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Regular Article

Neural response to errors among mothers with a history of recurrent depression and their adolescent daughters

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Abstract

Depression is transmitted within families, but the mechanisms involved in such transmission are not clearly defined. A potential marker of familial risk is the neural response to errors, which may play a role in depression symptoms and is known to be partially heritable. Here, 97 mother-daughter dyads completed a Flanker task while electroencephalography markers of error monitoring were recorded: the error-related negativity (ERN) and response-locked delta and theta power. We assessed whether these measures of neural response to errors 1) were associated with history of recurrent major depressive disorder (MDD) and current depression symptoms among mothers, 2) were correlated among mother-daughter dyads, and 3) were associated with maternal history of recurrent MDD and maternal symptoms of depression among daughters. A history of recurrent MDD was associated with blunted delta and increased theta among mothers. Across mothers, delta and theta were negatively and positively associated, respectively, with current depression symptoms. Mothers' and daughters' ERN were positively correlated. Finally, current maternal depression symptoms were negatively associated with delta power in daughters. These results suggest that neural responses to errors may be implicated in the intergenerational transmission of depression. These results also support the relevance of delta oscillations to understanding pathways to depression.

Keywords: depression; electroencephalography; event-related potentials; intergenerational transmission; mother-daughter dyads; time-frequency analyses

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Introduction

Depression is transmitted within families. Depression symptoms often correlate in parent-child dyads (e.g., Griffith et al., 2021; Lewis et al., 2011; Loechner et al., 2020). Multiple studies have also demonstrated that a parental history of depression confers risk for depression in offspring (Goodman, 2020; Gotlib et al., 2020, 2023) with some additional evidence showing particularly strong effects from mothers to their daughters (Connelly & O'Connell, 2022). Depression is more prevalent in women than in men (Salk et al., 2017; Xu et al., 2024), and this gender imbalance begins in early adolescence (Cyranowski et al., 2000; Morken et al., 2023). Because depression has a major impact on individual functioning as well as significant societal costs (König et al., 2019; Kessler et al., 2010), identifying mechanisms that may support the intergenerational transmission of risk for depression – especially among mother-daughter dyads – is important to develop methods to limit such transmission.

One process that could constitute a risk marker for the development and transmission of depression is the neural response to errors. When someone makes an error in a speeded-response task, a negative deflection can be seen in the electroencephalogram (EEG). That deflection – the error-related negativity (ERN) – appears approximately 0–100 ms after an error and is usually measured at frontocentral electrodes (Falkenstein et al., 1991; Ullsperger et al., 2014). It is primarily generated by the anterior cingulate cortex, a brain region that is known to be involved in performance and conflict monitoring (Brázdil et al., 2005; Keil et al., 2010; Ko et al., 2009; O'Connell et al., 2007). The ERN is thought to reflect neural processes that are triggered by error detection or response conflict (Gehring et al., 2012; Holroyd & Coles, 2002; Kieffaber et al., 2023). It can be used to assess individual differences pertaining to how the brain monitors and adjusts behavior in response to errors and conflicting situations (Olvet & Hajcak, 2008; Riesel et al., 2013).

A large body of literature suggests that the ERN is a viable risk marker for some forms of psychopathology, and particularly anxiety and related disorders. For instance, an enhanced ERN has been observed in individuals with anxiety disorders (Riesel et al., 2019; Riesel, 2019; Weinberg, Kotov, et al., 2015), is associated with trait anxiety (Moser et al., 2013; Riesel et al., 2022), and appears to prospectively predict anxiety symptoms (Meyer et al., 2017, 2021). Yet, despite criterion overlap and high degrees of comorbidity

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between anxiety and depression (Kessler et al., 2015; Zbozinek et al., 2012), the association between the ERN and depression is less clear. Consistent with the close association between depression and anxiety, several studies have also reported an enhanced ERN in individuals with depression (Aarts et al., 2013; Chiu & Deldin, 2007; Holmes & Pizzagalli, 2008, 2010). However, others have found no difference between depressed individuals and controls (Hanna et al., 2018; Olvet et al., 2010; Schrijvers et al., 2009; Weinberg, Kotov, et al., 2015), and still others have reported a blunted ERN in youth (Dell'Acqua et al., 2023; Ladouceur et al., 2012) and adults (Fissler et al., 2017; Schoenberg, 2014; Schrijvers et al., 2008; Weinberg, Liu, et al., 2016) with depression. The high degrees of comorbidity between anxiety and depression may be responsible for some inconsistency. While the ERN is usually enhanced in anxiety, comorbid depression may have a blunting effect on the ERN in people with anxiety disorders (Weinberg et al., 2012; Weinberg, Kotov, et al., 2015).

Task differences may also account for some discrepancies across studies. The most frequently used tasks in studies involving the ERN and depression are the Stroop and the flanker tasks. Both tasks involve interference control, but they differ in several aspects, such as the involvement of verbal vs. spatial interference and the type of information that needs to be filtered during task performance (Yeung et al., 2020). An enhanced ERN has been associated with depression when a Stroop task is used (Holmes & Pizzagalli, 2008, 2010). This is less frequently observed in studies that have used the Flanker task (Weinberg, Dieterich, et al., 2015); in fact, studies using a flanker task more typically find evidence of a blunted ERN associated with depression (Ladouceur et al., 2012; Schrijvers et al., 2008; Weinberg, Meyer, et al., 2016). Moreover, recent data suggests that a blunted ERN elicited during a flanker task can prospectively predict depression symptoms in both children (Lawler et al., 2021) and adults (Sandre et al., 2023). Several studies reporting null effects have also assessed the ERN using the Flanker task (Hanna et al., 2018; Olvet et al., 2010; Schrijvers et al., 2009; Weinberg, Kotov, et al., 2015), but it is possible that some of these studies lacked the necessary power to detect group differences. In addition, differences in reliability across the different tasks used to assess the ERN (Clayson, 2020; Riesel et al., 2013), or even across different variations of the Flanker task (Clayson et al., 2024), may also account for some of the aforementioned discrepancies.

Evidence that a blunted ERN can prospectively predict increases in depression symptoms is consistent with other evidence that the ERN may be a stable marker of vulnerability that could be useful in understanding transmission within families. For instance, this blunted ERN does not appear to be state-dependent, but instead can be observed in currently euthymic individuals with remitted depression (Weinberg, Liu, et al., 2016), who are at increased risk for subsequent episodes. The magnitude of the ERN is also subject to genetic contributions in adolescent twin samples (Anokhin et al., 2008; Burwell et al., 2016), and abnormalities in the magnitude of the ERN have been observed in unaffected family members of individuals with anxiety and related disorders (Carrasco et al., 2013; Riesel et al., 2011, 2019). Additionally, there is evidence that neural measures of error-monitoring are correlated between parents and their children. From early childhood and across adolescence, positive associations between mothers' and daughters' ERN have been reported (Moser et al., 2018; Suor et al., 2022). Finally, and of interest to the current study, a blunted ERN has been observed in the never-depressed children (ages 9 to 17) of mothers with recurrent depression (Meyer et al., 2018). Combined, these data suggest that the magnitude of the ERN may be familial and related to risk for depression. However, studies that have assessed familiality of the ERN have typically been in unselected samples, and studies that have assessed high-risk offspring have typically not collected data from parents.

