position error, conceptual error) were submitted to repeated-measures ANOVA separately for toddlers and adults (see Table 2 for descriptive statistics). A significant effect of condition was found for both toddlers ($F(2, 102) = 12.18$, $p < .001$, $\eta^2_p = .19$) and adults ($F(2, 26) = 4.74$, $p < .05$, $\eta^2_p = .27$). Planned comparisons revealed that the difference between

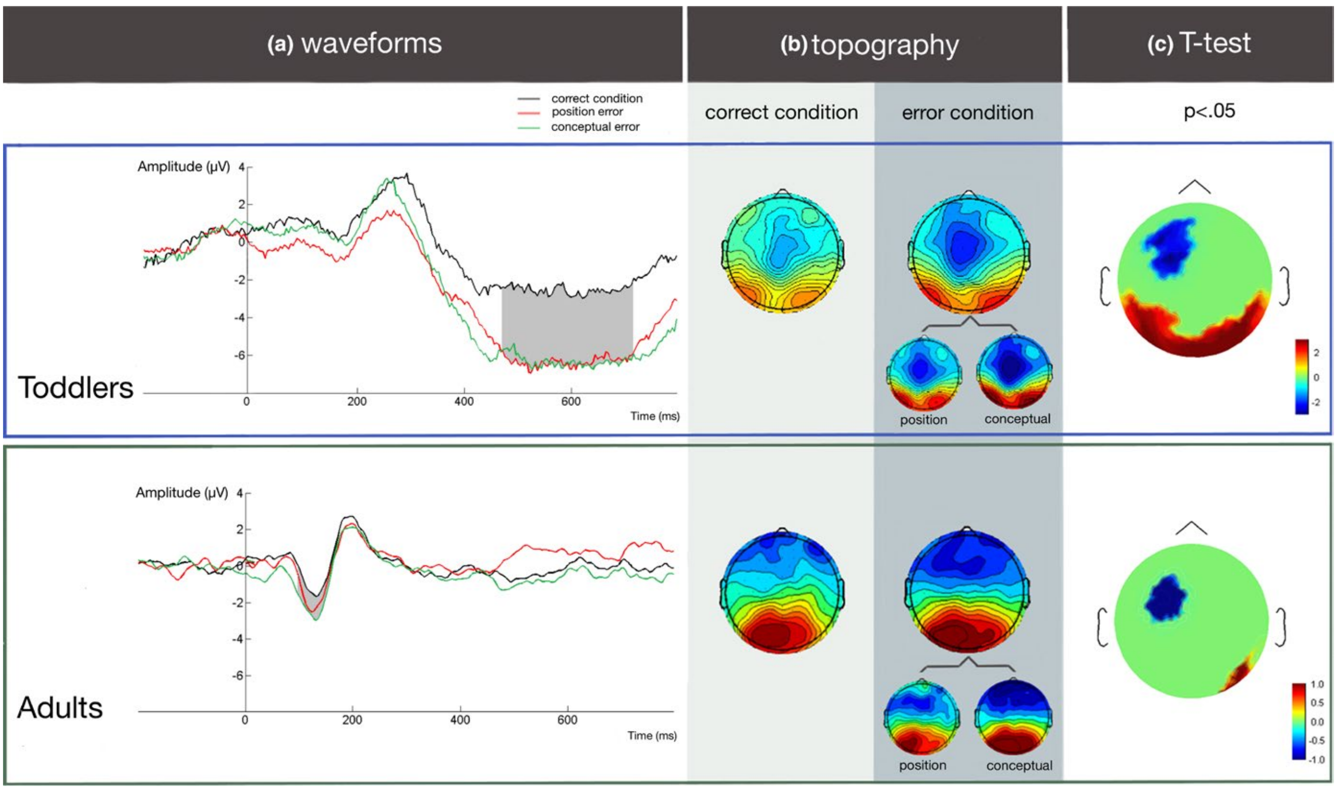

FIGURE 2 ERPs waveforms (a) and topographic maps (b) for correct and error conditions. ERPs were locked to the presentation of the third piece of the puzzle. *T*-test comparing amplitude differences between correct and incorrect (merged for position and conceptual errors) (c) [Correction added on 07 February 2017, after first online publication: Figure 2 has been replaced with a better resolution version.]

