

Neural reinstatement of context memory in adults with autism spectrum disorder

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Autism spectrum disorder (ASD) is associated with episodic memory impairment. However, episodic memories include a variety of contextual details, and it is difficult to solely rely on behavioral data to assess how specifically (i.e. event-specific reinstatement) an event is remembered. We applied encoding-retrieval representational similarity (ERS) analysis to EEG data to assess event-specific ERS for object-context associations in a sample of 34 adults (17 with, 17 without ASD). Participants studied objects presented alongside 2 contextual features: scene/color, and attention was directed toward one object-context relationship. At retrieval, memory was assessed for the object and both contexts. Behavioral results revealed no group differences in item or context memory performance. ERS results revealed group temporal differences in reinstatement. Results may indicate differences in both encoding (i.e. fewer perceptual details) and retrieval (i.e. ineffectively skipping through memory fragments) in ASD and should be further investigated in studies modulating the perceptual detail required for memory decisions. Results highlight the utility of ERS as a methodology used to evaluate episodic reinstatement even in the absence of behavioral differences in memory performance.

Key words: autism spectrum disorder; episodic memory; EEG; encoding-retrieval similarity; representational similarity.

Introduction

Autism spectrum disorder (ASD) is considered one of the most common neurodevelopmental disorders (see [Salari et al. 2022](#) for review), characterized by socio-communicative deficits and restrictive, repetitive behavioral patterns ([American Psychiatric Association 2013](#)). Though typically diagnosed in childhood ([van 't Hof et al. 2021](#)), ASD is a lifelong disorder with increasingly poor quality of life outcomes in adulthood (see [Mason et al. 2021](#) for meta-analysis). As the population of adults with autism is aging, more ASD research assesses studies of the adult lifespan ([Dietz et al. 2020](#); [Wise 2020](#)).

The memory profile associated with ASD ([Desaunay et al. 2020](#); [Griffin et al. 2021](#)) includes specific impairment in episodic memory. Episodic memory involves encoding a variety of contextual details to distinguish events from one another. Episodic memory in ASD is typically characterized by intact recognition or familiarity-based judgments and impaired recollection (see [Cooper and Simons 2019](#) for review). For example, many studies utilizing Remember/Know paradigm have shown that individuals with ASD often indicate they “know” an item but struggle to “remember” specific contextual details ([Bowler et al. 2000, 2007](#); [Tanweer et al. 2010](#); [Cooper et al. 2015](#); [Gaigg et al. 2015](#)).

Emerging evidence from neurotypical populations suggests that providing orienting instructions that explicitly direct attention to task-relevant associations (e.g. “is this scene (context) a likely location for this object (item)?”), rather than item-only or non-contextual details, can improve both younger and older adults’ context memory performance ([Naveh-Benjamin et al.](#)

[2007](#); [Glisky and Kong 2008](#); [Dulas and Duarte 2013, 2014](#)). These instructions may strengthen item-context associations during encoding ([Uncapher et al. 2006](#)) and/or reduce executive function demands during retrieval ([Cohn et al. 2008](#)). However, our daily environment is highly complex and when deciding what to attend to and remember we must also decide what to tune out. Inhibitory control deficits associated with ASD ([Geurts et al. 2014](#); [Schmitt et al. 2018](#)) would undermine the ability to tune out irrelevant details, resulting in diminished context memory accuracy.

We recently investigated the role of selective attention on behavioral context memory performance in adults with and without ASD ([Justus et al. 2021](#)). We explicitly directed attention to the relationship between a to-be-remembered item and one of 2 simultaneously presented contexts (i.e. item-scene or item-color) during encoding. Participants were instructed to direct their attention to one context (i.e. attended) while ignoring the other (i.e. unattended). At retrieval, memory was assessed for both the attended and unattended contexts. Behavioral results revealed no significant impairment in context memory performance in adults with ASD compared with NT adults. These results were surprising given the existent literature on episodic memory deficits in ASD. However, we suggest that supportive task procedures at both encoding (i.e. orienting instructions) and retrieval (i.e. recognition judgment of re-presented item-context pairs) may have attenuated behavioral differences in performance. A similar explanation was offered in a recent neuroimaging study ([Hogeveen et al. 2020](#)) comparing ASD and NT adults in relational memory performance

using a task with supportive encoding procedures (Ragland et al. 2012).

With behavioral data alone, it is difficult to know how specifically an event is remembered. That is, while our prior behavioral results indicated that NT and ASD adults show similar context memory accuracy, they do not necessarily indicate similar memory specificity (i.e. event-specific reinstatement) across groups. Neurobiological memory models theorize that reinstatement of encoding-related neural activity supports successful episodic memory retrieval (Norman and O'Reilly 2003). fMRI studies support this reinstatement idea showing stronger correlations between activity within particular cortical regions between encoding and retrieval for successful than unsuccessful memory trials (Ritchey et al. 2013; Gordon et al. 2014). More recent studies have used this encoding-retrieval similarity (ERS) approach to show that neural reinstatement of event-specific activity, above and beyond category- or task-related activity, supports episodic memory success (Wing et al. 2015; Danker et al. 2016; Trelle et al. 2020). EEG and MEG have similarly been used to show episodic reinstatement effects (Jafarpour et al. 2014; Lu et al. 2015; Sommer et al. 2019; Hokett et al. 2022; Lee et al. 2022). By quantifying the strength of trial-specific reinstatement, ERS is optimally suited for studying memory specificity. While research is lacking on episodic memory reinstatement in ASD populations, a few studies have suggested reductions as evidenced by ASD adults' reduced ERS of eye fixations (i.e. proportion of eye movements at retrieval directed toward areas previously attended to during encoding) during successful recollection (Cooper et al. 2017) and reduced specificity of autobiographical memory details (Crane et al. 2012).

In the current study, we measured oscillatory EEG during encoding and retrieval to assess event-specific ERS for object-context associations in NT and ASD adults. If less specific perceptual and/or conceptual details underlie context memory performance in ASD compared with NT adults, we predict reduced event-specific ERS patterns in ASD. EEG allowed us to assess the temporal dynamics of ERS and group differences therein. For example, early (<500 ms) encoding-related activity linked to early perceptual or semantic categorization processes could be reinstated later during retrieval (>500 ms) in which products of reinstatement may be subject to continued monitoring to make context memory decisions (Jafarpour et al. 2014; Lee et al. 2022). Existing studies would predict dysfunction in such cognitive control processes in ASD (see Demetriou et al. 2018 for meta-analysis).