In addition to the ERN, time-frequency decompositions of neural oscillations may provide relevant information related to error monitoring processes and their associations with depression and risk for depression. While the time-domain ERN only indexes phase-locked neural activity, decomposition of time-frequency total power provides information about both phase-locked and non-phased locked neural activity (Buzzell et al., 2022). Increased response-locked power in the delta and theta frequency bands has been observed during response monitoring tasks (Sandre & Weinberg, 2019; Völker et al., 2018; Yordanova et al., 2004). However, theta power appears to increase following both errors and correct responses (although to a lesser degree), whereas delta power appears specifically increased following errors (Yordanova et al., 2004). This suggests that oscillations in these bands index partially dissociable processes. Theta may reflect generic response monitoring processes (Yordanova et al., 2004), signaling that cognitive control needs to be implemented (Buzzell et al., 2019; Cavanagh & Frank, 2014; Cavanagh & Shackman, 2015). In contrast, the functional significance of error-related delta is less understood. It has been suggested that delta could reflect more elaborative processes, such as strategic adjustments in behavior, after the theta response has signaled the need for cognitive control (Sandre & Weinberg, 2019). Error-related delta has also been associated with the motivational salience of errors (Umemoto et al., 2021). Furthermore, while error-related theta is modulated by dopaminergic activity (Pezzetta et al., 2022), this is not the case with delta, which has been associated with norepinephrine activity (Pezzetta et al., 2023). These two neurotransmitters are known to contribute to the pathophysiology of depression, although they could be associated with different symptom profiles (Liu et al., 2018; Nutt, 2008; Werner & Coveñas, 2010). Given these specificities, assessing error-related delta and theta, in addition to the ERN, may improve our understanding of the association between neural responses to error and depression and risk for depression (Weinberg et al., 2022). However, the few studies that have examined associations between power in delta and theta in depression have reported mixed findings. One study reported decreased error-related theta in pediatric depression (Dell'Acqua et al., 2023), while another in adults found no significant links (Muir et al., 2020). Additionally, neither study reported significant differences between depressed individuals and controls in the amplitude of their delta oscillations. Despite the relevance of delta and theta oscillations in the study of depression, their role in the familial transmission of risk for depression has not been studied.

Our first objective was to identify how neural correlates of error monitoring are associated with a lifetime history of recurrent major depressive disorder (MDD) and current depression symptoms in mothers. Given the blunted ERN seen in adults with remitted depression (Weinberg, Liu, et al., 2016), we expected that mothers with a history of recurrent MDD would show a blunted ERN relative to mothers without a history of depression. We also expected that a blunted ERN would be associated with more severe current symptoms of depression. Our second objective was to assess how mothers' and daughters' neural responses to errors were associated. We hypothesized that mothers' and daughters' ERN would be positively associated (Moser et al., 2018; Suor et al., 2022). Our third objective was to assess how

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neural measures of error monitoring in daughters were associated with maternal history of depression and current depression symptoms. Consistent with previous work (Meyer et al., 2018), we expected that a maternal history of recurrent MDD and higher current maternal depression symptoms would be associated with a blunted ERN in daughters. For all three objectives, we did not formulate hypotheses for delta and theta power as these analyses were exploratory.

Methods

Participants

Mothers and their biological daughters were recruited from the Greater Montreal area using online and print advertisements (Ethridge et al., 2022; Freeman et al., 2022). Our recruitment strategy targeted two groups: mothers reporting a history of recurrent MDD and mothers with no history of MDD. Eligibility was verified through a phone screening, using an adapted version of the Mini International Neuropsychiatry Interview (MINI; Sheehan et al., 1998). To be included in the study, mothers needed to have a daughter aged 10–19 years old, live with them at least 50% of the time, and both had to be able to read and write in English. For all mothers, exclusion criteria consisted of (i) a history of head injury resulting in loss of consciousness for more than 10 minutes and (ii) a history of psychosis or mania, or current substance abuse. Additionally, for mothers without a history of recurrent MDD, a lifetime history of any psychiatric disorder was exclusionary (except for specific phobia (n = 3 in this group), given that it is less heritable, impairing, and predictive of children's risk for depression compared to other disorders (Kendler et al., 1992)). Daughters with a history of head injury resulting in loss of consciousness for more than 10 minutes were also excluded. Following screening, 109 mother-daughter dyads were invited to the lab for testing. Maternal eligibility was updated after enrollment by interviews with the Structured Clinical Interview for DSM–5 (SCID-5; First et al., 2016). Further exclusion criteria from the analyses of the current study were (i) no member of the dyad completed the Flanker task (n = 7), and (ii) no member of the dyad had valid EEG data with sufficient error trials after data preprocessing (n = 5). Thus, 97 mother-daughter dyads were included in the current study (44 mothers had a lifetime history of recurrent MDD). Demographics of the sample are presented in Table 1.

Mothers provided written informed consent for themselves and written parental consent for their daughter (if aged less than 18 years old). Daughters aged less than 18 years old provided assent and those aged 18 and above provided consent. All procedures were approved by McGill University ethics board and the study was conducted according to the principles of the Declaration of Helsinki.

Procedures

Clinical interviews

Semi-structured interviews were conducted in both mothers (Structured Clinical Interview for DSM-5 Disorders (SCID-5); First et al., 2016) and daughters (Mini International Neuropsychiatric Interview for Children and Adolescents (MINI-KID); Sheehan et al., 2010) to identify diagnoses of current and lifetime anxiety, mood, obsessive-compulsive, psychotic, substance use, trauma and stressor-related disorders. Interviews were conducted by graduate students and supervised by AW. Interrater reliability (Landis & Koch, 1977) for unipolar mood disorders, which are of primary interest in the current study, was assessed by 4 interviewers from a subset (n = 20) of interviews and was found to range from $\kappa = .70$ in daughters to $\kappa = .88$ in mothers.

Measures

Participants completed questionnaires assessing their own current depression symptoms. In adolescent daughters, depression symptoms were assessed with the 32-item Mood and Feelings Questionnaire (MFQ; Angold et al., 1995), which showed excellent internal consistency in our sample ($\alpha = .95$). Mothers' current depression symptoms were assessed with the 20-item General Depression scale from the expanded version of the Inventory of Depression and Anxiety Symptoms (IDAS-II; Watson et al., 2012). This scale demonstrated high internal consistency in our sample ($\alpha = .92$).

