Archival Report

Preserved Spontaneous Mentalizing Amid Reduced Intersubject Variability in Autism During a Movie Narrative

Margot Mangnus, Saskia B.J. Koch, Kexin Cai, Miriam Greidanus Romaneli, Peter Hagoort, Jana Bašnáková, and Arjen Stolk

ABSTRACT

BACKGROUND: While individuals with autism often face challenges in everyday social interactions, they may demonstrate proficiency in structured theory of mind (ToM) tasks that assess their ability to infer others' mental states. Using functional magnetic resonance imaging and pupillometry, we investigated whether these discrepancies stem from diminished spontaneous mentalizing or broader difficulties in unstructured contexts.

METHODS: Fifty-two adults diagnosed with autism and 52 neurotypical control participants viewed the animated short *Partly Cloudy*, a nonverbal animated film with a dynamic social narrative known to engage the ToM brain network during specific scenes. Analysis focused on comparing brain and pupil responses to these ToM events. Additionally, dynamic intersubject correlations were used to explore the variability of these responses throughout the film.

RESULTS: Both groups showed similar brain and pupil responses to ToM events and provided comparable descriptions of the characters' mental states. However, participants with autism exhibited significantly stronger correlations in their responses across the film's social narrative, indicating reduced interindividual variability. This distinct pattern emerged well before any ToM events and involved brain regions beyond the ToM network.

CONCLUSIONS: Our findings provide functional evidence of spontaneous mentalizing in autism, demonstrating this capacity in a context that affords but does not require mentalizing. Rather than responses to ToM events, a novel neurocognitive signature—interindividual variability in brain and pupil responses to evolving social narratives—differentiated neurotypical individuals from individuals with autism. These results suggest that idiosyncratic narrative processing in unstructured settings, a common element of everyday social interactions, may offer a more sensitive scenario for understanding the autistic mind.

https://doi.org/10.1016/j.bpsc.2024.10.007

Autism spectrum condition (ASC) is a neurodevelopmental disorder marked by difficulties in social communication and interaction across multiple contexts (1). These difficulties are frequently associated with theory of mind (ToM)—the ability to attribute mental states to oneself and others, also known as mentalizing (2,3). While initial findings suggested diminished ToM abilities in autism (4,5), subsequent studies have painted a more complex picture owing to a variety of factors.

First, the reliability of established ToM assessments, such as the False Belief Test, Strange Stories, and the Reading the Mind in the Eyes Test, has increasingly come under scrutiny. These tests have shown inconsistent effect sizes compared with earlier, smaller-scale studies and exhibited limited correlations with one another, despite their aim to measure similar or identical ToM constructs (6–9). Second, many studies have not adequately matched autistic individuals with neurotypical (NT) control participants based on language abilities, which are crucial to varying degrees for these tasks (10). This lack of language matching is particularly significant given the

generally lower performance in verbal learning and memory observed in the autism population (11). Lastly, recent research highlights the remarkable proficiency of autistic individuals in ToM tasks, especially in situations that require strategic mental state reasoning (12,13), such as deception (14).

Faced with these empirical challenges, researchers have turned to more implicit ToM measures. This includes the analysis of anticipatory eye movements concerning an actor's false beliefs (15) and measuring neural activity in the Animated Triangles Task, where participants attribute mental states to moving shapes (16). Recent findings indicate that while autistic individuals do show anticipatory gaze responses, these responses tend to be generally slower, regardless of whether the character's beliefs are true or false (17,18). In the Animated Triangles Task, both autistic and NT participants show comparable brain activation in key ToM regions, such as the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), and precuneus (19). However, individuals with autism typically underperform in both the mentalizing and nonmentalizing conditions of this

task, which combined with their generally slower anticipatory gaze responses, points to broader difficulties in implicit task settings (20). The extent to which autistic individuals engage in spontaneous mentalizing, particularly in unstructured settings that lack an explicitly defined task, as is common in everyday social interactions, remains largely unknown.

In this study combining functional magnetic resonance imaging (fMRI) and pupillometry, we aimed to bridge this knowledge gap by investigating how individuals with and without autism respond to mental state events embedded in a dynamic movie narrative. Additionally, we sought to provide insights into how these individuals process stimuli in less structured environments that more closely resemble everyday social interactions. Everyday interactions require a continuous assessment of stimuli within an evolving narrative (21-23), as can be seen in how even seemingly minor behaviors like a voluntary cough or a brief silence can carry significant implications in certain contexts (24). Failure to recognize these narrative cues could lead to misunderstandings in scenarios that require high levels of interpretation, such as irony or sarcasm, which are areas known to pose challenges for autistic individuals (25,26). However, capturing this narrative processing is challenging because it likely unfolds differently over time among individuals exposed to the same stimuli. We reasoned that narrative processing could manifest as interindividual variability in responses to movie stimuli, which should be particularly diminished among those less inclined to interpret stimuli through a narrative lens (27-30). We investigated this possibility using intersubject correlation analysis (31), applying it to 2 complementary methods for assessing cognitive processing: brain imaging and measurements of pupil size (32).

To probe spontaneous mentalizing and narrative processing, we recorded participants' brain and pupil responses as they viewed the nonverbal animated movie Partly Cloudy (33-35). Although movies cannot fully replicate the complexities of real-world social interactions (36), they offer an effective platform for immersing participants in an evolving narrative under uniform stimulus conditions. To assess differences in narrative processing between autistic and NT participants at various points during the movie, we augmented our intersubject correlation analysis with a dynamic sliding window technique and an adaptive clustering algorithm (37). The movie Partly Cloudy was chosen for its proven ability to evoke neural activations within the ToM network through distinct mental state events (34,38), making it suitable for evaluating spontaneous mentalizing. After viewing, we analyzed participants' verbal descriptions of the movie, focusing on their use of language related to mental states. This experimental approach enabled us to simultaneously probe spontaneous mentalizing and narrative processing, thereby providing insights into how these cognitive functions interact in individuals with autism.