Materials and methods

Participants

ASD participants included a subset from a previous study (Justus et al. 2021) who had quality EEG data. We first removed one participant who did not have EEG data at both encoding and retrieval. After preprocessing (described below), one additional participant was rejected. Finally, 4 additional participants were removed for not having enough context correct or incorrect EEG trials (2+) at both encoding and retrieval. NT participants included a subsample who had participated in one or more of our prior studies (James et al. 2016; Strunk et al. 2017; Powell et al. 2018; Justus et al. 2021; Mirjalili et al. 2022) who were matched to the ASD participants based on age, gender, and education. The final sample in this study included 17 ASD (ages 19–58, $M = 28 \pm 11.97$) and 17 NT (ages 18–57, $M = 27.12 \pm 12.65$) adults. All participants were native English speakers, right-handed, with

normal or corrected-to-normal vision. Participants were recruited from the Georgia Institute of Technology psychology research participant pool and the surrounding community through subway advertisements, word of mouth, and referrals from local programs serving adults with ASD. Participants were compensated with either \$10/h or course credit. Participants completed informed consent forms approved by the Georgia Institute of Technology IRB prior to participation. No participants reported psychiatric disorders, neurological disorders, vascular disease, or use of psychoactive medications. Participants completed a standardized neuropsychological battery including immediate and delayed recall subtests from the Memory Assessment Scale (Williams et al. 1991), letter fluency, trails A and B subtests of the Halsted-Reitan Neuropsychological Test Battery (Reitan and Wolfson 1985), Module 4 from the Autism Diagnostic Observation Schedule-2 (ADOS-2; Lord et al. 2012) was used to confirm ASD diagnosis using the following inclusion criteria: (i) prior diagnosis of ASD and (ii) met the ADOS-2 diagnostic cutoff score (>7) and Social Responsiveness Scale-2 (SRS-2; Constantino and Gruber 2012) diagnostic cutoff (>60). Demographics and neuropsychological test scores are summarized in Table 1.

Materials and design

Each trial featured a single, nameable object (e.g. chair) centrally presented on a white background with 1 of 3 possible colored squares (brown, green, or red) and 1 of 3 possible scenes (cityscape, island, or studio apartment) on either side of the object. During encoding, participants were presented with 288 images. During retrieval, the 288 previously presented objects (i.e. "old trials") were presented along with 144 new objects that had not been previously studied. New objects were presented alongside the same possible color and scene contexts used during encoding.

Procedure

Figure 1 depicts encoding and retrieval structure and timing. During encoding, participants were instructed to make subjective judgments about the relationship of the object and one context per trial. For item-color association trials, participants were asked "is this color likely for the object?" For item-scene association trials, participants were asked "is this object likely to appear in this scene?" Participants responded to these orienting prompts with one of 2 key presses (Yes/No). Participants completed 288 trials, split across 4 blocks. Each of 4 encoding blocks was divided into 4 mini blocks, each containing 18 trials of each orienting task (i.e. color or scene).

During retrieval, participants were presented with old and new item-context pairs. Like encoding, each trial included a single object flanked on opposing sides (left/right) by a colored square and scene. Old trials include equal numbers of trials in which (i) both color and scene matching encoding, (ii) only color matching, (iii) only scene matching, and (iv) neither color nor scene matching. Color and scene contexts were always located on the same side of the object as during encoding. Participants completed 432 trials, split across 4 blocks. Each block included 108 randomized trials (72 old, 36 new). Participants made a series of key press responses, first indicating whether the object shown was "old" or "new." If "new" was selected, the next trial began after a 2,000 ms delay. If "old" was selected, participants made 2 additional context memory judgments. These context judgments also included judgments of confidence—participants responded with one of 4 key presses ranging from 1 (*certain match*) to 4 (*certain mismatch*). Counterbalancing ensured the order of which context judgment

Table 1. Participant demographics.

Measure	ASD (12 M/5F) ^a			TD (12 M/5F) ^a		
	M	SD	Range	M	SD	Range
Age ^a	28.00	11.97	19–58	27.18	12.65	18–57
Education ^a	14.93	1.67	12–18	14.81	1.76	12–18
Letter fluency	13.47	4.53	4.33–20.67	14.69	4.44	9.33–26.67
List recall (immediate)	9.53	2.58	2–12	10.00	1.27	7–12
List recall (delayed)	10.19	1.87	5–12	11.00	1.51	7–12
Trails A (in s)	31.71	17.34	14.32–77.17	24.14	7.81	13.00–45.97
Trails B (in s)	68.90 ^b	25.17	26.67–110.78	48.23 ^b	16.96	25.78–80.00
ADOS-2 module 4 ^c						
Communication	4.00	1.12	2–6	—	—	—
Reciprocal social interaction	8.24	1.95	5–11	—	—	—
Combined total	12.24	2.68	8–16	—	—	—
SRS-2 (T-score) ^d						
Social awareness	58.12	7.46	44–72	—	—	—
Social cognition	64.29	8.99	48–81	—	—	—
Social communication	67.29	8.48	52–86	—	—	—
Social motivation	64.59	10.54	42–79	—	—	—
Restricted interests behavior	68.88	8.71	57–85	—	—	—
Combined total	67.06	8.22	60–85	—	—	—

Note. ^aindicates variables used for matching. ^bindicates significant group difference ($P < 0.05$). ^cAutism Diagnostic Observation Schedule-2 (ADOS-2), module 4. ^dSocial Responsiveness Scale-2, adult form self-report (SRS-2).