Flanker task

Participants performed an arrow version of the Flanker task (Eriksen & Eriksen, 1974). Stimuli were presented and responses were recorded with the Presentation software (Neurobehavioral Systems, Inc.; Albany, CA), running on an Intel Core i7 computer. On each trial of the task, 5 horizontally aligned arrowheads were presented at the center of a 19-inch computer monitor. The central arrowhead was the target stimulus and the two arrowheads on each side were the flankers. Half of the trials were congruent (i.e. the target and flanker stimuli point in the same direction) and the other half were incongruent (i.e. the target and flanker stimuli point in opposite directions). Trial order was randomized throughout the task. Participants were instructed to press the left or right button on a mouse according to the direction of the target stimulus. On each trial, stimuli were presented for 200 ms. A white fixation cross was then presented on a black screen for 1,800 ms or until a response was given. The intertrial interval then followed, which also consisted of a white fixation cross on a black screen for a duration ranging randomly from 1,000 to 2,000 ms.

Before beginning the task, participants performed a 6-trial practice session. They were told to be as fast and accurate as possible. Participants then performed the actual task, which was separated in five blocks of 30 trials, for a total of 150 trials. Performance-based feedback was displayed on-screen at the end of each block. If accuracy was 80% or above, participants were instructed to "Please try to respond faster," in order to increase the likelihood of committing errors. If accuracy was between 76 and 79%, the feedback was "You are doing a great job." If accuracy was 75% or below, participants were instructed to "Please try to be more accurate." Analyses pertaining to behavioral performance are presented in the Supplement.

EEG recordings

EEG was recorded at 1000Hz sampling rate from 32 electrodes mounted in the Easycap and placed according to the 10/20 system. The ground electrode was placed at FPz. Signals were recorded with BrainVision actiCHamp amplifier and Pycorder recording software (Brain Products, Munich, Germany). Electrical conducting gel was used to maintain electrode impedance below 10 kΩ throughout the recordings.

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Table 1. Demographic and clinical characteristics of study participants

	Mothers			Daughters		
	Without history of recurrent MDD (n = 53)	With history of recurrent MDD (n = 44)	Test statistic	Without maternal history of recurrent MDD (n = 53)	With maternal history of recurrent MDD (n = 44)	Test statistic
Age in years, mean (SD)	46.4 (4.9)	44.4 (7.5)	$t_{92} = 1.48$	14.7 (2.5)	14.1 (2.7)	$t_{93} = 0.95$
Ethnicity, number (%)			$\chi_7 = 8.02$			$\chi_7 = 6.38$
Caucasian	42 (79.2)	32 (72.7)		32 (60.4)	29 (65.9)	
Hispanic	2 (3.8)	1 (2.3)		2 (3.8)	0 (0.0)	
African-American	0 (0.0)	2 (4.5)		2 (3.8)	1 (2.3)	
Arab/West Asian	1 (1.9)	1 (2.3)		2 (3.8)	2 (4.5)	
Native/First Nation/Aboriginal	0 (0.0)	2 (4.5)		0 (0.0)	2 (4.5)	
Chinese	2 (3.8)	0 (0.0)		2 (3.8)	0 (0.0)	
Other	4 (7.5)	5 (11.4)		11 (20.8)	7 (15.9)	
Prefer not to answer/did not answer	2 (3.8)	1 (2.3)		2 (3.8)	3 (6.8)	
Family income, number (%)			$\chi_4 = 6.02$			
$0 – $49,999	12 (22.6)	12 (27.3)				
$50,000 – $99,999	7 (13.2)	13 (29.5)				
$100,000 – $199,999$	18 (34.0)	9 (20.5)				
$200,000+	3 (5.7)	3 (6.8)				
Prefer not to answer/did not answer	13 (24.5)	7 (15.9)				
History of anxiety disorder, number (%)	5 (9.4)	16 (36.4)	$\boldsymbol{\chi_1 = 9.98}$**	11 (20.8)	12 (27.3)	$\chi_1 = 0.59$
History of MDD, number (%)	53 (100)	44 (100)	–	13 (24.5)	12 (27.3)	$\chi_1 = 0.06$
Clinical scales, mean (SD)						
IDAS-II General Depression	34.1 (9.4)	45.9 (13.9)	$\boldsymbol{t_{91} = 69.7}$***			
MFQ				16.6 (15.0)	16.6 (13.1)	$t_{92} = 0.02$

Note: Income is reported in Canadian dollars (CAD). IDAS-II: Inventory of Depression and Anxiety Symptoms-II, MDD: major depressive disorder, MFQ: Mood and Feelings Questionnaire, SD: standard deviation.
**: $p < .01$, ***: $p < .001$

EEG signal treatment and feature extraction

EEG preprocessing

Continuous EEG signals were preprocessed with the Maryland Analysis of Developmental EEG (MADE) pipeline (Debnath et al., 2020), running on Matlab 2020a. The MADE pipeline relies on EEGLAB's (Delorme & Makeig, 2004) functions and data structure. Data were preprocessed separately for event-related potentials (ERP) and time-frequency analyses. The first step consists of offline filtering using EEGLAB's firfilt plugin. Continuous data were filtered with a Hamming window finite impulse response filter, with a 0.1 Hz high-pass filter (0.1 Hz transition width). A 30 Hz low-pass filter was used for ERP analyses and a 50 Hz low-pass filter was used for time-frequency analyses (10 Hz transition width in both cases). The stopband attenuation was 53 dB. The channel_properties function from EEGLAB's FASTER plugin (Nolan et al., 2010) was used to identify and remove flat or noisy channels according to three-values: Hurst exponent, correlation with other channels, and channel variance. After this step, residual flat channels were removed from the data if their standard deviation across the whole recording was smaller than 1. Independent component analysis (ICA) was used to remove non-neural artifacts such as blinks, saccades, and muscle artifacts. Given that ICA performs better on data filtered with a 1 Hz high-pass filter, the ICA was performed on a copy of the recordings. This copied dataset was first epoched into 1-second segments. Those 1-second epochs with very low/high amplitude (± 1000 μV) or excessive EMG activity (below −30 and above 100 dB between 20–40 Hz) were marked as bad epochs. Channels containing more than 20% of these epochs, suggesting bad channels missed by FASTER, were removed from both the copied and the original datasets. These bad epochs were then removed from the copied dataset. ICA was then conducted on the copied dataset with EEGLAB's runica function. ICA weights were transferred to the original dataset. The adjusted-ADJUST toolbox (Leach et al., 2020; Mognon et al., 2011) was used to automatically identify artifactual independent components in the original dataset, which were then rejected. Continuous data were epoched from −500 ms to 1,000 ms relative to response onset for ERP analyses, and from −1,000 ms to 2,000 ms for time-frequency analyses. Longer epochs are needed for time-frequency analyses, which however comes with the cost of losing participants due to artifacts in the longer epochs (see results). A threshold-based rejection method was used to deal with residual artifacts. For frontal electrodes near the eyes (Fp1, Fp2), any epoch with voltage exceeding ±100 μV was removed. For other electrodes, epochs for which voltage exceeded ±100 μV in more than 10% of electrodes were removed. For remaining epochs, individual channels were interpolated with a spherical spline procedure at the epoch level if voltage exceeded the ±100 μV threshold. Channels that were removed in the first steps of the pipeline were also interpolated with a spherical spline procedure. Finally, electrodes were re-referenced to the average of both mastoids (TP9 and TP10).