METHODS AND MATERIALS

Preregistration and Data Availability

The study comprised 2 sets of preregistered analyses (39). The first set focused on spontaneous pupil and brain responses to movie events anticipated to elicit mental state inferences complemented by a questionnaire that examined participants' use of related vocabulary to describe the movie. The second

set of analyses explored dynamic intersubject correlations to investigate idiosyncratic narrative processing throughout the entire movie. Unlike the event-related analyses, these exploratory analyses were not limited to specific movie segments. All resulting pupillometry and fMRI data are publicly available for additional research (40).

Participants

A total of 104 participants were enrolled in the study, 52 adults diagnosed with ASC and 52 NT participants. Recruitment occurred through Radboud University's database, social media, campus postings, and outpatient clinics in Nijmegen and Arnhem, the Netherlands. Eligibility for the ASC group required a formal diagnosis from a clinician (1), while exclusion criteria for all participants included the use of psychotropic drugs, severe cognitive impairment, systemic diseases, or neurological treatment history. As shown in Table 1, both groups were demographically matched for sex, age (Kullback-Leibler divergence = 0.05, $F_{51.51}$ = 0.29), and both verbal and nonverbal IQ, which were verified through the Similarities and Vocabulary subscales of the Wechsler Adult Intelligence Scale (41) (Kullback-Leibler divergence = 0.02, $F_{51.51}$ = 0.74) and Raven's Progressive Matrices (42) (Kullback-Leibler divergence = 0.01, $F_{51,51}$ = 0.63). Notably, participants with ASC scored higher on the Autism Spectrum Quotient (43), confirming group distinctions. Data collection involved MRI scans (n = 104) and pupillometry (n = 100) while participants viewed the film followed by a postviewing questionnaire completed by most participants (n = 101). All participants provided written informed consent, which was approved by the local ethics committee (Committee for Human-Subject Research, region Arnhem-Nijmegen; file No. 2019-6059), and received compensation for their participation.

Experimental Design

Participants watched the 5-minute and 45-second animated short called *Partly Cloudy*, which depicts the evolving friend-ship between a stork and a cloud through various social interactions integral to its narrative. After viewing, participants described the plot to assess narrative comprehension and articulation of characters' mental states. Descriptions were analyzed by independent raters, who categorized words into mental state terms or other content-related categories, using the mental state word list from Bang *et al.* (44). An independent *t* test was used to compare the frequency of mental state words used between groups. The movie featured 3 types of

Table 1. Demographic Characteristics

	ASC Group, $n = 52$	NT Group, $n = 52$	Group Difference
Sex, Female:Male	29:23	32:20	$\chi^2 = 1.73, p = .19$
Age, Years	27.7 (6.3)	25.9 (5.5)	$t_{102} = 1.74, p = .08$
Verbal IQ, WAIS-III	126 (16)	124 (16)	$t_{102} = 0.51, p = .61$
Nonverbal IQ, RPM	103 (9)	104 (11)	$t_{102} = -0.46, p = .64$
Autism Quotient	31 (9)	12 (6)	t_{102} = 12.2, p < .001

Values are presented as n or mean (SD).

ASC, autism spectrum condition; NT, neurotypical; RPM, Raven's Progressive Matrices; WAIS, Wechsler Adult Intelligence Scale.

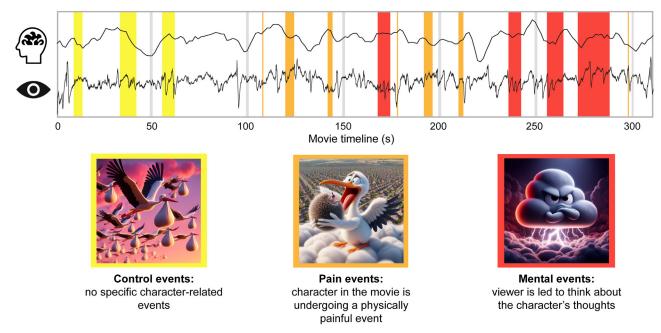


Figure 1. Participants with autism and neurotypical participants viewed a 6-minute animated movie portraying the evolving friendship between a stork and a cloud, while their pupil and brain responses were recorded. Originally used by Jacoby et al. (34) as a theory of mind (ToM) localizer, the movie includes 3 types of events—mental, pain, and control—each marked on the movie timeline. Mental and pain events were expected to prompt inferences about characters' mental and physical states, whereas control events featured no characters in the foreground. The event images shown were generated using Copilot in Bing for copyright purposes to closely resemble scenes from the movie.

events, coded by the original research team that introduced it as a ToM localizer task (34). These included mental, pain, and control events, each annotated on the movie's timeline in Figure 1. Mental events, which totaled 44 seconds across 4 events, were expected to elicit inferences about characters' mental states, depicting scenarios like characters feeling distressed while observing others enjoying a cheerful interaction or mistakenly perceiving betrayal by a friend. Pain events, which totaled 26 seconds across 7 events, depicted instances where characters experienced physical discomfort, such as being shocked by an eel or bitten by a crocodile. Control events, which totaled 24 seconds across 3 events, showcased serene moments like birds in flight or panoramic views of clouds. As detailed in later sections, these categorizations facilitated the analysis of ToM-related pupillary and neural responses.