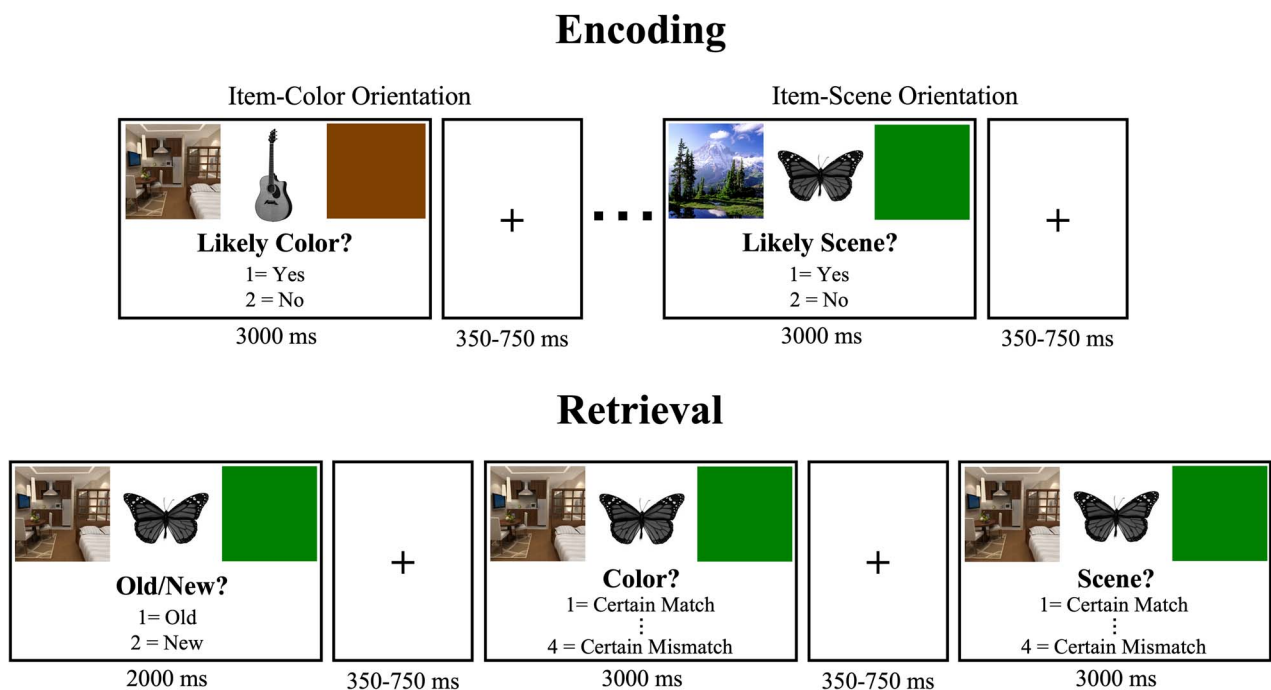


Fig. 1. Description of the task design and trial timing. Stimuli included 432 grayscale images of objects from the Hemera technologies photo-object DVDs and Google images. Color/scene contexts were counterbalanced so that they appeared equal times on the right and left sides of the object. Object and context images spanned a maximum horizontal and vertical visual angle of $\sim 3^\circ$. Attention was directed to the item-color and item-scene association equal number of times. Old/new status for objects was also counterbalanced across participants. The task featured 4 encoding blocks of 72 trials per block (288 total encoding trials) and 4 retrieval blocks of 108 trials per block (432 total retrieval trials). All 4 encoding blocks were completed followed by all 4 of the retrieval blocks. Participants were given both verbal and written instructions and completed practice blocks before beginning the encoding and retrieval task until understanding of each task was demonstrated (~ 5 min). Participants were offered the opportunity to take brief breaks in between each block. The start time of each block was used to evaluate average block time (i.e. task + break time) and found no group differences, $t(32) = 1.45$, $P = 0.16$, Cohen's $d = 0.49$.

was prompted first (item-color match, item-scene match) across participants.

Behavioral analysis

Statistical analyses were performed using JASP and SPSS (IBM Corp 2021; JASP Team 2022). Relationships between

neuropsychological tests and task performance were explored using correlation analyses. We collapsed across context type (color and scene) and confidence for all analyses as we found no context type or confidence effect in prior analyses (Justus et al. 2021). Only 4 participants total (2 per group) was older than age 50 years and therefore we did not perform specific analyses

of age. However, we did control for age as a covariate given the wide age range. Item recognition accuracy was estimated using d' prime discrimination index. Context memory accuracy was also computed as d' prime for attended and unattended context features separately: i.e. $d' = z$ (proportion of “match” responses to contexts that matched those presented at encoding) $- z$ (proportion of “match” responses to contexts that mismatched those shown at encoding). ANCOVAs were utilized to explore differences in memory performance within and between groups while controlling for age. Bayes factors (null/alternative; BF01; Lee and Wagenmakers 2014) were computed when nonsignificant main effects or interactions with Group (TD vs. ASD) were observed, where < 0.33 or > 3 is considered noteworthy.

EEG acquisition and preprocessing

Continuous scalp-recorded EEG data were collected during encoding and retrieval using 32 Ag-AgCl electrodes with an ActiveTwo amplifier system (Biosemi, Amsterdam, the Netherlands). Electrodes were positioned based on the extended 10–20 system (Nuwer et al. 1998). Electrodes were placed at midline locations (Fz, Cz, Pz, and Oz) and left/right hemisphere locations (FP1/FP2, AF3/AF4, F3/F4, F7/F8, FC1/FC2, FC5/FC6, C3/C4, T7/T8, CP1/CP2, CP5/CP6, P3/P4, P7/P8, PO3/PO4, and O1/O2). Electrodes on left and right mastoids were placed for offline referencing. Four additional electrodes (i.e. above and below right eye and one on outer canthus of each eye) were placed to monitor vertical (VEOG) and horizontal (HEOG) electrooculogram. The EEG sampling rate was 512 Hz with 24-bit resolution. Offline preprocessing was performed using EEGLAB (Delorme and Makeig 2004), ERPLAB (Lopez-Calderon and Luck 2014), and FIELDTRIP (Oostenveld et al. 2011). First, continuous data were down-sampled to 256 Hz and re-referenced to the average of the left and right mastoid electrodes. Data were then band-pass filtered between 0.5 and 100 Hz, and 60 Hz line noise was removed using EEGLAB PREP plugin (Bigdely-Shamlo et al. 2015). Continuous EEG data were then epoched into time windows from $-1,000$ ms before to $3,000$ ms after the onset of the first retrieval question (i.e. old/new judgment). Each epoch was baseline corrected using the 200 ms prior to object onset for both encoding and retrieval. Artifacts were removed by first removing non-ocular artifacts (e.g. large drift, electrode spikes, and saturation). Independent component analysis was then used to remove additional ocular artifacts from remaining epochs (Delorme and Makeig 2004). Epochs containing uncorrected artifacts (± 150 mV) were removed.

