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SHORT REPORT

Intact memory storage but impaired retrieval in visual memory in autism: New insights from an electrophysiological study

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Abstract

In a recent study on visual episodic memory (Desaunay, Clochon, et al., 2020), we have shown event-related potentials (ERPs) differences associated with priming (150–300 msec), familiarity (350–470 msec), and recollection (600–700 msec), in young people with autism spectrum disorders (ASD) compared with typical development (TD). To go further into the study of the processes of storage and retrieval of the memory trace, we re-analyzed Desaunay, Clochon, et al's data using time-frequency analysis, that is, event-related synchronization and desynchronization (ERS/ERD). This allows a decomposition of the spectral power within frequency bands associated with these ERPs. We focused both on the same time windows and the same regions of interest as previously published. We mainly identified, in ASD compared with TD, reduced ERS in low-frequencies (delta, theta) in early time-windows, and non-significant differences in ERD in higher frequencies (alpha, beta1) in all time-windows. Reduced ERS during recognition confirmed previously reported diminution of priming effects and difficulties in manipulation and retrieval of both semantic and episodic information. Conversely, preserved ERD corroborates a preservation of memory storage processes. These observations are consistent with a cognitive model of memory in ASD, that suggests difficulties in cognitive operations or executive demand at retrieval, subsequent to successful long-term storage of information.

Lay Summary

We assessed the EEG synchronization and desynchronization, during visual episodic recognition. We observed, in youth with Autism, reduced synchronization in low-frequencies (delta, theta), suggesting reduced access to and manipulation of long-term stored information. By contrast, non-significant differences in desynchronization at higher frequencies (alpha, beta frequency bands), that support long-term stored semantic and episodic information, suggested preserved memory traces.

KEYWORDS
alpha, associative memory, autism, delta, episodic memory, ERS/ERD, theta

INTRODUCTION

Visual memory in autism spectrum disorder (ASD) is characterized by a complex pattern of preserved functions and difficulties, depending on memory processes and type of stimuli (Desaunay, Briant, et al., 2020; Griffin et al., 2021). Recently, using event-related potentials (ERPs) in an associative recognition task with picture pairs, we demonstrated decreased amplitudes on the potentials indexing priming (150–300 ms) and familiarity (350–470 ms) in ASD compared with typical development (TD), suggesting that these processes are reduced in ASD. This was followed by a more widespread potential indexing recollection (600–700 ms), suggesting a compensatory increase in associative retrieval processes (Desaunay, Clochon, et al., 2020) in ASD. Visual episodic recognition typically involves low and high frequency bands (Herweg et al., 2020; Klimesch, 2012), whose EEG power is atypical in ASD (Wang et al., 2013). To assess how our results may relate to EEG power specificities in ASD, we performed here time-frequency analysis, that is, event-related synchronization and desynchronization (ERS/ERD), which allows a decomposition of the spectral power within frequency bands associated with these ERPs.

ERS/ERD correspond to the percentage increase/decrease in the EEG power during paced events, relative to the EEG power at baseline, for a specific frequency band, and provides an index of increased or decreased brain activity (Clochon et al., 1996; Pfurtscheller & Lopes Da Silva, 1999). Theta and alpha are the most commonly identified frequencies in ERS/ERD during episodic recognition in TD. Theta ERS have been associated working memory maintenance and updating mainly (Eschmann et al., 2018), and with subprocesses during priming, familiarity, and recollection, which allow access to and manipulation of stored information in episodic memory (Hsieh & Ranganath, 2014; Klimesch et al., 2010; Mitchell et al., 2008; Wynn et al., 2019). Desynchronization within alpha/beta bands has been related to long-term storage of both semantic and episodic information (the *information* via *desynchronization hypothesis*, Hanslmayr et al., 2012). During episodic retrieval, alpha/beta (notably beta1) ERD may index the reactivation of the sensory features of a memory trace (Hanslmayr et al., 2012), that is, the representation of information retrieved from episodic memories (Griffiths et al., 2019; Karlsson et al., 2020).

ERS/ERD studies in ASD have primarily identified reduced beta ERD compared with TD, following motor imitation (Buard et al., 2018; Ewen et al., 2016; Honaga et al., 2010), and during processing of emotional faces (Mennella et al., 2017). Recent investigations have also identified decreased occipital theta and gamma synchronization during photograph viewing in minimally-verbal children with ASD (Ortiz-Mantilla et al., 2019), increased temporal theta to low-gamma ERS when watching audiovisual movies in children with ASD and high-sensory profile (Matsuzaki et al., 2021), and reduced alpha ERD during attentional capture in children with ASD (Keehn et al., 2017).