Pupillometry and MRI Data Acquisition

Pupil size was continuously tracked using an SR Research Eyelink 1000 plus eyetracker at 1000 Hz. MRI data were acquired using a Siemens 3T MRI scanner with a 32-channel head coil. Structural images were obtained with a T1 magnetization-prepared rapid acquisition gradient-echo sequence (repetition time = 2200 ms, inversion time = 1100 ms, echo time = 2.6 ms, flip angle = 11°, voxel size = 0.8 mm³, acceleration factor = 2). Functional images were acquired with a multiband multiecho sequence (repetition time = 1500 ms, echo time = 13.4/34.8/56.2 ms, flip angle = 75°, voxel size = 2.5 mm³, acceleration factor = 2). Analysis of head movement through framewise displacement showed no significant

differences between the ASC and NT groups. Mean framewise displacement was mean \pm SD = 0.15 \pm 0.05 for the ASC group and 0.16 \pm 0.09 for the NT group ($t_{102} = -0.78$, p = .43), with maximum framewise displacement values at 0.81 \pm 0.79 for the ASC group and 1.03 \pm 1.31 for the NT group ($t_{102} = -1.09$, p = .28). Additionally, assessments of total head motion, calculated from translation and rotation during the realignment process, indicated no significant differences (translation: 109.5 \pm 74.6 vs. 114.3 \pm 99.5, $t_{102} = 0.28$, p = .78; rotation: 2.0 \pm 0.98 vs. 2.2 \pm 1.2, $t_{102} = 0.74$, p = .46).

Pupillometry Data Analysis

Pupillometry data underwent preprocessing with a combination of established and custom MATLAB (version 2020a; The MathWorks, Inc.) routines. Blinks were removed using a noisebased detection algorithm (45). Squints, marked by unusually small pupil sizes (46), and gaze jumps, indicative of excessive translational eye movements, were both identified and eliminated through visual inspection. After these adjustments, $89.3\% \pm 9.4\%$ of the data remained usable for the ASC group, and 88.4% \pm 10.6% remained usable for the NT group (t_{98} = 0.48, p = .63). Fixations and saccades were distinguished using an adaptive velocity threshold (47). Pupil time series were normalized (z-scored) and adjusted for global luminance fluctuations modeled using the Im() function from the R stats package (48) up to the fifth polynomial order, validated with data from 5 randomly selected participants. Luminance was quantified using red-green-blue color values based on the Rec. 709 formula (49).

Event-related pupil responses were analyzed through a 3×2 mixed-design analysis of variance with mean pupil size as the dependent variable and event condition (mental, pain, control) and participant group status (ASC, NT) as factors. Tukey's honest significant difference tests were used to investigate ToM-related contrasts further, specifically to compare mental with both pain and control conditions. To verify the robustness of our findings against variations in event timing, a control analysis was conducted by incorporating an additional time-based regressor into the lm() function during preprocessing. This adjustment, which was incremented by 1 every second, did not influence the main findings.

Intersubject variability was assessed using dynamic intersubject correlation analysis of the pupil time series. Using a leave-one-out approach, each participant's time series was correlated with the composite average time series of all other group members (50). This analysis was conducted using a 30second sliding window at 100-ms intervals, generating a correlation time series for the entire movie duration per participant. All correlation time series were Fisher z-transformed and subjected to a nonparametric cluster-based permutation test (37). This test addresses the multiple comparisons problem in time-series analysis by clustering significant neighboring data points. These clusters are tested against a null distribution formed by randomly shuffling participant labels and recalculating statistics, allowing the identification of specific time points where significant differences in pupil response variability between groups occurred, while effectively controlling for false positives. Statistical testing was performed using a 2sided independent samples t test with 10,000 permutations to establish the null distribution. Clusters that reached a Monte Carlo p value of .05 or less were considered statistically significant.

fMRI Data Analysis

Functional images were preprocessed using SPM12, initially consolidating multiple echoes into single volumes through echo-weighted combinations. These volumes were realigned to the initial image using rigid-body transformations and second-degree B-spline interpolation and subsequently unwarped with participant-specific field maps to minimize spatial distortions and signal dropout. Anatomical images were coregistered to the mean functional image and segmented into gray matter, white matter, and cerebrospinal fluid categories using SPM's tissue probability maps, enabling normalization to Montreal Neurological Institute space. An 8-mm full width at half maximum kernel was applied for spatial smoothing. Firstlevel regressors estimated activations for mental, pain, and control events and included adjustments for head movement (using squared and cubic terms together with first and second derivatives) and tissue signal intensities. A 0.6 threshold masking was applied to ensure optimal brain coverage.

Two 2×2 mixed-design analyses of variance were conducted to analyze ToM activations across mental, pain, and control conditions and participant groups (ASC, NT). The first contrast (mental > pain) sought to confirm previous findings of enhanced ToM network activity (34), while the second contrast (mental > control) extended these findings to scenes that lack foreground characters. Results were subjected to whole-brain

cluster-level correction (familywise error-corrected p [p_{FWE}] < .05), with anatomical locations identified using the SPM Anatomy Toolbox (51). Additionally, a region of interest analysis focused on 3 peak brain regions and was complemented by Bayesian analysis (52) to evaluate consistent neural activation within the ToM network across groups, reporting evidence with Bayes factors (BFs). Robustness against event timing variations was confirmed through a control analysis with a first-level regressor added that incremented with each volume.