Before wavelet decomposition and RSA analyses, each subject's data were represented using an $n \times 32 \times 1024$ matrix, with n being the number of trials and every trial consisted of band-pass filtered EEG signal at 32 electrodes and 1,024 time-bins (i.e. the sampling rate of 256 Hz over each 4-s trial). Subsequently, each epoch was converted into a time-frequency representation using Morlet wavelets (Percival and Walden 1993) with 78 linearly spaced frequencies from 3 to 80 Hz, then downsampled from 256 to 50 Hz. Throughout wavelet transformation, each epoch was decreased to the time range of interest (i.e. 0–2,000 ms after onset). Thus, the data dimension changed to $n(\text{trials}) \times 32(\text{electrodes}) \times 78(\text{frequencies}) \times 100$ power values for 100 20 ms time bins (i.e. the sampling rate of 50 Hz over 2 s). We focused this study on power values in the 3–40 Hz range as prior scalp EEG studies (Hanslmayr et al. 2016), including those from our lab, have shown memory-related neural activity within this frequency range. High frequency gamma activity was not assessed given difficulty separating cortical gamma from that induced by microsaccades (Yuval-Greenberg and Deouell 2009).

We divided the electrodes into 4, nonoverlapping electrode regions (see Fig. 2) and averaged over the electrodes within each electrode region. We analyzed EEG data across electrodes within 4 quadrants of the scalp in order to reduce the number of analyses while also preserving some spatial differences in effects of interest, should they exist. Preliminary analyses using smaller numbers of electrode clusters yielded similar patterns of results. In order to simplify the findings and the associated interpretations, we present results from the 4 electrode regions. We divided the wavelet transforms into 18,300 ms time windows where each consecutive time windows overlapped by 100 ms. A summary of these steps can be found in Fig. 2.

Representational similarity analysis

We averaged power within each 300 ms time window separately for every frequency value (in 1 Hz increments) from 3 to 40 Hz for each electrode separately. We log-transformed the averaged power values to make a vector of power values for each time window and electrode. Subsequently, we averaged each 300 ms window power signal vector within each individual electrode across the electrodes within a region (e.g. left frontal; see Materials and Design). Consequently, for each of the 18 300 ms time windows and 4 electrode regions, the associated “representational pattern” is a vector of 38 (i.e. 3–40 Hz) log-transformed average power values. In the next step, for each electrode region and 300 ms time window, we evaluated the extent of similarity between the frequency vectors for a particular encoding trial and the frequency vectors for a particular retrieval trial. We computed the Pearson correlation between every frequency vector for every 300 ms time window from the encoding period with the corresponding frequency vector for every 300 ms time window from the retrieval period (indicated in Fig. 2). We calculated the correlation of EEG signals' oscillatory power between the encoding and retrieval of a particular trial type for a specific electrode region and time window. This approach has been used in prior EEG studies (Yaffe et al. 2014; Staresina et al. 2016; Sommer et al. 2019).

For each subject, we calculated within-event similarity and between-event similarity for 4 context memory conditions: hits (i.e. correctly identifying a matched attended context as a match), misses (i.e. incorrectly identifying a matched attended context as a mismatch), correct rejections (i.e. correctly identifying a mismatched attended context as a mismatch), and false alarms (i.e. incorrectly identifying a mismatched attended context as a match). Match and mismatch trials were defined according to the context that was attended to during encoding (collapsed across scene and color contexts). In other words, a match trial hit is one in which the previously attended context (e.g. red square) is shown again during retrieval and for which an individual correctly states “match,” regardless of whether the scene context matched between study and test. Similarly, a mismatch trial correct rejection is one in which the previously attended context (e.g. cityscape) is replaced with a different within-category context (e.g. beach) and an individual correctly states “mismatch,” regardless of whether the color context matched between study and test. Given that unattended context performance was at chance for both groups, we collapsed across unattended contexts for these analyses. Within-event similarity was calculated as explained above for a trial at retrieval and the associated matching trial at encoding (i.e. same object). Between-event similarity was calculated for a trial at retrieval and all the trials at encoding of the same category (i.e. hit and miss).

Importantly, the number of hits, misses, correct rejections, and false alarms was not equal for the participants. To ensure the

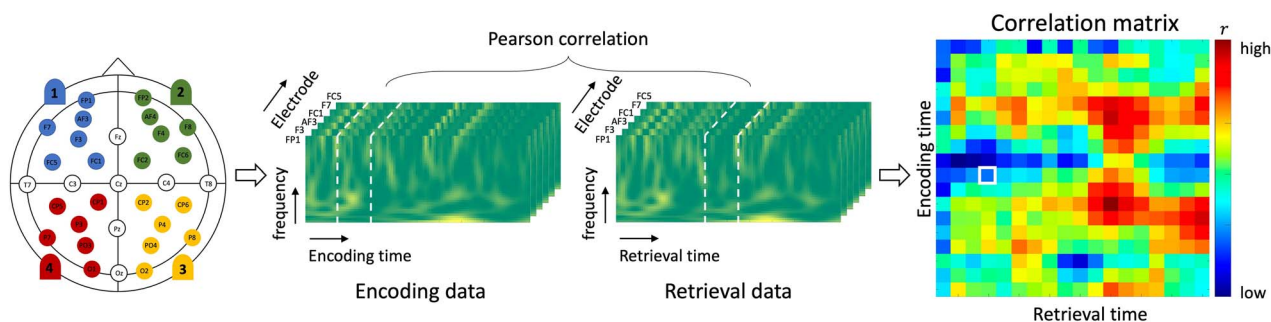


Fig. 2. Description of the methodology used for representational similarity analyses. We averaged power within each 300 ms time window separately for each frequency for each electrode separately. Subsequently, we averaged each 300 ms window log-transformed power signal averages within an individual electrode across the electrodes within an electrode region to form a vector of 38 (i.e. 3–40 Hz) log-transformed average power values for each electrode. We then averaged these vectors of 38 (i.e. 3–40 Hz) log-transformed average power values across the electrodes within an electrode region to end up with an averaged vector of 38 (i.e. 3–40 Hz) log-transformed average power values for each electrode region. These vectors are known as representational patterns. In this figure, the time window 300–600 ms from encoding (the left pattern) and 800–1,100 ms from retrieval (the right pattern) for the left frontal electrode region is chosen and shown with dashed white lines. The associated representational patterns will be correlated using Pearson correlation as the related correlation coefficient is shown with the white square on the correlation matrix. We repeat the same process to correlate the representational patterns for all time intervals during encoding and the representational patterns for all time intervals during retrieval leading to the correlation matrix. Note that a similar approach is used for other electrode regions as well, but we have not shown them here (more details can be found in [Supplementary Method](#)).

analyses do not have an imbalance (e.g. having different signal to noise ratios when averaging across similarity matrices of trials of different conditions), we artificially generated trials using the synthetic minority oversampling technique (SMOTE) so that all conditions have an equal number of trials ([Chawla et al. 2002](#); [Mirjalili et al. 2022](#)) for each participant. As a control analysis, we repeated the analyses without SMOTE and the results were generally similar to the presented results.