TABLE 2 Descriptive statistics of ERN amplitude and change in theta power per experimental condition. Means and standard deviations are provided for toddlers' and adults' data

	Measure	Condition	Mean	*SD*
Toddlers	ERP amplitude (μV)	correct	−2.32	4.84
		position error	−5.38	5.49
		conceptual error	−5.86	6.08
	Theta power (standardized change)	correct	8.19	7.34
		error	11.90	9.79
Adults	ERP amplitude (μV)	correct	−2.03	1.48
		position error	−3.42	3.07
		conceptual error	−3.55	2.44
	Theta power (standardized change)	correct	6.27	3.37
		error	12.03	7.36

error conditions (both position and conceptual) and the correct condition was significant for both toddlers (position error vs. correct condition: $F(1, 51) = 15.04$, $p < .001$; conceptual error vs. correct condition: $F(1, 51) = 17.18$, $p < .001$) and adults (position error vs. correct condition: $F(1, 13) = 6.64$, $p < .05$; conceptual error vs. correct condition: $F(1, 13) = 8.41$, $p < .05$), whereas there were no significant differences between error conditions in any group (toddlers: $F(1, 51) < 1$; adults: $F(1, 13) < 1$). Therefore, data from the two types of errors were merged for subsequent analyses. The difference wave was calculated by subtracting correct from error conditions. No gender differences were found in the ERN amplitude for the toddlers' group ($t(51) < 1$).

3.2 | Time frequency analysis results

Both toddlers and adults showed an increase in relative theta power at Fcz (electrode 12) for the error compared to the correct condition (see Figure 3). This difference in theta power between conditions was statistically significant in the theta frequency range between 6 and 7 Hz in both cases, matching the ERN time window. Theta power differences between error and correct conditions were significant between 300 and 600 milliseconds after stimulus presentation in toddlers ($t(51) = 2.37$, $p < .05$, $d = .64$). No gender differences were found ($t(51) < 1$). Adults showed a significant correct vs. error difference in theta power in the time window between 240 and 450 milliseconds ($t(14) = 2.91$, $p < .05$, $d = .77$).

3.3 | Correlation analyses between SES and electrophysiological brain measures

We ran Pearson's correlations to test whether (1) the amplitude of the ERN, and (2) the correct vs. error difference in standardized change in theta power were correlated to SES indicators and the general index of SES. Results of the correlation analyses are presented in Table 3. The ERN amplitude was significantly associated with parental education, parental occupation and family income, as well as to the general index of SES. A larger difference between error and correct condition in amplitude of ERN was related to higher family SES. Furthermore, children of highly educated parents demonstrated a significantly greater increment in theta power in the error condition relative to the correct condition. These observed individual differences in ERN amplitude and theta power were not related to age ($r = -.099$, $p = .24$, and $r = .076$, $p = .26$, respectively).