Feature extraction

ERP analyses were performed with ERPLAB (Lopez-Calderon & Luck, 2014). Error and correct trials were averaged separately and baseline-corrected (−500 to −300 ms). Only participants with at least 6 error trials were included (Meyer et al., 2013; Olvet & Hajcak, 2009; Sandre et al., 2020). In the current study, mothers committed fewer errors than daughters. We therefore excluded more mothers than daughters from EEG analyses due to insufficient error trials. Among the 97 dyads included in this study, 90 daughters and 55 mothers had at least 6 error trials. Mothers with insufficient trials did not differ from those with at least 6 trials regarding depression symptoms or history of recurrent MDD (all p-values > .31). Given these sample sizes, our study was powered to detect medium group differences ($d \approx .6$) and correlations ($r \approx .3$) in daughters, and large groups differences ($d \approx .8$) and medium correlations ($r \approx .35$) in mothers.

A difference wave was computed by subtracting the ERPs to correct responses from that of errors. The ΔERN was assessed as the difference wave's mean amplitude in the 0–100 post-response interval at electrode Cz. Time-frequency transforms were performed with the time-frequency principal components analysis (TF-PCA) approach (Bernat et al., 2005; Buzzell et al., 2022). First, and similarly to the procedure used in Buzzell et al. (2019), we used a subsampling procedure to match the number of trials across conditions. Six trials were randomly selected without replacement across all valid trials in a condition and averaged. This procedure was repeated 25 times. The resulting 25 estimates were bootstrapped 100 times; the mean of the bootstrapped samples was used in further analyses. Second, delta and theta frequencies were filtered separately, given that lower frequencies (such as delta) have larger magnitudes than higher frequencies. Thus, for delta TF-PCA analyses, data were filtered with a 4 Hz Butterworth low-pass filter. For theta TF-PCA analyses, data were filtered with a 2 Hz Butterworth high-pass filter. Theta was averaged from 4 medial frontal electrodes (Fz, Cz, FC1, FC2), whereas delta was averaged from 4 medial parietal electrodes (Cz, Pz, CP1, CP2). Given that the highest frequency of interest in the current study was theta, data were downsampled to 32 Hz to reduce computing time.

Following this, Cohen's class reduced interference distributions was used to obtain a time-frequency decomposition of response-locked average power across trials of the two different conditions (i.e., error and correct trials). For both delta and theta frequency bands, the first PCA factor was selected. Like the approach taken by Buzzell et al. (2019), we used a hybrid approach where we derived PCA factors from averaged power and applied those factors to total power. Total power, unlike average power, is computed at the trial-level before being averaged across trials and thus includes both phase-locked and non-phased locked brain activity (Cohen, 2014).

Similar to the ΔERN, brain oscillations to correct responses were subtracted from that of errors to obtain the Δdelta and Δtheta. Split-half reliability coefficients for the EEG measures of interest fell in the moderate range in daughters (ΔERN: $r = .55$; Δdelta: $r = .51$; Δtheta: $r = .59$) and in the low to moderate range in mothers (ΔERN: $r = .46$; Δdelta: $r = .59$; Δtheta: $r = .49$).

Statistical analyses

For our first objective, t-tests were performed to compare EEG markers of error monitoring (ΔERN, Δdelta, and Δtheta) between mothers with and without a lifetime history of depression. Pearson's correlations were also performed between mothers' EEG markers of error monitoring and their current symptoms of depression. For our second objective, Pearson's correlations were performed between daughters' and mothers' EEG markers of error monitoring. For our third objective, t-tests were performed to compare daughters' EEG markers of error monitoring according to their mother's lifetime history of recurrent MDD. Pearson's correlations were also performed between daughters' EEG markers of error monitoring and their mothers' current symptoms of depression. Since these latter analyses aimed to identify whether

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Table 2. Bivariate associations between study variables

	Total group		Mothers without a history of recurrent MDD		Mothers with a history of recurrent MDD										
Variable	*M*	*SD*	*M*	*SD*	*M*	*SD*	1	2	3	4	5	6	7	8	9
1. Daughters' ΔERN (μV)	−3.49	6.32	−3.07	6.94	−3.97	5.56	–								
2. Daughters' Δdelta (μV^2/Hz)	0.20	0.58	0.29	0.51	0.09	0.64	.41**	–							
3. Daughters' Δtheta (μV^2/Hz)	0.05	0.05	0.05	0.05	0.05	0.06	−.35**	.03	–						
4. Mothers' ΔERN (μV)	−2.79	4.74	−2.1	4.60	−3.59	4.97	.41**	.28	−.07	–					
5. Mothers' Δdelta (μV^2/Hz)	−0.03	0.31	0.05	0.32	−0.12	0.28	.03	.14	.23	.04	–				
6. Mothers' Δtheta (μV^2/Hz)	0.03	0.03	0.02	0.02	0.04	0.03	−.38**	−.36*	.25	−.36**	-.18	–			
7. Daughters' age	14.49	2.63	14.65	2.50	14.14	2.70	−.20	−.26*	.13	.13	.03	−.05	–		
8. MFQ (daughters)	48.47	14.06	48.50	15.02	48.43	12.95	.01	−.06	.01	.25	.03	−.12	.23*	–	
9. IDAS-II General Depression (mothers)	39.55	12.99	34.06	9.39	45.90	13.85	−.05	−.30**	.09	−.20	−.28*	.28*	−.23*	.06	–

Note: IDAS-II: Inventory of Depression and Anxiety Symptoms-II, *M*: mean, MFQ: Mood and Feelings Questionnaire, *SD*: standard deviation. *: $p < .05$, **: $p < .01$.

error monitoring mechanisms in mothers may constitute a risk marker for future depression in their daughters, independent of daughters' mood states, daughters with a lifetime history of depression (n = 25) were excluded from this set of analyses, leaving 67 daughters for these analyses. Finally, all analyses were repeated while taking into account several other potential confounding factors, such maternal symptoms of anxiety and history of anxiety disorders, daughters' symptoms of anxiety and history of anxiety disorders, maternal and daughters' age, as well as family income (Online supplement).