Intersubject variability at the neural level was assessed using dynamic intersubject correlation analysis of voxel time series adjusted for head movement and tissue signals. Mirroring the pupillometry analysis, a leave-one-out and sliding window method generated whole-brain correlation time series for each participant. For computational efficiency, the data were spatially and temporally downsampled by a factor of 3, which resulted in a voxel resolution of 7.5 mm and a sampling interval of 4.5 seconds. These data underwent a nonparametric cluster-based permutation test (37), which corrected for multiple comparisons across voxels and time points using a 2sided independent samples t test with 10,000 permutations (Monte Carlo p < .05). The analysis was further refined with a spatially adaptive clustering algorithm that identified variations in brain response patterns between groups. The spatial distribution of the identified spatiotemporal brain cluster was visualized by summing t values across all time points, producing a 3-dimensional representation of significant variability. The degree of overlap between this cluster and the ToM network was quantified by comparing their spatial volumes. Lastly, a supplementary analysis without the sliding window approach calculated correlations across the entire voxel time series, pinpointing a smaller cluster in the left supramarginal gyrus. Consistent with the main findings, this cluster demonstrated reduced intersubject variability in the ASC group.

RESULTS

Postviewing Movie Descriptions

After the film viewing, participants were asked to recount the story of the stork and the cloud's evolving friendship in their own words. We analyzed these descriptions for the use of mental state words and other content-related terms (Figure 2A). Statistical analysis revealed no significant differences in the frequency of mental state word usage between the autistic and NT participants (mean_{ASC} = 0.063, mean_{NT} = 0.054, $t_{99} = 0.84$, p = .40) (Figure 2B), with a BF in favor of the null hypothesis (BF_{Null} = 3.49). This finding suggests that participants in the autistic and NT groups engaged similarly with the mental states depicted in the film.

Event-Related Pupil Responses

Participants' pupil sizes were continuously tracked throughout the movie to assess responses to events expected to elicit mental state inferences, such as the cloud reflecting on the stork's actions. We also analyzed responses to events expected to evoke physical state inferences, like the stork experiencing pain, as well as to control scenes that were devoid of character interactions. Pupillometry analysis

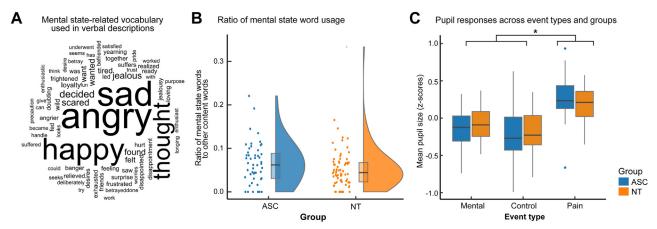


Figure 2. Comparable mental state descriptions and pupil responses across groups. (A) Word cloud depicting the frequency of mental state—related vocabulary used by participants in their postviewing movie descriptions. The size of each word corresponds to its frequency of use. (B) Bar graphs displaying the ratio of mental state words to other content-related terms in these descriptions, which show no significant differences between the 2 groups. (C) Pupil responses across all event conditions, which reveal similar response patterns in both the autistic and neurotypical (NT) groups. Asterisks denote significant differences between event conditions (all ps < .001), with no significant differences observed between groups. Outliers are represented by dots, while whiskers display a 1.5 interquartile range. ASC, autism spectrum condition.

identified distinct responses to these 3 event types ($F_{2,196} = 73.0$, p < .001, BF_{Null} = 0.00) (Figure 2C), with the largest pupil dilation occurring during pain events (mean = 0.22, z score), followed by mental events (mean = -0.12) and control events

(mean = -0.20). Comparisons of pupil responses between autistic and NT participants revealed no significant differences ($F_{1.98} = 0.03$, p = .86, BF_{Null} = 7.8) or interaction effects between participant groups and event types ($F_{2.196} = 2.1$, p = .12,

A Whole-brain responses to mental state events

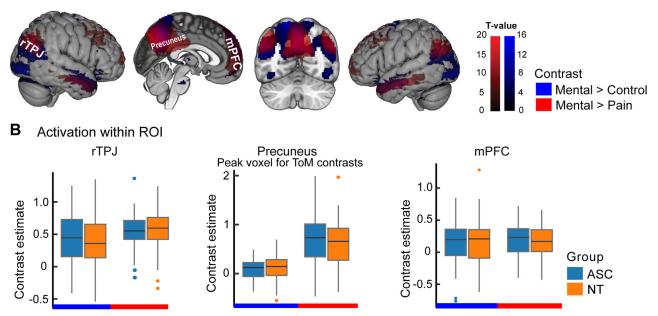


Figure 3. Comparable neural activation patterns during mental state events across groups. (A) Brain sections showing whole-brain responses specific to mental state events, as assessed through the mental > control and mental > pain contrasts. There were no significant differences in activation for either contrast between the autistic and neurotypical (NT) groups. (B) Box plots depicting the contrast estimates for the mental > control (in blue underlining) and mental > pain (in red underlining) comparisons across various regions of interest (ROIs) for both groups. The right temporoparietal junction (rTPJ) and medial prefrontal cortex (mPFC) were selected as ROIs based on theory of mind literature, while the precuneus was selected because of the peak voxel being located in that region for both theory of mind contrasts. Across all ROIs and contrasts, no significant differences were observed between the groups. Outliers are represented by dots, while whiskers display a 1.5 interquartile range. ASC, autism spectrum condition.

BF_{Null} = 2.5). This suggests that both groups reacted similarly to the different event types in the movie.