Next, we deduced between-event similarity matrices from within-event similarity matrices for every trial. We averaged the obtained event-specific, time–time similarity matrices across trials with the same trial type for each participant, resulting in average event-specific, time–time similarity matrices for every electrode region and trial type. We deduced average event-specific miss similarity from average event-specific hit similarity [i.e. (within-hit – between-hit) – (within-miss – between-miss)] and average event-specific false alarm similarity from average event-specific correct rejection similarity [i.e. (within-correct rejection – between-correct rejection) – (within-false alarm – between-false alarm)].

Deriving group difference clusters

We compared memory-related neural similarity of different time windows during encoding and retrieval for subjects with ASD and neurotypical subjects. The details are presented in the [Supplementary Material](#).

Results

Behavioral results

Demographics and neuropsychological test results are shown in [Table 1](#). Adults with ASD exhibited significantly lower performance than NT adults on Trails B [$t(31) = 2.75$, $P = 0.01$, Cohen's $d = 0.96$, equal variances not assumed as Levene's test were significant]. There were no other significant group differences (t 's < 1.59, P 's > 0.12, Cohen's d 's < 0.56).

Item and context memory performance values are presented in [Table 2](#). Both groups showed above chance (0) performance for item recognition, [$t(16)$'s > 7.31, P 's < 0.001, Cohen's d 's > 1.77], which did not differ between groups, [$t(23.4) = 1.58$, $P = 0.064$,

Cohen's $d = 0.54$, equal variances not assumed as Levene's test were significant]. Bayes factor analyses support weak evidence in favor of an absence of a Group effect ($BF_{01} = 0.73$). Both groups showed above chance (0) memory performance for attended [$t(16)$'s > 5.14, P 's < 0.001, Cohen's d 's > 1.25] and unattended contexts [$t(16)$'s > 2.24, P 's < 0.02, Cohen's d 's > 0.54]. A Context (Attended, Unattended) \times Group (NT, ASD) ANOVA revealed a main effect of Context [$F(1, 32) = 62.53$, $P < 0.001$, $\eta^2_p = 0.66$] but no effect of Group [$F(1, 32) = 2.09$, $P = 0.157$, $\eta^2_p = 0.06$] or Context \times Group interaction [$F(1, 32) = 4.09$, $P = 0.052$, $\eta^2_p = 0.11$]. This suggests that the attention manipulation during encoding (i.e. orienting instructions) was effective in enhancing context memory accuracy for the attended context for both groups. There is moderate evidence for the absence of a main effect of Group ($BF_{01} = 8.92$) and weak evidence for the absence of a Group \times Context interaction ($BF_{01} = 0.72$). This pattern of effects remained significant after controlling for age [ANCOVA effects: Context [$F(1, 31) = 24.11$, $P < 0.001$, $\eta^2_p = 0.44$], Group, [$F(1, 31) = 2.05$, $P = 0.162$, $\eta^2_p = 0.06$], Context \times Group [$F(1, 31) = 4.12$, $P = 0.051$, $\eta^2_p = 0.12$].

The information regarding the response time and the number of trials that ended up in each memory condition is shown in [Table 3](#). We did not find any significant differences between the response times of the 2 groups for any of the memory conditions (all t 's < 1.43, all P 's > 0.088).

EEG results

Match attended context trials

We computed spatiotemporal clusters reflecting event-specific ERS sensitive to context memory accuracy (context hit – context miss) that differed between ASD and NT groups. The results for matches are shown in [Fig. 3](#). [Figure 3a](#) shows the time intervals in which the memory-related ERS for attended context match trials significantly differed between groups. Bar plots showing the magnitude of the effects are seen in [Fig. 3b](#). For the largest significant cluster within each electrode region (which is selected based on the number of encoding–retrieval time intervals included in the cluster and is marked with an X), the associated electrode region, time intervals, t -statistic, and P -value are presented in [Table 4](#). The details for all clusters are shown in [Supplementary Table 1](#).

Table 2. Hit rate, false alarm rate, and discriminability (d') for item and context memory.

Measure	Hit rate	False alarm rate	d'
Item recognition			
NT	0.75 (0.15); range 0.49–0.96	0.05 (0.03); range 0.02–0.16	2.40 (0.54); range 1.57–3.31
ASD	0.73 (0.18); range 0.40–0.97	0.17 (0.24); range 0.02–0.94	1.94 (1.09); range 0.22–3.93
Attended context			
NT	0.78 (0.13); range 0.45–0.91	0.35 (0.11); range 0.08–0.49	1.23 (0.65); range 0.16–2.68
ASD	0.69 (0.19); range 0.31–0.96	0.40 (0.12); range 0.22–0.65	0.83 (0.66); range –0.24 to 1.94
Unattended context			
NT	0.53 (0.11); range 0.28–0.75	0.50 (0.10); range 0.30–0.70	0.09 (0.16); range –0.19 to 0.46
ASD	0.52 (0.17); range 0.25–0.88	0.46 (0.16); range 0.18–0.84	0.15 (0.18); range –0.08 to 0.56

Note. Mean (SD).

Table 3. Hit rate, false alarm rate, and discriminability (d') for item and context memory.

Measure	Hit	Miss	Correct rejection	False alarm
Response time				
NT	1.22 (0.18); range 0.97–1.63	1.22 (0.19); range 0.74–1.61	1.20 (0.20); range 0.76–1.54	1.25 (0.18); range 0.99–1.63
ASD	1.26 (0.27); range 1.04–1.92	1.31 (0.31); range 0.95–1.86	1.29 (0.27); range 0.90–1.93	1.33 (0.37); range 0.87–2.41
Number of trials				
NT	46 (25.0); range 10–94	25 (16.5); range 4–55	28 (10.6); range 13–47	44 (29.5); range 7–103
ASD	32 (21.9); range 5–91	22 (16.6); range 6–62	21 (14.7); range 5–52	34 (27.4); range 4–102

Note. Mean (SD).