Results

Measures of depression symptoms

All bivariate associations between study variables are presented in Table 2. From this table, we can see that there was no concordance in depression symptoms between mothers and daughters. According to established cutoffs of ≥29 for the MFQ (Daviss et al., 2006) and ≥47 for the IDAS General Depression scale (De la Rosa-Cáceres et al., 2023; Stasik-O'Brien et al., 2018), 16 daughters and 26 mothers reported clinically significantly levels of depression.

Impact of lifetime depression history and current depression on EEG correlates of error monitoring in mothers

Fifty-five mothers had valid ERP data and 53 had valid time-frequency data. Among those, 23 had a lifetime history of recurrent MDD. We found that mothers with a lifetime history of recurrent MDD had reduced Δdelta [$t(50) = 2.09$, $p = .042$, $d = .59$] and increased Δtheta [$t(50) = -2.18$, $p = .034$, $d = .58$] power relative to those without a history of recurrent MDD. There was no significant between-group difference in ΔERN amplitude [$t(52) = 1.14$, $p = .26$, $d = .31$]. Similarly, we found that current depression symptoms, as assessed by the IDAS-II General Depression scale, were significantly associated with decreased Δdelta [$r(50) = -.28$, $p = .045$] and increased Δtheta [$r(50 = .28$, $p = .049$] power across the whole sample of mothers with valid EEG data. There was no significant association between depression symptoms and ΔERN amplitude [$r(52) = -.20$, $p = .15$] (Figure 1).

Familiality of electrophysiological correlates of error-monitoring

Across our sample, there were 48 dyads with valid ERP data for both the daughter and the mother, and 46 with valid time-frequency data. Correlation analyses revealed that mothers' and daughters' ΔERN were significantly correlated [$r(46) = .41$, $p = .004$] (Figure 2). However, Δdelta [$r(44) = .14$, $p = .34$] and Δtheta [$r(44) = .25$, $p = .095$] were not significantly correlated in mother-daughter dyads.

Association between mothers' lifetime history of depression and current depression symptoms and daughters' neural responses to errors

After excluding daughters with a lifetime history of depression, there were 67 daughters remaining with valid EEG data. Among those, 31 (46.3%) had a mother with a history of recurrent MDD. In daughters, none of the three neural measures were significantly associated with a lifetime history of recurrent MDD in mothers [ΔERN: $t(65) = 1.28$, $p = .21$, $d = .31$; Δdelta: $t(65) = 1.75$, $p = .086$, $d = .71$; Δtheta: $t(65) = 0.45$, $p = .66$, $d = .11$]. Additionally, in daughters, neither ΔERN [$r(62) = -.17$, $p = .19$] nor Δtheta [$r(62) = .11$, $p = .41$] was associated with maternal depression symptoms. However, daughters' Δdelta response was significantly correlated with maternal symptoms of depression [$r(62) = -.37$, $p = .002$], such that daughters of mothers with more current symptoms of depression showed decreased delta power following errors (Figure 3).

We also conducted several sensitivity analyses to assess the effect of other variables on our primary analyses. When accounting for maternal anxiety symptoms, most results remained significant. When accounting for maternal history of anxiety disorder, only the association between maternal depression symptoms and Δdelta in daughters, as well as the analysis pertaining to the familiality of the ERN, remained significant (**Table S1**). Nevertheless, all effects remained of similar magnitude and in the same direction. Those differences when including maternal history of anxiety as a covariate may be due to low power given that few (n = 16) mothers had a history of anxiety disorder. All analyses remained significant when controlling for daughters' anxiety symptoms and history of

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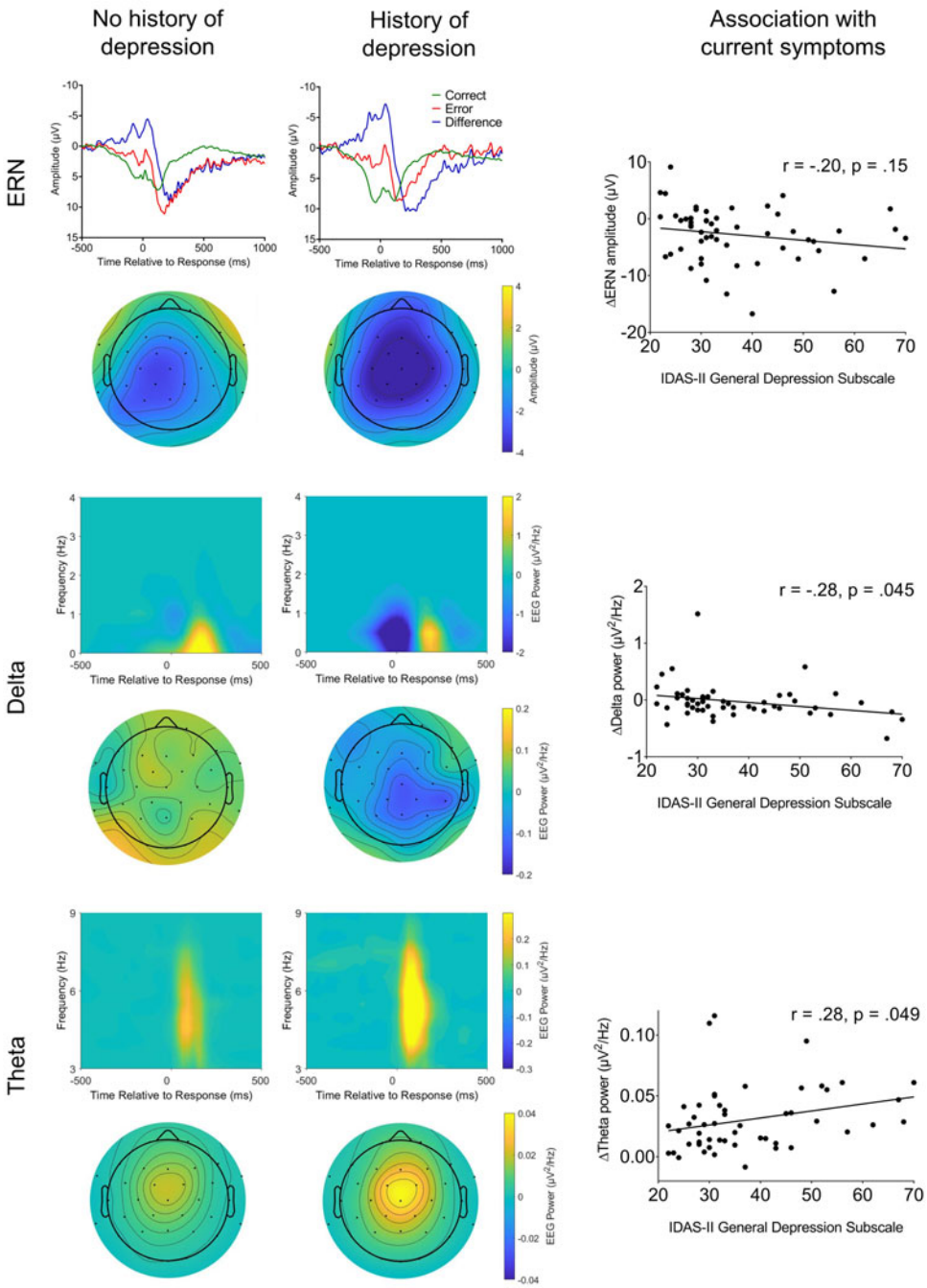