Thus, in the present study, we reanalyzed EEG results from Desaunay, Clochon, et al.'s (2020) ERP study, using the ERS/ERD method on both same time windows, and same and adjacent regions of interest (ROIs) as previously identified. We focused on low (i.e., delta, theta), and high (i.e., alpha, beta1) frequency bands, hypothesizing reduced ERS/ERD in ASD. The link between visual memory and visual cognition was also investigated using the group embedded figures test (GEFT).

METHOD

The present study was conducted on data collected in Desaunay, Clochon, et al. (2020). We report briefly the methods, described in details in the previous publication, with a focus on ERS/ERD analyses. The visual associative recognition paradigm (Figure 1) was derived from a prior pilot study (Desaunay et al., 2017).

The sample consisted of 22 participants with ASD and 32 TD matched controls (see Table 1). The diagnosis of ASD was based on the DSM-5 (American Psychiatric Association, 2013) criteria, using the ADI-R (Le Couteur et al., 2003) and/or the ADOS (Lord et al., 2000) methods. All participants signed for consent, and their parents for minors. The study was conducted in accordance with international (Declaration of Helsinki, 2008) and local (CPP Nord-Ouest, ID-RCB: 2014-A00481-46) ethics procedures.

EEG signal was recorded continuously (GES 300 amplifier, EGI Hydrocel Geodesic Sensor Net, 128 Ag/AgCl dense array sensors), referenced (vertex reference Cz, ground reference CPPz), sampled (1 kHz frequency). EEG recordings were then offline re-referenced to a common average reference, segmented into stimuli-synchronized epochs, from 250 ms before (baseline) and until 1000 ms post stimulus onset. Artifacts were excluded of the analysis by visual inspection.

The quantification of ERS/ERD of "identical" and "new" pairs conditions was performed on trials associated to correct behavioral responses with a minimum of 15 artifact free trials per condition for each participant. The data were band-pass filtered at the previously selected subject specific band, then, the Hilbert transform was applied to obtain the amplitude envelope of the oscillations (Clochon et al., 1996). EEG activity was then averaged across epochs separately for each condition. Synchronizations (i.e., ERS) and desynchronizations (i.e., ERD) corresponded to respectively positive and negative percentage changes.

For EEG analyses, we conducted a series of 2 (group: ASD, TD) $\times$ 2 (condition: identical, new pairs) analyses of variance (ANOVAs) separately for each time-window and each frequency band, using a general linear model (GLM) procedure, with *post-hoc* Tukey test corrected for multiple comparisons. Groups of electrodes were averaged together resulting in 15 ROIs, with 4–8 electrodes per region (Kurikawa, Mizuseki, & Fukai, 2020; Ross et al., 2015). ERS/ERD were analyzed on the three time-windows were significant results were previously identified (Desaunay, Clochon, et al., 2020): 150–300 ms, 350–470 ms, and 600–700 ms, focusing on delta (1.5–4 Hz), theta (4–7.5 Hz), alpha (7.5–13 Hz), and beta1 (13–18.5 Hz) frequency bands.