Table 4. The associated electrode regions, time intervals (at encoding and retrieval), t-statistics, and P-values for clusters in which the memory-related ERS for context match trials significantly differed between groups. Here, we have only shown the details for the biggest cluster in each electrode region. The details for all clusters are available in the [Supplementary Material](#).

	Region	Encoding interval (ms)	Retrieval interval (ms)	t-statistic	P-value
NT > ASD					
	Left frontal	100–400	900–1,300	2.825	0.006
	Left posterior	900–1,400	700–1,600	2.119	0.025
	Right posterior	900–1,300	1,300–1,700	2.526	0.011
	Right frontal	1,100–1,600	400–1,000	2.571	0.010
ASD > NT					
	Left frontal	1,200–1,500	400–700	2.032	0.030
	Left posterior	1,500–2,000	1,600–1,900	1.754	0.049
	Right posterior	100–600	700–1,300	1.954	0.034
	Right frontal	700–1000	300–600	2.136	0.024

Generally, the clusters showed that the memory-related ERS between later encoding periods and earlier during retrieval is the highest. However, for subjects with ASD, the memory-related ERS between later encoding periods is highest with later retrieval periods compared with the ones for NT adults. Two of the clusters in [Fig. 3a](#) are highlighted as examples to show this delayed effect in ASD. The details of the associated temporal analyses and results are shown in the [Supplementary Material](#).

Moreover, we identified spatiotemporal clusters reflecting event-specific ERS sensitive to context memory accuracy (context hit – context miss) that were similar between ASD and NT groups. The details for these results are shown in the [Supplementary Material](#).

Mismatch attended context trials

We computed spatiotemporal clusters reflecting event-specific ERS sensitive to context memory accuracy that differed between ASD and NT groups. The results for mismatches are shown in [Fig. 4](#). [Figure 4a](#) shows the time intervals in which the memory-related ERS for context mismatch trials significantly differ between groups. Bar plots showing the magnitude of the effects are seen [Fig. 4b](#). Moreover, for the largest significant

cluster within each electrode region (marked with an X), the associated electrode region, time intervals, t-statistic, and P-value are presented in [Table 5](#). The details for all clusters are shown in [Supplementary Table 2](#). Generally, the clusters showed the memory-related ERS between earlier encoding periods and later during retrieval is the highest. However, for subjects with ASD, the memory-related ERS between earlier encoding periods is highest with earlier retrieval periods compared with the ones for NT adults. Two of the clusters in [Fig. 4a](#) are highlighted as examples. The details of the associated temporal analyses and results are shown in the [Supplementary Material](#).

Moreover, we identified spatiotemporal clusters reflecting event-specific ERS sensitive to context memory accuracy (context correct rejection – context false alarm) that were similar between ASD and NT groups. The details for these results are shown in the [Supplementary Material](#).

Discussion

The goal of the present study was to test the hypothesis that, despite comparable context memory performance as indicated by behavioral indices, underlying neural activity may reveal

Differential group effects in differential memory-related Event-specific ERS for matching context trials

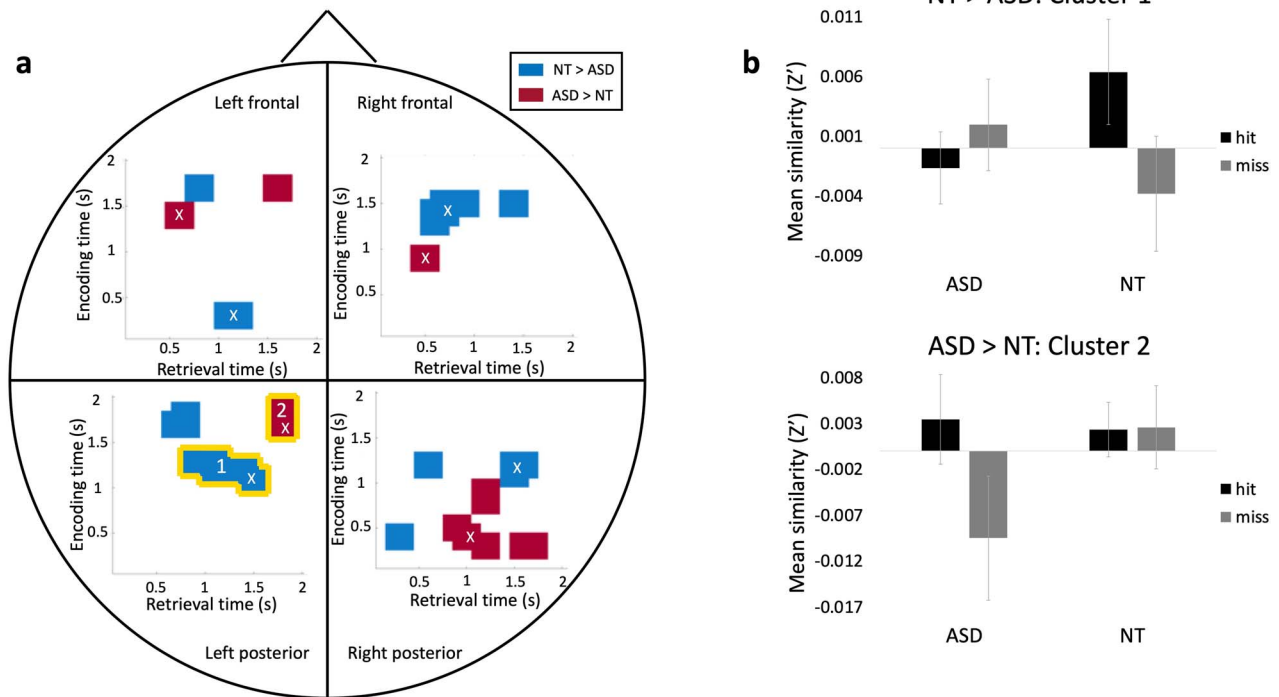


Fig. 3. a) The time intervals in which the memory-related ERS for matches is significantly greater for neurotypical subjects compared with subjects with ASD (blue), whereas the ERS for hits is significantly greater than ERS for misses for neurotypical subjects; and the time intervals in which the memory-related ERS is significantly greater for subjects with ASD compared with neurotypical subjects (red), whereas the ERS for hits is significantly greater than ERS for misses for ASD subjects b) the breakdown of memory-related neural similarity into average event-specific similarity for hits and average event-specific similarity for misses (with the associated 95% confidence intervals) for 2 of the clusters shown in part a). These 2 clusters are chosen as examples, and the pattern was similar for the other clusters.