Figure 1. Mothers' electroencephalogram (EEG) correlates of error-monitoring according to lifetime history/current symptoms of depression. ERP waveforms and time-frequency plots for Δdelta and Δtheta depicts EEG correlates of error-monitoring in mothers with and without a lifetime history of recurrent major depressive disorder. Scalp maps shows the topographical distribution of error-minus correct difference in the 0–100 ms post-response interval (ERN panel) and of the first component from TF-PCA (delta and theta panels). The scatterplots on the right show the associations between current depression symptoms and EEG correlates of error-monitoring.

anxiety disorder (**Table S2**). Finally, most results remained significant when controlling for mothers' and daughters' age, family income, and daughters' current symptoms of depression (**Table S3 and Table S4**)."

Discussion

In the current study, our aim was to better understand familial transmission of depression, and whether neural measures of error monitoring might be implicated in this transmission. To that end, we first looked at whether these neural measures differed in mothers with a history of recurrent depression. Next, we examined the extent to which these neural responses were correlated between mothers and daughters. Finally, we examined the extent to which maternal history of depression and current symptoms of depression were associated with neural measures of error-monitoring in daughters.

First, we found that mothers with a history of recurrent depression had reduced delta and increased theta power relative to mothers without a history of depression, although these groups did not differ significantly in terms of ERN amplitude. Mothers' current symptoms of depression also correlated significantly with EEG power in these two frequency bands, but not with the ERN. Although error-related delta and theta have only rarely been assessed in relation with depression, these results contrast somewhat with two previous studies in adults and adolescents. One of these reported no significant associations between theta and delta power and depression symptoms in an adult sample enriched

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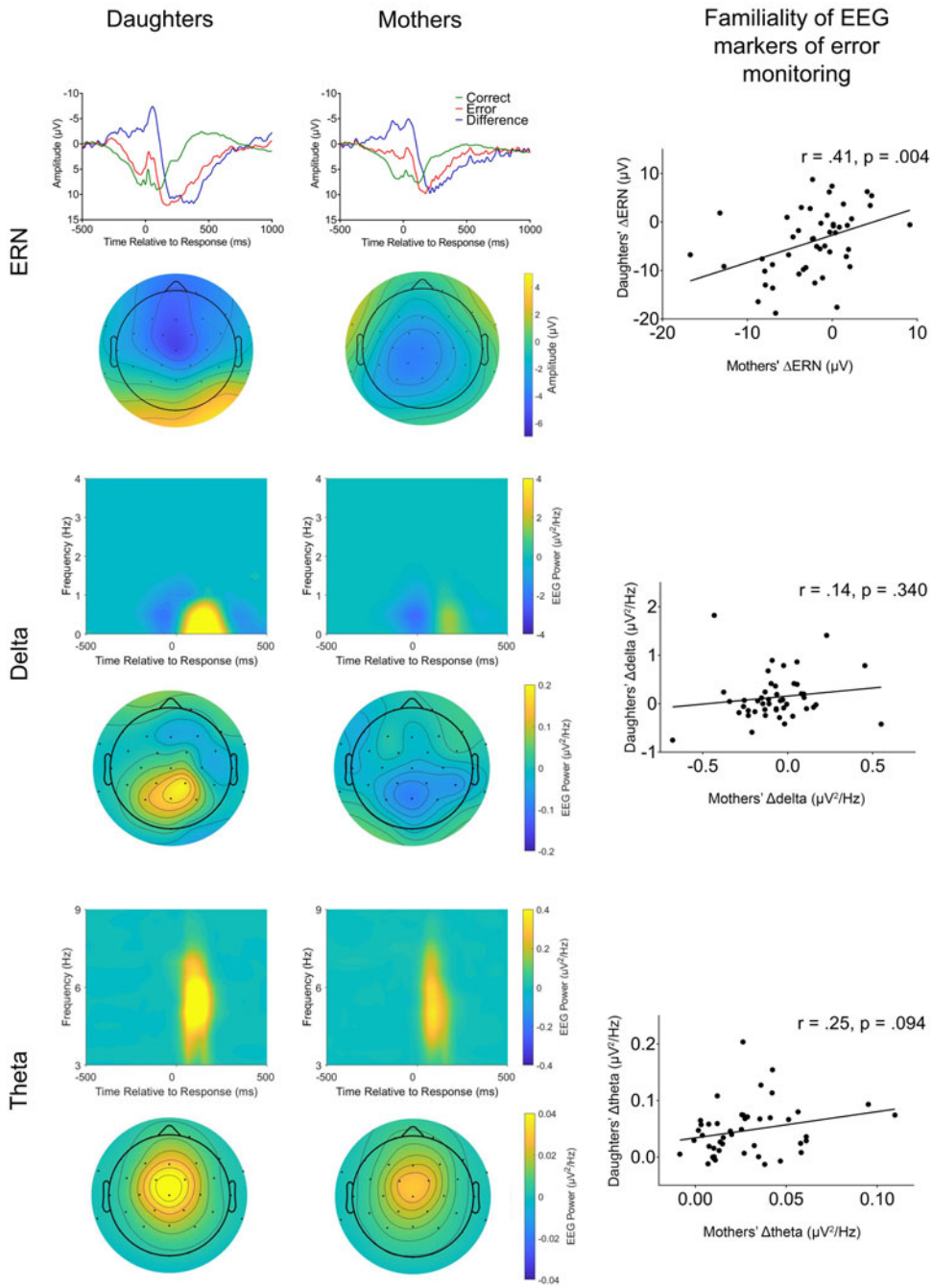

Figure 2. Associations between mother's and daughters' neural response to errors. The left part of the figure shows ERP waveforms and Δdelta and Δtheta time-frequency plots for mother-daughter dyads, as well as topographical distribution of the error minus correct difference for ERPs/electroencephalogram (EEG) power. The scatterplots on the right show associations between mothers' and daughters' EEG correlates of error-monitoring.

for MDD and generalized anxiety disorder (Muir et al., 2020). The other, in adolescents, reported decreased theta associated with depression, but, contrary to hypotheses, no significant reduction in delta power (Dell'Acqua et al., 2023). Further research is needed, but one possible explanation for these results is that the increases in theta and reductions in delta power observed in the current study appear later in life and are associated with the duration and recurrence of depressive episodes. Future studies in larger clinical samples will be necessary to explore this question.