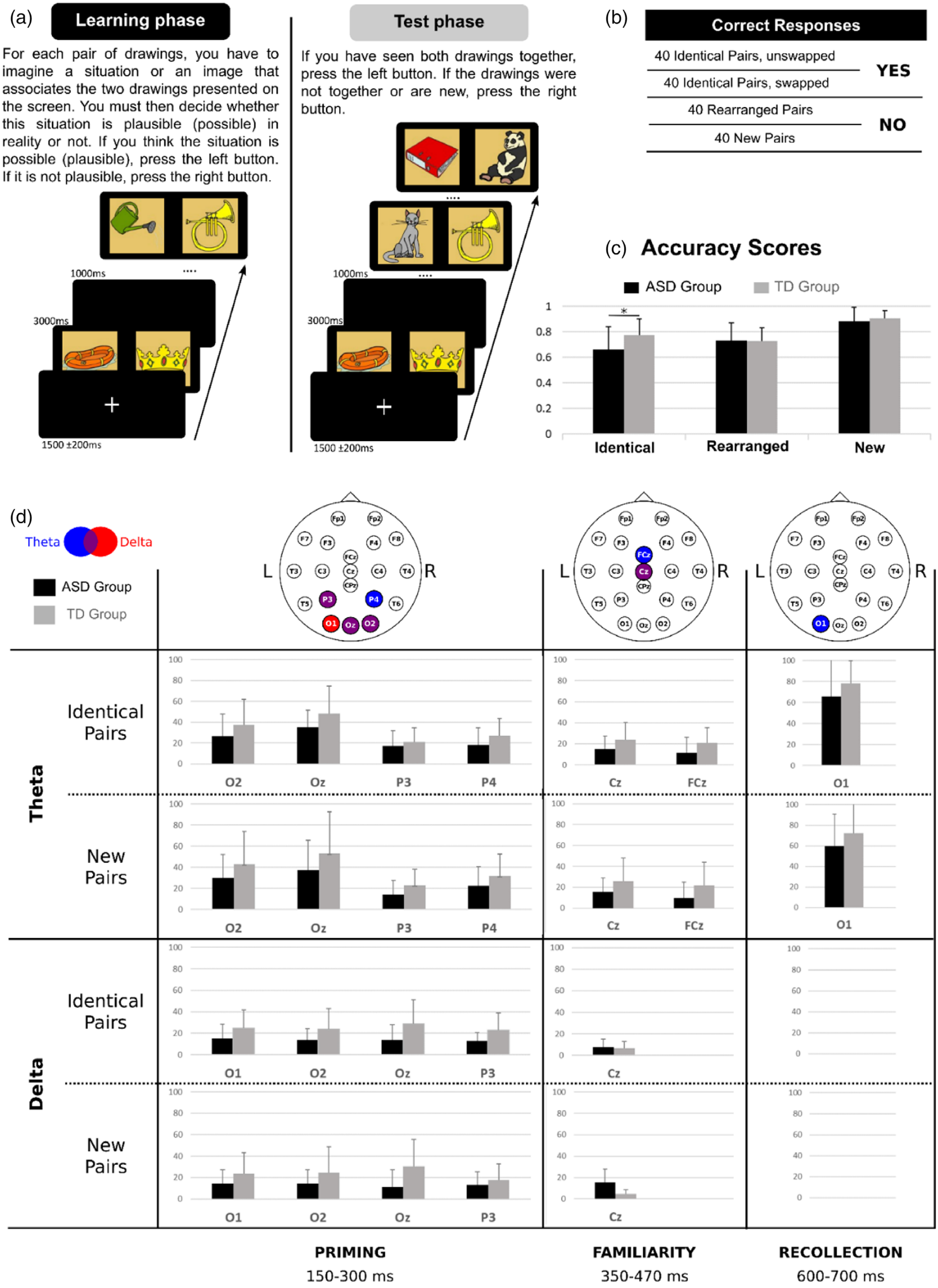

FIGURE 1 Legend on next page.

TABLE 1 Participant characteristics and independent samples *t* test

	Autism spectrum disorders group ($n = 22$, two female)		Typical development group ($n = 32$, two female)		
	Mean	SD	Mean	SD	*p* value
Age (years)	16.51 (10.4–25.75)	3.56	17.95 (12.3–25.6)	3.97	0.178
FSIQ	101.4 (72–132)	14.65	106.22 (86–134)	12.38	0.199
VCI	106.72 (69–145)	17.32	110.06 (77–143)	17.11	0.487
PRI	105.68 (72–142)	18.22	104.40 (84–130)	12.51	0.761

Abbreviations: FSIQ, full-scale intelligence quotient; PRI, perceptual reasoning index; S, standard deviation; VCI, verbal comprehension index.

To further explore visual cognition, participants performed the GEFT (Witkin et al., 1971), a timed version of the EFT. Individuals with ASD perform differently from TD participants on EFTs, in part based on their enhanced perceptual functioning (Cribb et al., 2016). Correlations with ERS/ERD were conducted using the Pearson coefficient.

We corrected for multiple comparisons by applying the false discovery rate (FDR) correction on p values (Benjamini & Yekutieli, 2001).