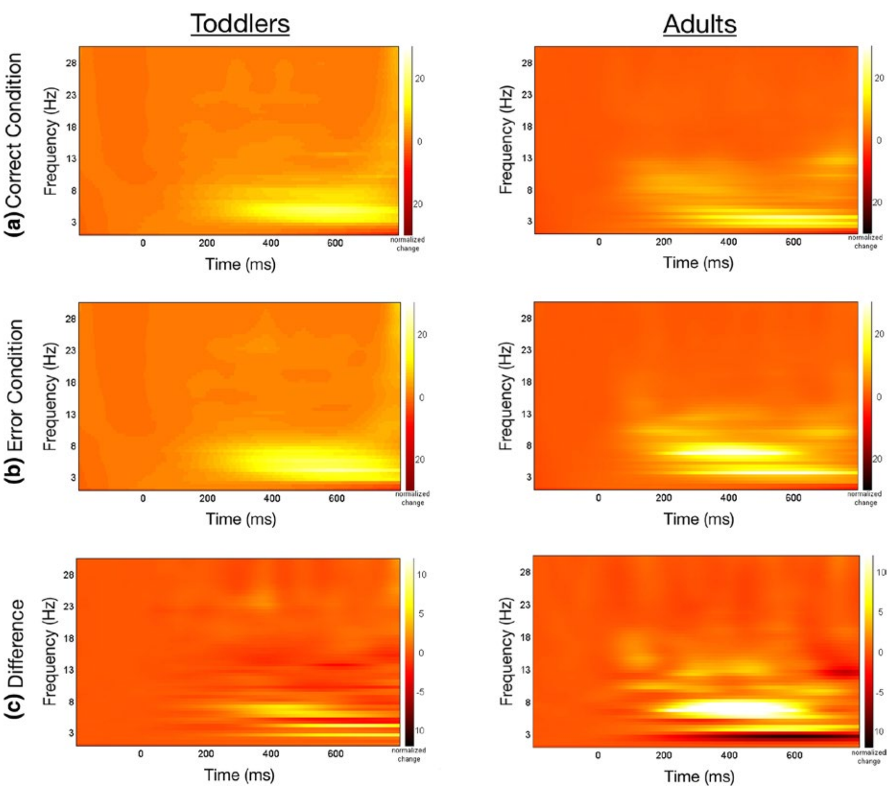

FIGURE 3 Time-frequency maps for adults and toddlers in the correct (a) and error condition (b). Maps at the bottom show the subtraction (incorrect − correct) of the signal (c) [Correction added on 07 February 2017, after first online publication: Figure 3 has been replaced with a better resolution version.]

TABLE 3 Pearson's correlations between SES and both ERN and change in theta power for errors

	ERN	Theta power
Parents' occupation	.37**	−.07
Parents' education	.31*	.23*
Family income-to-needs ratio	.24*	.11
SES (*z*-score)	.35**	.11

*$p < .05$; **$p < .01$.

3.4 | Linear regression analyses of SES on electrophysiological brain measures

Simple linear regression was performed to examine the association between SES and amplitude of the ERN in toddlers. The analysis revealed that SES significantly contributed to the amplitude of the ERN (β = .355, $F(1, 51) = 7.10$, $p < .05$). The amplitude of the ERN is predicted from SES by the following model: ERN amplitude = 6.25 + 3.29 × SES general index ($R^2 = .13$). We also ran additional simple linear regression analyses to test whether parental education was a predictor for both amplitude of the ERN and increase in theta power in response to errors. Parental education significantly contributed to the amplitude of the ERN (β = .31, $F(1, 51) = 5.03$, $p < .05$; $R^2 = .10$; see Figure 4) but was only marginally associated with theta power (β = .25, $F(1, 51) = 3.47$, $p < .07$; $R^2 = .07$; see Figure 5).

4 | DISCUSSION

The current study was designed to investigate the development of neural mechanisms underpinning executive control of attention during the second year of life and to explore the influence of SES on such mechanisms. To that end, we designed an experimental procedure in which toddlers' brain electrophysiological response to errors was registered. In adults, error detection has been extensively related to neurophysiological mechanisms involved in action regulation and EA (Luu et al., 2004). In babies, brain reaction to errors is considered a measure of the functional emergence of the EA network (Rothbart, Sheese, Rueda, & Posner, 2011). A recent study has shown that when babies observe unexpected events (e.g., a toy car that passes through a solid wall) they are more likely to engage in information-seeking behaviors, such as exploring objects that committed the violations in a hypothesis-testing mode (Stahl & Feigenson, 2015). The authors of this study argue that babies use violation of expectation as a way to select information from the environment that is most useful for learning. Although the ability of babies to regulate action based on the feedback inherent to error detection (for example, slowing responses after committing an error) seems not to be present until 36 months of age (Jones, Rothbart, & Posner, 2003), our data indicate that the sight of an unexpected puzzle completion (e.g., a chicken body being completed with an elephant head) causes greater engagement of the EA network related to the detection of conflict between what was expected (toddlers' mental representation of the cartoon animals created during familiarization) and what happened.

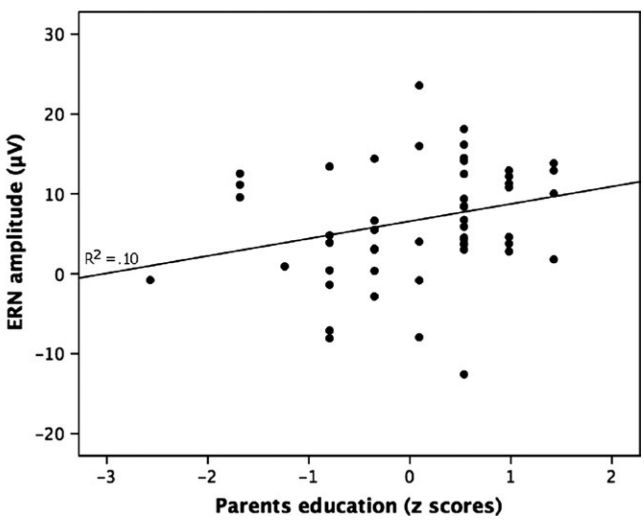

FIGURE 4 Linear regression model showing the association between amplitude of the ERN (error − correct difference in amplitude) and parental education