Table 5. The associated electrode regions, time intervals (at encoding and retrieval), t-statistics, and P-values for clusters in which the memory-related ERS for context mismatch trials significantly differed between groups. Here, we have only shown the details for the biggest cluster in each electrode region. The details for all clusters are available in the [Supplementary Material](#).

	Region	Encoding interval (ms)	Retrieval interval (ms)	t-statistic	P-value
NT > ASD	Left frontal	400–1,000	1,300–2,000	2.441	0.013
	Left posterior	1,100–1,500	1,300–1,800	4.429	< 0.001
	Right posterior	800–1,200	1,000–1,400	2.704	0.008
ASD > NT	Left frontal	1,500–1,900	300–1,100	2.050	0.029
	Left posterior	1,400–1,800	600–900	1.989	0.032
	Right posterior	1,100–1,400	200–500	2.321	0.017
	Right frontal	1,400–1,700	300–600	2.426	0.014

reduced event-specific reactivation of encoding-related neural activity during retrieval in ASD compared with NT adults. Event-specific ERS is a correlate of episodic reinstatement of event-specific features [e.g. specific perceptual (blue) or semantic features (indoor and kitchen) of the associated context, and/or decision processes supporting memory] that is related to memory accuracy. Reinstatement Behavioral data alone do not allow for this understanding of the quality of memory representations. Adults with and without ASD exhibited similar item- and context-memory performance. The null behavioral results were somewhat surprising given that studies tend to find impairments in episodic memory in ASD (see [Desaunay et al. 2020](#); [Griffin et al. 2021](#) for meta-analyses). ERS results were not consistent with generally reduced episodic reinstatement in ASD as predicted. However,

underlying group differences in ERS suggest qualitative and quantitative differences in event-specific, above and beyond general categorical (i.e. scene vs. color) reinstatement of encoding related neural activity during retrieval in ASD compared with NT. These results and their implications are discussed below.

The lack of group behavioral differences in our study aligns with [Bowler et al.'s \(2004\)](#) Task Support Hypothesis proposing that memory deficits in ASD will be attenuated on any task including supportive encoding and/or retrieval procedures. The present task featured orienting instructions at encoding, which could have attenuated behavioral differences between groups. A similar explanation was offered in [Hogeveen et al. \(2020\)](#). Executive dysfunction accounts (e.g. [Hill 2004](#)) suggest that ASD is characterized by a variety of cognitive

Differential group effects in differential memory-related Event-specific ERS for mismatching context trials

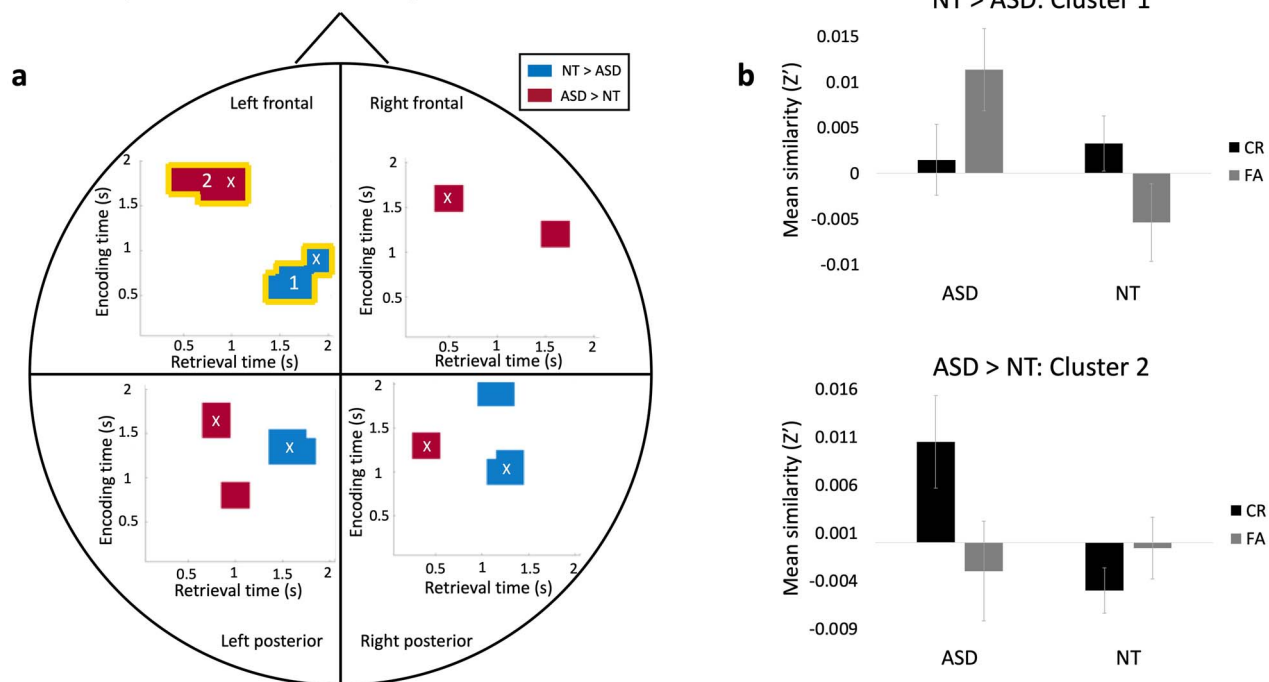


Fig. 4. a) The time intervals in which the memory-related ERS for mismatches is significantly greater for neurotypical subjects compared with subjects with ASD (blue), whereas the ERS for correct rejections is significantly greater than ERS for false alarms for neurotypical subjects; and the time intervals in which the memory-related neural similarity is significantly greater for subjects with ASD compared with neurotypical subjects (red), whereas the ERS for correct rejections is significantly greater than ERS for false alarms for ASD subjects b) the breakdown of memory-related neural similarity into average event-specific similarity for correct rejections and average event-specific similarity for false alarms (with the associated 95% confidence intervals) for 2 of the clusters shown in part a). These 2 clusters are chosen as examples, and the pattern was similar for the other clusters.

processes deficits including lifelong impairments in cognitive flexibility (Leung and Zakzanis 2014 for meta-analysis) and interference control (Geurts et al. 2014 for meta-analysis). ASD research has shown decreased episodic memory performance when cognitive control demands are high during encoding (Solomon et al. 2016; Williams et al. 2017). Furthermore, representation of object-context pairs at retrieval may have lessened demands on strategic retrieval operations. Future studies without these encoding and retrieval support measures (i.e. freely recall) may reveal context memory impairment in ASD.