RESULTS

The two-way ANOVAs mainly showed group effects (Table 2). In the 150–300 ms time-window, the ASD group showed reduced delta ERS (left, middle, right occipital, left parietal ROIs) and theta ERS (middle, right occipital, bilateral parietal ROIs), relative to the TD group. In the 350–470 ms time-window, the ASD group showed reduced delta ERS (middle central ROI) and theta ERS (middle frontocentral and middle central ROIs), relative to the TD group. In the 600–700 ms time-window, the ASD group showed reduced theta ERS (left occipital ROI), relative to the TD group. *Post-hoc* Tukey tests indicated lower ERS amplitudes in participants with ASD relative to TD, except for the higher delta ERS between 350–470 ms in the middle central ROI.

We also identified a group x condition interaction in the 350–470 ms time-window for delta ERS on the middle central ROI ($F_{(1,104)} = 4.09$, $p = 0.046$, $\eta_p^2 = 0.036$), with *post-hoc* Tukey test indicating a significantly higher ERS for new pairs in participants with ASD relative to TD ($p = 0.012$).

The ASD group showed reduced GEFT performance (mean = 9.05; SD = 5.04) relative to the TD group (mean = 11.78; SD = 4.46); a one-way ANOVA ($F_{(1,52)} = 4.42$, p = 0.04, $\eta_p^2 = 0.078$) indicated that this difference was significant. Significant correlations between GEFT scores and ERS/ERD were only found in the ASD group and theta ERS between 350 and 470 ms in middle central ROI, for both new pairs, and all pairs, that is, identical and new pairs merged (Table 3).

DISCUSSION

From the visual associative recognition task, main ERS results were as follow. In ASD relative to TD participants, there was decreased delta ERS between 150 and 300 ms in occipital and left parietal ROIs; decreased theta ERS, between 150 and 300 ms in occipito-parietal ROIs, 350–470 ms in middle central and middle frontocentral ROIs, then 600–700 ms in left occipital ROI. There were non-significant differences for alpha/beta1 ERD in all time-windows. Decreased ERS in low-frequencies (delta, theta), and non-significant ERD differences in high-frequencies (alpha, beta1) may be related to electrophysiological specificities in ASD, and indicate reduced priming effect and access to and manipulation of semantic and episodic information, contrasting with a preservation of memory traces (see Figure 1).

These reduced ERS may entail two pathophysiological processes. First, resting-state EEG studies have evidenced excessive power at low (delta, theta) and high (beta, gamma) frequencies in ASD, while reduced power in the middle-range frequency band (alpha) (i.e., the "*U-shaped profile of electrophysiological power alterations*"; Wang et al., 2013). In the current analysis, this excessive power at rest may limit the increase in power required during the memory task, resulting in reduced ERS. Second, low frequency waves (<20 Hz) emerge from synchronized activity of large neural assemblies, which gate small neural assemblies oscillating at high frequencies

FIGURE 1 (a) Material and procedure. (b) Number of picture pairs per condition, and correct responses. (c) Accuracy scores per condition: Means and standard deviations for identical (pooled swapped and unswapped pairs), rearranged, and new pairs; asterisk indicates a significant difference. (d) Significant between group differences for delta and theta ERS, on their corresponding time-windows (priming, 150–300 ms; familiarity, 350–470 ms; recollection, 600–700 ms) and regions of interest (ROIs). ASD, autism spectrum disorder; Cz, middle central ROI; FCz, middle frontocentral ROI; O1, left occipital ROI; O2, right occipital ROI; Oz, middle occipital ROI; P3, left parietal ROI; P4, right parietal ROI; TD, typical development.

TABLE 2 Significant group effects (ANOVAs) on the three time-windows (150–300 ms; 350–470 ms; 600–700 ms)

Time-windows	ERS / ERD	Regions of interest	F	P	Partial eta-squared	FDR correction	Comparison
150–300 ms	Delta ERS	O1	8.35	0.005	0.074	0.013	ASD < TD
		O2	8.05	0.005	0.072	0.013	ASD < TD
		Oz	18.16	<0.001	0.148	<0.001	ASD < TD
		P3	7.86	0.006	0.069	0.013	ASD < TD
	Theta ERS	O2	5.46	0.021	0.049	0.031	ASD < TD
		Oz	4.73	0.032	0.043	0.038	ASD < TD
		P3	4.93	0.028	0.045	0.037	ASD < TD
		P4	6.47	0.012	0.058	0.023	ASD < TD
350–470 ms	Delta ERS	Cz	5.81	0.018	0.0508	0.029	ASD > TD
	Theta ERS	FCz	9.78	0.002	0.086	0.013	ASD < TD
		Cz	8.44	0.004	0.075	0.013	ASD < TD
600–700 ms	Theta ERS	O1	4.23	0.042	0.039	0.046	ASD < TD

Note: Regions of interest: O1, left occipital; O2, right occipital; Oz, middle occipital; P3, left parietal; P4, right parietal; Cz, middle central; FCz, middle frontocentral. The last column indicates the direction of the amplitude difference.