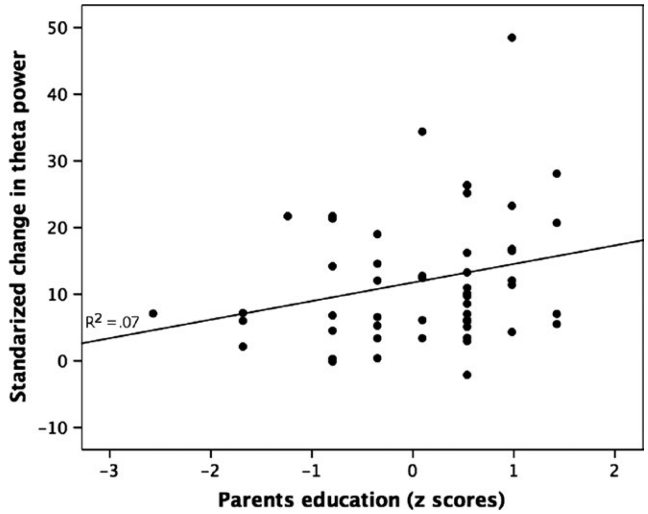

FIGURE 5 Linear regression model showing the association between theta power (error − correct difference in standardized change) and parental education

Consistent with our predictions, toddlers exhibited an increased fronto-central negativity, similar to the adults' ERN, following the observation of configuration errors when adding the final piece of the puzzles. Our experimental protocol included two types of error. Error trials differed in the type of information manipulated to create the mismatch: one involved completing the puzzle with a new piece (conceptual error), and the other involved completing the puzzle with the old piece in an unexpected orientation (position error). It could be argued that conceptual errors involve a novelty component, as children were not familiarized with the head of other animals, besides the three correct configurations, during phases I and II of the protocol. Importantly, both types of error produced a strikingly similar electrophysiological reaction over midfrontal channels, which was not statistically differentiable. This indicates that the observed brain response reflects a general cognitive mechanism dedicated to the processing of error and expectancy violations rather than to the processing of specific information or whether the final piece is novel or not. Nonetheless, novelty and surprise are inherent to errors when these consist of a mismatch between what was intended or expected and what finally occurred.

The results revealed substantial differences between toddlers and adults in the latency and temporal extension of the error-related response. Developmental differences in the latency of ERP components have been well documented in prior research (Abundis-Gutiérrez, Checa, Castellanos, & Rueda, 2014; Berger et al., 2006; Rueda, Posner, Rothbart, & Davis-Strober, 2004). The latency of functionally similar ERP components has been shown to be larger at younger ages (Rueda et al., 2004). Besides, delays in latency may not be independent of larger signal amplitude also exhibited at younger ages, an effect that is also observed in our data. Greater amplitudes and longer latencies are related to maturation processes such as skull thickening, synaptic density, and myelination of white matter fibers (Ponton, Eggermont, Kwong, & Don, 2000), which may also explain age-related changes in speed of processing.

The topography of the error-related negativity in 16–18-month-old toddlers in our study was comparable to that found in adults. Considering the common topography and functionality, this negative component can be seen as a precursor of the ERN as interpreted by other authors (Berger et al., 2006; Gehring, Liu, Orr, & Carp, 2011). In support of this conclusion, we also found an increase in theta-band power in error trials compared to correct ones. As previously reported in infants (Berger et al., 2006), the theta power burst was concurrent with the ERN-like component and is thought to be the result of a phase alignment of theta-band activity (Luu et al., 2004; Trujillo & Allen, 2007). Indeed, the increase in theta power in response to the perception of errors or unexpected events has been consistently reported (Bates et al., 2005; Reid et al., 2009; Tzur & Berger, 2009).

Nevertheless, in contrast to previous research with infants where results regarding theta band did not reach the significance level, we found that the increment of theta power in the error condition was statistically significant for both toddlers and adults. Recent research suggests that frontal theta is an important mechanism supporting changes in white matter fibers. Evidence from animal and human studies shows increases in myelination and connectivity following bursts of frontal theta mediated by activation of the protease calpain (Posner, Tang, & Lynch, 2014). Frontal theta activation in young children may thus be an important mechanism promoting the development of optimal structural connections between regions within the EA network.