Given that participants could potentially use familiarity to endorse a context color or scene feature as “matching” in the present task, it is unclear from the behavioral data alone whether participants with ASD could bring back to mind similar levels of episodic details as NT participants to make these behavioral judgments. Literature on compensation in ASD would suggest that behavioral performance may be supported by compensatory strategies that are mismatched (i.e. deficits persist) at the cognitive or neural level (Livingston and Happé 2017). Our ERS results showed significant asymmetrical ERS effects such that encoding activity was similar to retrieval activity occurring either earlier or later. For context-match trials, the observed clusters generally had later encoding periods that were reinstated earlier during retrieval. This pattern was more evident for NT adults, with reinstatement effects tending to occur *later* during retrieval for adults with ASD. These results are consistent with findings from animal models and emerging work in humans showing that episodic reinstatement occurs on a temporally compressed timescale relative to encoding (Yaffe et al. 2014; Michelmann et al. 2019).

Factors underlying temporal compression remain unclear (Schreiner and Staudigl 2020) but could include reinstatement of fragments of previous events and/or skipping less-informative fragments (Michelmann et al. 2019). Although the current study was not designed to explicitly test this idea, it is possible that adults with ASD do not effectively skip through memory fragments during retrieval, which could contribute to their later ERS effects. Future studies that employ dynamic stimuli coupled with explicit mental replay task instructions would be useful for investigating this idea (i.e. Michelmann et al. 2018, 2019).

For context-mismatch trials, the observed clusters generally had earlier encoding periods that were reinstated later during retrieval. Furthermore, this pattern was more evident for NT adults, with reinstatement effects tending to occur *earlier* during retrieval for adults with ASD.

These effects are generally consistent with recall-to-reject theories of memory in which subjects must recall the prior episodes to reject the new information as new (Rotello 2000). Prior studies suggest that earlier perceptual processes will be reconstructed later during remembering (Mecklinger et al. 2016; Linde-Domingo et al. 2019; Mirjalili et al. 2021). Thus, if one is reconstructing prior events to make a memory decision, earlier perception details would likely be recollected later during retrieval. As discussed above, if adults with ASD encoded fewer perceptual details than did NT adults, reconstruction may have been abbreviated. Future studies using designs that parametrically modulate the level of perceptual detail required to make episodic memory decisions would be useful for testing this idea.

This study has a few limitations. The small sample size, because of strict criteria used for selection, limits the potential

generalizability of these findings, and should be replicated in a larger sample. Null behavioral effects, including lack of group differences and the trending Group \times Context interaction ($P = 0.052$) could possibly be because of the small sample size yielding insufficient power to detect smaller effects. Furthermore, though our ASD sample varied considerably on the ADOS-2 and SRS-2 (see Table 1), we are underpowered to evaluate the relationship of ASD symptomatology with ERS. ASD is characterized by substantial heterogeneity and future studies with larger samples and diverse symptomatology should evaluate symptom severity as related to episodic memory ERS. Another limitation of the present study is that we did not match participants on Verbal IQ, which is often done in ASD literature, as we did not collect such data in this sample. We instead employed one-to-one matching for age, gender, and education and resulting samples were comparable across neuropsychological tests that we did collect (Table 1). Lastly, while our sample features a wide age range (ages 18–58), our participants were predominantly younger (see Table 1) and therefore limited in our ability to investigate topics such as accelerated cognitive aging in ASD, which has mixed literature (Geurts and Vissers 2012; Powell et al. 2017; Pagni et al. 2022; Torenvliet et al. 2022, 2023). ASD could be a risk factor for accelerated cognitive decline, given the higher prevalence of neurodegenerative disorders in adults with ASD (Hand et al. 2020; Vivanti et al. 2021) but also could be a “phenotypic mimic” in which similar impairments are observed as with healthy aging but because of underlying biological differences (Torenvliet et al. 2023). ASD like other developmental conditions (e.g. ADHD and schizophrenia) can be complicated to study regarding cognitive aging as developmental changes because of diagnosis vs. late adulthood can be difficult to disentangle. Furthermore, research has suggested substantial variability in aging trajectories for individuals with ASD (Howlin et al. 2013, 2014; Simonoff et al. 2020). Nonetheless, it seems possible that ERS may be more sensitive to age in ASD compared with NT. If aging exacerbates memory impairments, and reduced memory specificity, in ASD, it could have implications in evaluating age-related trajectories of cognitive decline and corresponding quality of life in this population. Furthermore, decrease in ERS may predict the onset of pathological cognitive aging processes such as dementia, which has only recently been studied in ASD with emergent work suggesting greater prevalence for early onset compared with the general population (Vivanti et al. 2021). Future studies, with wide age range and larger sample sizes, should explore these ideas.

To our knowledge, this is the first study to use pattern analyses to explore episodic memory in ASD. We show that ERS can be used in conjunction with behavioral indices to further dissociate memory accuracy and the underlying event-specific neural reinstatement that supports performance and as a novel approach for identifying the nature of episodic memory differences between NT adults and those with ASD.

Acknowledgments

We are thankful for all our volunteers who participated in this study. The authors report no biomedical financial interests or potential conflicts of interest.

Author contributions

Sidni A. Justus (Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Writing—original draft,

Writing—review & editing), Soroush Mirjalili (Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Writing—original draft, Writing—review & editing), Patrick S. Powell (Data curation), and Audrey Duarte (Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing—original draft, Writing—review & editing)

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

Funding

The National Science Foundation Grant (award #1125683 to AD); a Ruth L. Kirschstein NRSA Institutional Research Training Grant from the National Institutes of Health (National Institute on Aging) (award #5T32AG000175).

Conflict of interest statement: None declared.

Data availability

Data used in the current study are available upon request from the corresponding author.

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