Abbreviations: ASD, participants with autism spectrum disorder; FDR, false discovery rate correction; TD, participants with typical development.

TABLE 3 Correlations between theta ERS, in 350–470 ms time-window in central (Cz) ROIs, for new pairs or all pairs, and GEFT scores

		GEFT scores				
		ASD			TD	
		r	*p*	FDR correction	*r*	*p*
Theta ERS, 350–470 ms, central ROI (Cz)	New pairs	−0.58	<0.01	0.010	−0.21	0.252
	All pairs	−0.49	<0.001	0.002	−0.13	0.305

Abbreviations: ASD, participants with autism spectrum disorder; FDR, false discovery rate correction; TD, Participants with typical development.

(>40 Hz). For low frequencies, the increase in power–and thereby the amplitude ERS change–results from the increment in synchronized firing of these large neural assemblies (Fellner & Hanslmayr, 2017). This process may be limited in ASD, due to altered coordination of cortical activity (Simon & Wallace, 2016).

These results provide new insights on memory functioning in ASD. Interestingly, there was non-significant between-group difference on alpha/beta1 ERD, notably in time-windows associated with familiarity and recollection, which are linked to the semantic and episodic memory systems respectively (Yonelinas, 2002). As alpha and beta desynchronization has been associated with the reactivation of long-term stored information (Hanslmayr et al., 2012), including semantic memories (Klimesch, 1996; Klimesch et al., 1997) and high-fidelity representation of episodic memories (Griffiths et al., 2019; Karlsson et al., 2020), this result might suggest a relative preservation of stored information in ASD. By contrast, the conjunction of early reduced theta and delta ERS (150–300 ms), in occipito-parietal ROIs, may underlie a decrease in visual attention and priming (Freunberger et al., 2007; Karakaş, 2020; Lee et al., 2020). In later time-windows, reduced theta ERS suggests weaknesses in electrophysiological processes supporting access to and manipulation of both semantic and episodic information (Düzel et al., 2003; Hsieh & Ranganath, 2014; Klimesch et al., 2010; Mitchell et al., 2008; Wynn et al., 2019). This theta ERS decrement between 600–700 ms was however limited to the left occipital ROI, which is consistent with results of associative memory fMRI studies showing similar posterior brain activity, including the hippocampus, in ASD as in TD (Cooper et al., 2017; Greimel et al., 2012; Hogeveen et al., 2020).

In addition, we observed in the ASD group only, negative correlations between theta ERS and GEFT scores, associated with diminished performance when compared with the TD group. This result may seem unexpected but the version of the test used here is a time limited EFT version that may have affected participants with autism. The negative correlations suggest that participants with ASD were more successful at the GEFT when top-down processes such as memory strategies were disengaged (Karakaş, 2020). Instead, their ability to perform the GEFT may have been more supported by bottom-up processes, e.g., enhanced perceptual processing (Cribb et al., 2016), and local visual processing bias (Bölte et al., 2007). By contrast, non-significant correlations in the TD group seem related to behavioral results showing only weak correlations between EFT performance and measures of memory (Huygelier et al., 2018).

The lack of statistical power may limit our results, as there was no condition effect in our samples; this may also be related to the general processing demands of the episodic memory system (Klimesch et al., 2001). The low EEG spatial resolution did not allow to identify precisely the generators associated with reduced ERS.

In conclusion, reduced delta/theta ERS and non-significant differences alpha/beta1 ERD indicate reduced priming effects, as well as reduced access to and manipulation of semantic and episodic information, which contrasts with a preservation of memory traces. This conclusion corroborates the cognitive model of memory in ASD formulated in Desaunay, Briant, et al.'s (2020) meta-analysis, which suggests preserved long-term stored information–supported here by alpha/beta1 ERD–but difficulties in memory tasks involving substantial cognitive operations or executive demand–indexed herein by reduced delta/theta ERS. Finally, our results confirm that the ERS/ERD method offers a promising approach, complementary to the use of ERPs, to explore cognition in ASD.

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CONFLICT OF INTEREST

There are no conflicts of interest for any of the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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