Event-Related Brain Responses

A whole-brain fMRI analysis was conducted to examine neural activations during mental events compared with control and pain events. As depicted in Figure 3A, this analysis identified robust activation in key areas of the ToM network (53), specifically in the right and left TPJ (right TPJ: Montreal Neurological Institute coordinates [x, y, z] = [48, -62, 32], t = 16.85, $p_{\text{EWF}} < .001$; left TPJ: [-46, -62, 32], t = 16.92, $p_{\text{EWF}} < .001$), the precuneus ([6, -64, 40], t = 20.64, $p_{FWE} < .001$), mPFC $([-6, 52, 38], t = 7.33, p_{EWE} < .001)$, and left middle temporal gyrus ([-52, 2, -26], t = 11.51, ρ_{FWE} < .001). Echoing the pupillometry findings, no significant differences in neural activation were observed between autistic and NT participants. Complementary region of interest analysis (Figure 3B) and Bayesian analysis reinforced these findings, providing evidence favoring the null hypothesis over alternative models suggesting group differences. This was consistently demonstrated across all evaluated regions of interest for both mental > pain contrasts (right TPJ: BF_{Null} = 4.83, precuneus: BF_{Null} = 1.73, mPFC: BF_{Null} = 4.01) and mental > control contrasts (right TPJ: $BF_{Null} = 3.43$, precuneus: $BF_{Null} = 3.63$, mPFC: BF_{Null} = 4.71), underscoring a similarity in neural processing of mental states among autistic and NT individuals.

Movie-Driven Variability in Pupil Responses

Having observed comparable pupil and brain responses to mental state events and similar verbal descriptions from both autistic and NT participants, we expanded our investigation to narrative processing differences across the entire movie through dynamic intersubject correlation analysis of the pupil time series. This analysis revealed an interval from 40 to 71 seconds when individuals with autism demonstrated significantly stronger correlations in pupil responses, indicating reduced intersubject variability, than NT participants $(mean_{ASC} = 0.61, mean_{NT} = 0.55, cluster stat = 777, p = .045)$ (Figure 4). This interval preceded any mental state events and coincided with scenes featuring storks flying through the air and clouds morphing into baby animals. Although this reduced variability continued throughout the film, it did not reach statistical significance outside this interval after adjustment for multiple comparisons. Furthermore, differences in variability were not due to variations in saccadic eve movements because their frequency and variability remained consistent between groups (Figure S1).

Movie-Driven Variability in Brain Responses

When applied to the fMRI data, dynamic intersubject correlation analysis identified a spatiotemporal cluster where individuals with autism showed significantly stronger correlations in their brain responses than NT participants (Figure 5). This cluster spanned the entire movie (cluster stat = 1332, p = .002) and included peaks in the right and left supramarginal gyrus (right supramarginal gyrus: [52, -34, 32], $t_{\text{max.}} = 3.88$; left supramarginal gyrus: [-54, -40, 32], $t_{\text{max.}} =$ 4.54), the right inferior temporal gyrus ([54, -22, -28], $t_{\text{max.}} =$ 5.90), and the left calcarine gyrus ([6, -102, -10], $t_{\text{max.}} = 4.20$). The reduced variability was consistent across these regions for most of the movie (Figure S2), and it emerged well before and continued after any mental state events. The cluster's overlap with the ToM network was minimal, comprising <20% of the total cluster size (Figure 6). This indicates that the observed reduced variability in brain responses among autistic participants extended beyond regions involved in mental state processing, suggesting broader differences in neural processing between the groups.

DISCUSSION

Using fMRI and pupillometry, this study provides functional evidence of spontaneous mentalizing abilities in individuals

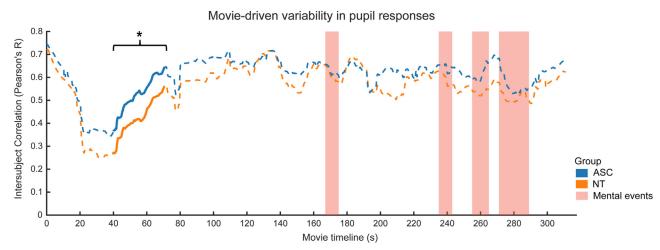


Figure 4. Reduced pupil response variability in autistic participants. Dynamic intersubject correlation analysis initially showed comparably high levels of correlation in both the autistic and neurotypical (NT) groups at the start of the movie. However, a significant divergence emerged around the 40-second mark, when individuals with autism showed stronger correlations in their pupil responses, indicating reduced intersubject variability, than NT participants. This pattern of reduced variability emerged well before the mental state events highlighted by the pink areas. Solid lines delineate statistically significant intervals, as determined by a cluster-based permutation test. ASC, autism spectrum condition. $^*p < .05$.

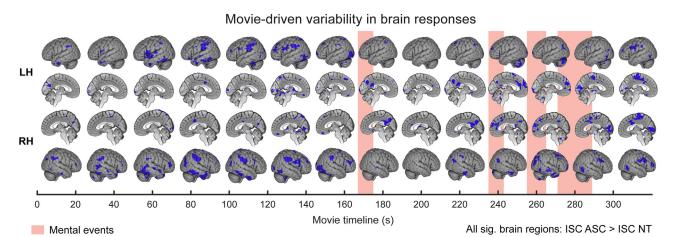


Figure 5. Reduced brain response variability in autistic participants. Dynamic intersubject correlation (ISC) analysis identified a spatiotemporal brain cluster where autistic individuals demonstrated significantly stronger correlations in their brain responses, indicating reduced intersubject variability, than neurotypical (NT) participants. This cluster persisted throughout the movie and featured peaks in the right and left supramarginal gyrus, the right inferior temporal gyrus, and the left calcarine gyrus. Echoing the pupillometry data, this pattern of reduced variability in autistic participants emerged well before the mental state events highlighted by the pink areas. ASC, autism spectrum condition; LH, left hemisphere; RH, right hemisphere.

with autism. Compared with NT participants matched on sex, age, and both verbal and nonverbal IQ, individuals with autism exhibited similar brain and pupil responses during movie scenes known to activate the ToM network (34,38). Activity in the ToM network was enhanced during scenes that encouraged viewers to contemplate the actions and mental states of depicted characters. Conversely, scenes that prompted physical state inferences, such as characters experiencing physical discomfort, or control scenes that lacked central characters, resulted in weaker ToM activations. Verbal descriptions provided by participants after the movie corroborated these findings, indicating an engagement with the mental state events depicted in the movie on par with that of NT participants. These results extend previous evidence of preserved mentalizing in autism (19,54), showcasing this capacity in a situation that affords but does not require mentalizing.