A second important piece of evidence provided by our study is that family SES was associated with the magnitude of the brain response to errors. This result shows that SES influences the functional development of the EA network from very early on. The influence of SES in early attention development is supported by prior behavioral studies, which demonstrated that infants coming from low-SES families show poorer performance in the A/not-B task (Lipina et al., 2005) and greater inattention (Clearfield & Jedd, 2013) compared to those raised in high-SES environments. We found that the impact of SES can also be observed at the level of brain function. This is consistent with recent evidence showing that children from low-SES backgrounds show diminished gray matter volume in frontal and parietal regions during the first years of life (Hanson et al., 2013). Reduced gray matter volume in structures within the EA network may contribute to the poorer functional efficiency of this network for error detection observed in our study. Likewise, infants raised in low-SES families show reduced power in frontal gamma oscillations while seeing video clips with familiar objects (Tomalski et al., 2013), an oscillatory activity thought to support processes related to object perception and attention (Engel, Fries, & Singer, 2001).

In our study, the reduced ERN shown by low-SES toddlers could be due to either a weakened representation of the correct configuration of cartoons for which toddlers had only limited experience, a poorer activation of EA mechanisms of conflict detection, or both. The experimental protocol in our study included a standardized familiarization phase that was intended to make the experience with the puzzles comparable for all children. In spite of that, children from high-SES families might have formed richer and stronger representations of correct puzzle configurations compared to low-SES children. Evidence shows that parents with a higher education level speak far more to their children and use richer vocabulary compared to parents from low-SES families, which influences children's lexical development (Hoff, 2006). Restricted linguistic interactions together with the greater probability of suffering stress contribute to poorer quality parent–child interactions in low-SES families (Farah, Hackman, & Meaney, 2010). These factors might have contributed to poorer learning capacities in toddlers from lower-SES backgrounds as well as diminished function of brain mechanisms of EA. Both effects can account for the more immature pattern of brain activation exhibited by low-SES children for error detection in our study. It has been argued that SES disparities during infancy and toddlerhood explain individual differences in cognitive achievement even later in childhood (Hackman, Gallop, Evans, & Farah, 2015). Our study was limited by the lack of information about possible intervening variables that contribute to the association between SES and cognitive function, such as nutrition, stress, attachment, parent–child interactions, or language (Bradley & Corwyn, 2002; Farah et al., 2010). Consequently, more research is required to delineate the factors that modulate the relationship between SES and early development of EA.

Electrophysiological ERN and related frontal theta oscillations related to error detection have the potential to act as biomarkers of EA function in infancy and toddlerhood. Emerging evidence indicates that deficits in EA are central to a number of developmental disorders such as Autism Spectrum Disorder (ASD), Attention-Deficit Hyperactivity Disorder (ADHD), and language delay (Johnson, 2012), as well as conditions such as prematurity (van de Weijer-Bergsma, Wijnroks, & Jongmans, 2008). Atypical fronto-medial theta responses have been observed in ADHD (Groom et al., 2010), and abnormalities in EEG connectivity in the theta range have been observed in children diagnosed with autism (García Domínguez, Stieben, Pérez Velázquez, & Shanker, 2013). The new ERN protocol utilized in this study can be used with pre-verbal children in order to have an early neural measure of error monitoring and associated theta power. This can be of use in identifying individual differences that are not necessarily noticeable at the behavioral level at this age, opening a window to early detection and prevention of risk for developmental psychopathology.

Likewise, poverty and low SES have been recognized as a risk factor for the later development of behavioral problems, attention deficits, psychopathology, learning disabilities and low academic achievement (Morgan, Farkas, Hillemeier, & Maczuga, 2009; Palardy, 2008; Shaw et al., 1998; Wadsworth & Achenbach, 2005). Our results show that the effect of a disadvantageous environment can be observed from very early in development, making it clear that intervention to prevent the negative impact of SES on cognitive development should start as early as possible. However, future research aimed at identifying mediators of the effect of SES on attention development will be key to developing multifaceted prevention programs at early age.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Figure S1 Puzzle combinations included and excluded to build the conceptual error condition in the experimental phase of the study.

Figure S2 Topographical location of electrodes selected for the statistical analyses in toddlers and adults.

Table S1 Probability for all possible animal puzzle combinations (included and not included in the study) of being perceived as incorrect