The results in mothers are also consistent with previous evidence that error-related oscillations in delta and theta bands reflect at least partially distinct processes (Yordanova et al., 2004). On the one hand, the increase in error-related theta may suggest that signals indicating the need for cognitive control (Cavanagh & Frank, 2014) are preserved or even enhanced in mothers with a history of depression. On the other hand, delta oscillations have been suggested to reflect strategic adjustments in behavior after the need for cognitive control has been signaled (Sandre & Weinberg, 2019). Given that delta oscillations are known to be involved in motivational processes (Knyazev, 2007, 2012) and that error-related delta may reflect the motivational salience of errors (Umemoto et al., 2021), decreased error-related delta in mothers with a history of depression may reflect decreased motivation to implement cognitive control. Also, while blunted error-related delta has not yet been reported in depression, blunted delta power has been observed in other contexts, such as following monetary reward (Foti et al., 2015; Nelson et al., 2018), social feedback (Jin et al., 2019), or when viewing pleasant pictures (Dell'Acqua, Brush,

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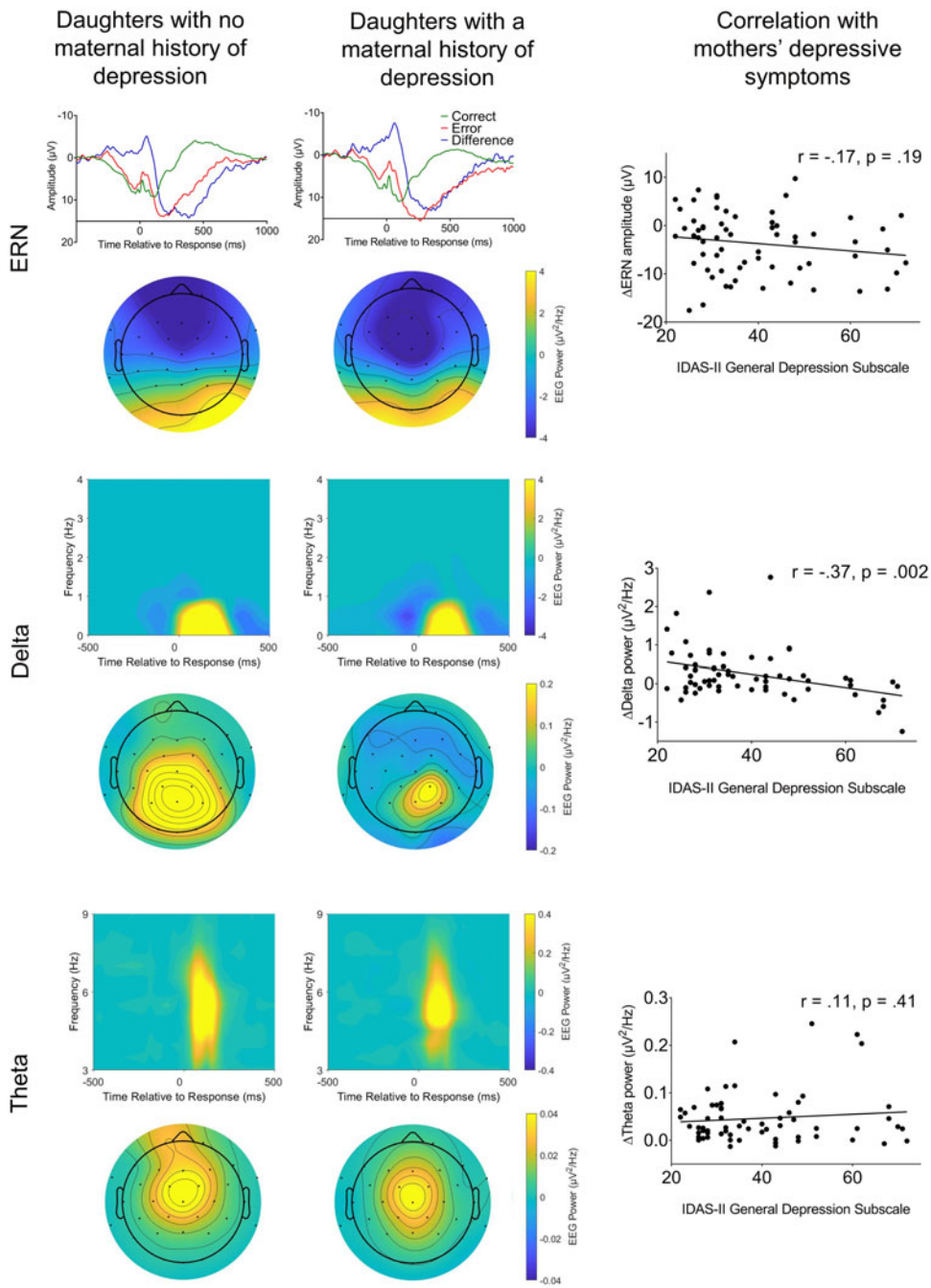

Figure 3. Link between mothers' lifetime history of depression/current depression symptoms on daughters' electroencephalogram (EEG) markers of error monitoring. ERP waveforms and time-frequency plots for Δdelta and Δtheta depicts EEG correlates of error-monitoring in daughters according to their mothers' lifetime history of recurrent major depressive disorder. Scalp maps shows the topographical distribution of the error minus correct difference for ERPs/EEG power. The scatterplots on the right shows the associations between mothers' current depression symptoms and daughters' EEG correlates of error-monitoring.

et al., 2022; Dell'Acqua, Dal Bò, et al., 2022). Decreased response to and engagement with both positive and negative stimuli and events is consistent with the emotion context insensitivity theory of depression, which suggests that depressed individuals have decreased emotional reactivity (Bylsma et al., 2008; Bylsma, 2021; Rottenberg et al., 2005). Thus, given that blunted delta is observed not only in the context of error monitoring but for other psychological processes as well, it may represent a more general effect of reduced motivation associated with depression.