While individuals with and without ASC showed comparable brain and pupil responses during mental state events, dynamic intersubject correlation analysis revealed significant differences in the correlation of these responses over extended movie intervals. Participants with autism exhibited significantly stronger correlations, indicating reduced interindividual variability, across several brain regions outside the ToM network. These included the right and left supramarginal gyrus, linked to empathic judgment (55,56); the right inferior temporal gyrus, associated with narrative comprehension (57); and the left calcarine gyrus, crucial for visual processing (58). This reduced

variability was not due to differences in bottom-up processing, as autistic and NT groups exhibited similar saccadic eye movement patterns throughout the film. The most pronounced differences emerged during early scenes featuring storks flying through the air and clouds morphing into baby animals, which likely introduced significant narrative ambiguity. This ambiguity may have prompted NT viewers to idiosyncratically interpret how these visual elements fit into the evolving storyline, resulting in less consistent responses. In contrast, autistic participants' responses appeared to be more consistently aligned with the movie's stimuli, possibly reflecting a heightened focus on specific details rather than the broader narrative context (59-63). Importantly, these differences manifested in cognitive and neural processing rather than in eye movements, suggesting that the variability observed in NT responses may represent a neurocognitive signature of top-down processing.

The neuroanatomical bases of the observed changes in response variability are consistent with existing research on autism and social interaction. Previous studies have documented structural alterations in the gray matter of both the right and left supramarginal gyrus in individuals with autism (64–66), as well as reduced anatomical connectivity in the right inferior temporal cortex (67,68). This region exhibits prolonged activations during tasks that involve story comprehension and interactive communication (57,69), highlighting its role in integrating stimuli within an evolving narrative. This integration is crucial for complex social interactions, which necessitate the

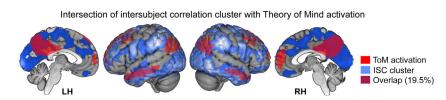


Figure 6. Limited spatial overlap between brain regions showing reduced intersubject variability in autistic participants and theory of mind (ToM) activation. The overlap comprised <20% of the total cluster size. For clarity, the cluster is visualized using a cumulative *t* value threshold of ≥20. Lateral brain images provide an overlay with a search distance of 10 mm. ISC, intersubject correlation; LH, left hemisphere; RH, right hemisphere.

continuous assessment of diverse stimuli to maintain narrative coherence with others (21–23). A key direction for future research is to examine how response variability in the identified brain regions differs across various social contexts. Such investigations will not only help to illuminate the specific challenges faced by autistic individuals in everyday social situations but could also inform the development of interventions by identifying environments that promote effective social interaction (70).

It is worth noting that our intersubject correlation patterns differ from previous studies that demonstrated greater brain response variability in autistic individuals than in NT participants (71-78). Several factors could explain these discrepancies. First, our study used an animated film with fictional characters as opposed to the more realistic human portrayals used in other studies. Although the type of characters may influence brain responses in autism (79), greater neural variability has been noted with fictional characters (74). Second, we implemented an adaptive clustering algorithm to identify spatiotemporal clusters of brain response variability within 30second intervals. This approach is potentially more sensitive to brain response variations associated with subtle shifts in interpretation than whole-movie analyses, which emphasize consistent patterns over significantly longer durations (10-67 minutes). This approach may more effectively capture the hypothesized increased reliance on bottom-up sensory stimulation in autism (80), possibly leading to less variability in neural signals related to narrative interpretation. More generally, our findings invite a reconsideration of theories that propose precise neural synchronization as a means to manage individual perspectives in daily interactions (81). These theories suggest that aligning neural responses to external cues helps individuals achieve a common viewpoint, thereby facilitating social interaction (82,83). However, contrary to expectations based on their social difficulties, participants with autism in our study displayed stronger neural correlations when exposed to the same external stimuli, thereby challenging the assumed role of precise neural synchronization in social interaction (84).

Conclusions

This study offers functional evidence of spontaneous mentalizing in autism, showcasing this capacity in a context affording but not requiring mental state inferences. More distinctively, our findings identify a novel neurocognitive signature—interindividual variability in brain and pupil responses to evolving social narratives—that differentiates NT individuals from individuals with autism. These results underscore the importance of idiosyncratic narrative processing in unstructured settings, a common feature of everyday social interactions, as a potentially more sensitive framework for understanding the autistic mind.

ACKNOWLEDGMENTS AND DISCLOSURES

This work was supported by the Gravitation Grant from the Netherlands Organization for Scientific Research (NWO) (Grant No. 024.001.006) awarded to the Language in Interaction Consortium (to AS and JB).

A previous version of this article was published as a preprint on bioRxiv: https://doi.org/10.1101/2024.03.08.583911.

All authors report no biomedical financial interests or potential conflicts of interest.

ARTICLE INFORMATION

From the Donders Institute for Brain, Cognition, and Behaviour, Radboud University, Nijmegen, the Netherlands (MM, SBJK, MGR, PH, JB); Psychological and Brain Sciences, Dartmouth College, Hanover, New Hampshire (KC, AS); and Max Planck Institute for Psycholinguistics, Max-Planck-Gesellschaft, Nijmegen, the Netherlands (PH).

JB and AS contributed equally to this work.