We also found significant concordance of neural responses to errors in mother-daughter dyads, although only for the ERN. While there was no such significant familial concordance for power in the delta and theta bands, the associations were in the expected direction. It should be noted that our familiality analyses were limited by a small number of dyads in which both members had sufficient error trials. Nevertheless, concordance of the ERN amplitude is consistent with prior studies showing similar associations in mother-child dyads (Moser et al., 2018; Suor et al., 2022). The similarity in the neural response to errors in mothers and daughters could partially be explained by similarity in brain structures. For instance, intergenerational concordance of gray matter structure in several regions brain regions, including the anterior cingulate cortex – an important generator of the ERN – has been reported in depressed mothers and their never-depressed daughters (Minami et al., 2022). However, parenting behaviors associated with depression have also been associated with variation in the ERN in offspring (Banica et al., 2019; Brooker & Buss, 2014; Chong et al., 2020; Meyer & Wissemann, 2020), suggesting another

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pathway for familial transmission of error monitoring processes; in other words, rather than direct transmission of biological risk for atypical brain function, it may be that parents with a blunted ERN parent in a way that results in a blunted ERN in their offspring. Finally, certain psychological characteristics that have been associated with an enhanced ERN, such as perfectionism (Meyer & Wissemann, 2020) or the tendency to worry (Moser et al., 2013), can be transmitted from parents to children through observational learning (Carmo et al., 2021; Pavlova et al., 2022). Thus, the mother-daughter concordance in ERN amplitude might also reflect vicarious transmission of specific psychological traits that in turn enhance the ERN. Future longitudinal studies will be helpful in identifying specific mechanisms of intergenerational transmission of neural responses to errors.

Finally, we also assessed how the brain correlates of error monitoring in daughters were associated with their mothers' history of depression or current depression symptoms. For this set of analyses, we excluded daughters with a history or current diagnosis of MDD, given that it can be challenging when someone has already met criteria for MDD to know whether observed alterations to neural markers precede symptoms, are themselves a symptom of the disorder, or are a consequence of the disorder. In contrast to previous work (e.g., Meyer et al., 2018), we did not find an association between adolescent's ΔERN and their mother's symptoms of depression. However, mothers' depression symptoms were significantly associated with daughters' error-related delta power. Also, while error-related delta power did not significantly differ in daughters according to maternal history of recurrent MDD, we found a medium-to-large effect size ($d = .71$), suggesting that we may have lacked the necessary power to detect a difference. This also highlights the importance of examining continuous relationships between neural response to errors and depression symptoms, as it allows assessing the whole spectrum of depression severity and the dimensional nature of depression (Lahey et al., 2022). Only focusing on diagnoses overlooks the functional impairment associated with subthreshold symptoms of depression (Balázs et al., 2013; Cuijpers & Smit, 2004). Nevertheless, diagnostic measures allow to capture information about depression across the lifespan. We thus advocate for a balanced use of both diagnoses and dimensional measures. As previously noted, there seems to be a consistent association between depression symptoms and blunted delta across tasks tapping different motivational and affective processes. For instance, in addition to error processing, blunted delta in depression has been associated with other performance monitoring processes, such as reward processing (Foti et al., 2015; Jin et al., 2019; Nelson et al., 2018). We may thus see similar effects across metrics of different performance monitoring processes. However, such a phenomenon may not be specific to performance monitoring, as blunted delta during affective picture viewing has also been observed (Dell'Acqua, Brush, et al., 2022; Dell'Acqua, Dal Bò, et al., 2022), suggesting broad motivational disengagement. Blunted error-related delta in adolescent girls whose mothers have increased depression symptoms may thus constitute a risk marker for future depression, especially since blunted delta was associated with depression in their mothers, and given that blunted reward-related delta prospectively predicts depression onset in adolescents girls (Nelson et al., 2018).

The current results also raise some important questions. For example, although daughters' and mothers' error-related delta power were both associated with maternal depression symptoms, significant familial concordance of error-related neural response was only found for the ERN. While those differences may partly be attributable to a small sample size, it also raises questions about the differences in the functional significance of the ERN, delta, and theta, and how those differences affect familial transmission of the risk for depression. Previous work has shown that time-frequency decomposition of ERPs may reveal unique associations between neural measures and individual differences (Cavanagh et al., 2017). Thus, it is possible that some processes that are specifically indexed by error-related delta, such as evaluation of the motivational salience of errors (Umemoto et al., 2021), are particularly involved in the risk for developing depression. Additionally, though we only observed significant familial concordance for the ERN and not for error-related delta/theta, associations for spectral measures were in the expected direction. It is possible that the ERN receives additional contributions from neural oscillations outside the delta/theta range (Carp & Compton, 2009; Koelewijn et al., 2008; Völker et al., 2018), and that power in these frequency bands may be more concordant in mother-daughter dyads.

We must also note that although error-related delta and theta were associated with depression symptoms in mothers, we did not find such associations in daughters for any of our neural measures of response to errors. This may be related to the fact that, for these analyses, we excluded daughters who had already had a depressive episode. Though this decision was made to better explore the association between neural markers of performance monitoring and risk for depression, it may also have obscured associations between these markers and daughters' current symptoms. In this sample of adolescent girls, blunted error-related delta may also better reflect risk for future increases in depression. For instance, prior research has shown an association between a blunted ERN and increases in depression symptoms over time, without a significant cross-sectional correlation at baseline (Sandre et al., 2023). Since this study was cross-sectional, we cannot assess whether the intergenerational transmission of the neural response to errors is associated with the development of depression in adolescence. Future studies should use a longitudinal design among mother-daughter dyads to test this hypothesis. These results must also be interpreted in the light of further limitations. First, our sample only included mothers and their adolescent daughters. While internalizing disorders are more common in women and girls and thus the mother-daughter dyad is the most at risk for intergenerational transmission of depression (Connell & Goodman, 2002), our experimental design precludes assessment of the mother-son and father-child relationships. Recent research has found links between the father-child relationship and offspring internalizing symptoms (Bilodeau-Houle et al., 2020; Gregory et al., 2019), as well as paternal transmission of depression (Dachew et al., 2023), highlighting the importance of looking at dyadic relationships with both parents. Additionally, mothers committed fewer errors than daughters, resulting in more data loss in mothers and a smaller sample size in analyses that included EEG data from mothers. Future studies might explore ways to encourage participants to better balance accuracy and speed to result in sufficient error trials. However, in such tasks, participants from different experimental groups may use different strategies (e.g., Wylie et al., 2009), therefore introducing additional experimental challenges.

Despite these limitations, our results may have relevant clinical implications. Prior research has shown that targeted interventions can affect the amplitude of the ERN (Klawohn et al., 2020; Meyer et al., 2020; Nelson et al., 2017). If a blunted neural response to errors constitutes a vulnerability for depression that is transmitted

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from mother to daughter, early assessment of that response and intervention to change it may have beneficial impact in youth. Future research should assess whether increasing a previously blunted neural response to errors can protect from developing depression later in life. In sum, results from this study suggest that neural response to errors is impacted by history of recurrent depression and current depression symptoms in adult women, is transmitted in mother-daughter dyads, and, in adolescent girls, is associated with their mothers' current symptoms of depression. Future longitudinal studies will be necessary to assess whether neural responses to errors, especially delta power, can prospectively predict the onset of depression in adolescents.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0954579424001780.

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Competing interests. The authors report no conflict of interest.

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