In memory of Kexin Cai, who contributed to this paper.

Address correspondence to Margot Mangnus, M.Sc., at margot. mangnus@donders.ru.nl.

Received Sep 5, 2024; revised Sep 30, 2024; accepted Oct 18, 2024. Supplementary material cited in this article is available online at https://doi.org/10.1016/j.bpsc.2024.10.007.

REFERENCES

- American Psychiatric Association (2013): Diagnostic and Statistical Manual of Mental Disorders: DSM-5, 5th ed. Arlington, VA: American Psychiatric Association.
- Premack D, Woodruff G (1978): Does the Chimpanzee Have a Theory of Mind? Behav Brain Sci 1:515–526.
- Wimmer H, Perner J (1983): Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. Cognition 13:103–128.
- Baron-Cohen S, Leslie AM, Frith U (1985): Does the autistic child have a "theory of mind"? Cognition 21:37–46.
- Happé FGE (1994): An advanced test of theory of mind: Understanding of story characters' thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. J Autism Dev Disord 24:129–154.
- Gernsbacher MA, Yergeau M (2019): Empirical failures of the claim that autistic people lack a theory of mind. Arch Sci Psychol 7:102–118.
- Higgins WC, Kaplan DM, Deschrijver E, Ross RM (2024): Construct validity evidence reporting practices for the Reading the Mind in the Eyes Test: A systematic scoping review. Clin Psychol Rev 108:102378.
- Schaafsma SM, Pfaff DW, Spunt RP, Adolphs R (2015): Deconstructing and reconstructing theory of mind. Trends Cogn Sci 19: 65–72.
- Yeung EKL, Apperly IA, Devine RT (2024): Measures of individual differences in adult theory of mind: A systematic review. Neurosci Biobehav Rev 157:105481.
- Betz N, Hoemann K, Barrett LF (2019): Words are a context for mental inference. Emotion 19:1463–1477.
- Velikonja T, Fett AK, Velthorst E (2019): Patterns of nonsocial and social cognitive functioning in adults with autism spectrum disorder: A systematic review and meta-analysis. JAMA Psychiatry 76:135–151.
- Bowler DM (1992): "Theory of mind" in Asperger's Syndrome. J Child Psychol Psychiatry 33:877–893.
- Pantelis PC, Kennedy DP (2017): Autism does not limit strategic thinking in the "beauty contest" game. Cognition 160:91–97.
- van Tiel B, Deliens G, Geelhand P, Murillo Oosterwijk A, Kissine M (2021): Strategic deception in adults with autism spectrum disorder. J Autism Dev Disord 51:255–266.
- Senju A, Southgate V, White S, Frith U (2009): Mindblind Eyes: An absence of spontaneous theory of mind in Asperger syndrome. Science 325:883–885.
- Abell F, Happé F, Frith U (2000): Do triangles play tricks? Attribution of mental states to animated shapes in normal and abnormal development. Coop Dev 15:1–16.
- Glenwright M, Scott RM, Bilevicius E, Pronovost M, Hanlon-Dearman A (2021): Children with autism spectrum disorder can attribute false beliefs in a spontaneous-response preferential-looking task. Front Commun 6.
- Schuwerk T, Sodian B, Paulus M (2016): Cognitive mechanisms underlying action prediction in children and adults with autism spectrum condition. J Autism Dev Disord 46:3623–3639.
- Moessnang C, Baumeister S, Tillmann J, Goyard D, Charman T, Ambrosino S, et al. (2020): Social brain activation during mentalizing in

- a large autism cohort: The Longitudinal European Autism Project. Mol Autism 11:17.
- Wilson AC (2021): Do animated triangles reveal a marked difficulty among autistic people with reading minds? Autism 25:1175–1186.
- Goffman E (1974): Frame Analysis: An Essay on the Organization of Experience. Cambridge, MA: Harvard University Press, 586. ix.
- Johnson SGB, Bilovich A, Tuckett D (2022): Conviction Narrative Theory: A theory of choice under radical uncertainty. Behav Brain Sci 46:e82.
- Stolk A, Bašnáková J, Toni I (2022): Joint epistemic engineering: The neglected process in human communication. The Routledge Handbook of Semiosis and the Brain. Routledge, 259–278.
- Kendon A (1994): Do gestures communicate? A review. Res Lang Soc Interact 27:175–200.
- Deliens G, Papastamou F, Ruytenbeek N, Geelhand P, Kissine M (2018): Selective pragmatic impairment in autism spectrum disorder: Indirect requests versus irony. J Autism Dev Disord 48:2938–2952.
- Zalla T, Amsellem F, Chaste P, Ervas F, Leboyer M, Champagne-Lavau M (2014): Individuals with autism spectrum disorders do not use social stereotypes in irony comprehension. PLoS One 9:e95568.
- Chang LJ, Jolly E, Cheong JH, Rapuano KM, Greenstein N, Chen PA, Manning JR (2021): Endogenous variation in ventromedial prefrontal cortex state dynamics during naturalistic viewing reflects affective experience. Sci Adv 7:eabf7129.
- Finn ES, Corlett PR, Chen G, Bandettini PA, Constable RT (2018): Trait
 paranoia shapes inter-subject synchrony in brain activity during an
 ambiguous social narrative. Nat Commun 9:2043.
- Owen LLW, Manning JR (2024): High-level cognition is supported by information-rich but compressible brain activity patterns. Proc Natl Acad Sci U S A 121:e2400082121.
- Zhang C, Beste C, Prochazkova L, Wang K, Speer SPH, Smidts A, et al. (2022): Resting-state BOLD signal variability is associated with individual differences in metacontrol. Sci Rep 12:18425.
- Hasson U, Nir Y, Levy I, Fuhrmann G, Malach R (2004): Intersubject synchronization of cortical activity during natural vision. Science 303:1634–1640.
- Beatty J (1982): Task-evoked pupillary responses, processing load, and the structure of processing resources. Psychol Bull 91:276–292.
- 33. Sohn P (2009): Partly Cloudy [DVD]. Emeryville, CA: Pixar Animation
- Jacoby N, Bruneau E, Koster-Hale J, Saxe R (2016): Localizing Pain Matrix and theory of mind networks with both verbal and non-verbal stimuli. Neuroimage 126:39–48.
- Paunov AM, Blank IA, Fedorenko E (2019): Functionally distinct language and theory of mind networks are synchronized at rest and during language comprehension. J Neurophysiol 121:1244–1265.
- Wheatley T, Boncz A, Toni I, Stolk A (2019): Beyond the isolated brain: The promise and challenge of interacting minds. Neuron 103:186–188.
- Maris E, Oostenveld R (2007): Nonparametric statistical testing of EEG- and MEG-data. J Neurosci Methods 164:177–190.
- Richardson H, Lisandrelli G, Riobueno-Naylor A, Saxe R (2018): Development of the social brain from age three to twelve years. Nat Commun 9:1027.
- Mangnus M, Koch SBJ, Greidanus Romaneli M, Goltz F, Cai K, Hagoort P, Bašnáková J, Stolk A (2022): Theory of Mind in autism spectrum conditions: A task-based neuroimaging approach. Available at: https://doi.org/10.17605/OSF.IO/8F2NK. Accessed June 30, 2022.
- Mangnus M, Koch SBJ, Cai K, Greidanus Romaneli M, Hagoort P, Bašnáková J, Stolk A (2024): Neural and Pupillary Responses to a Narrative Movie From Autistic and Neurotypical Individuals, version 1. Radboud University. Available at: https://doi.org/10.34973/1pth-1493, 2002. Accessed March 8, 2024.
- Wechsler D, Psychological corporation (1997): WAIS-III: Administration and Scoring Manual: Wechsler Adult Intelligence Scale. San Antonio, TX: Psychological corporation.
- Raven J (1989): The raven progressive matrices: A review of national norming studies and ethnic and socioeconomic variation within the United States. J Educ Meas 26:1–16.

- 43. Baron-Cohen S, Wheelwright S, Skinner R, Martin J, Clubley E (2001): The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. J Autism Dev Disord 31:5–17.
- 44. Bang J, Burns J, Nadig A (2013): Brief report: Conveying subjective experience in conversation: Production of mental state terms and personal narratives in individuals with high functioning autism. J Autism Dev Disord 43:1732–1740.
- Hershman R, Henik A, Cohen N (2018): A novel blink detection method based on pupillometry noise. Behav Res Methods 50:107–114.
- Mathôt S (2018): Pupillometry: Psychology, Physiology, and Function. J Cogn 1:16.
- Nyström M, Holmqvist K (2010): An adaptive algorithm for fixation, saccade, and glissade detection in eyetracking data. Behav Res Methods 42:188–204.
- Bates D, Mächler M, Bolker B, Walker S (2015): Fitting linear mixedeffects models using Ime4. J Stat Softw 67:1–48.
- International Telecommunication Union I: Parameter values for the HDTV standards for production and international programme exchange. Available at: https://www.itu.int/dms_pubrec/itu-r/rec/bt/rrec-bt.709-6-201506-il!pdf-e.pdf. Accessed January 8, 2024.
- Nastase SA, Gazzola V, Hasson U, Keysers C (2019): Measuring shared responses across subjects using intersubject correlation. Soc Cogn Affect Neurosci 14:667–685.
- Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles K (2005): A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25:1325–1335.
- JASP Team (2022): JASP, version 0.16.4. Computer software. Available at: https://jasp-stats.org/. Accessed January 8, 2024.
- Schurz M, Radua J, Aichhorn M, Richlan F, Perner J (2014): Fractionating theory of mind: A meta-analysis of functional brain imaging studies. Neurosci Biobehav Rev 42:9–34.
- Dufour N, Redcay E, Young L, Mavros PL, Moran JM, Triantafyllou C, et al. (2013): Similar brain activation during false belief tasks in a large sample of adults with and without autism. PLoS One 8:e75468.
- Silani G, Lamm C, Ruff CC, Singer T (2013): Right supramarginal gyrus is crucial to overcome emotional egocentricity bias in social judgments. J Neurosci 33:15466–15476
- Wada S, Honma M, Masaoka Y, Yoshida M, Koiwa N, Sugiyama H, et al. (2021): Volume of the right supramarginal gyrus is associated with a maintenance of emotion recognition ability. PLoS One 16: e0254623.
- Youssofzadeh V, Conant L, Stout J, Ustine C, Humphries C, Gross WL, et al. (2022): Late dominance of the right hemisphere during narrative comprehension. Neuroimage 264:119749.
- Woldorff MG, Liotti M, Seabolt M, Busse L, Lancaster JL, Fox PT (2002): The temporal dynamics of the effects in occipital cortex of visual-spatial selective attention. Brain Res Cogn Brain Res 15:1–15.
- Losh M, Capps L (2003): Narrative ability in high-functioning children with autism or Asperger's syndrome. J Autism Dev Disord 33:239–251.
- Tager-Flusberg H (1995): 'Once upon a ribbit': Stories narrated by autistic children. Br J Dev Psychol 13:45–59.
- Barnes JL, Baron-Cohen S (2012): The big picture: Storytelling ability in adults with autism spectrum conditions. J Autism Dev Disord 42:1557–1565.
- Geelhand P, Papastamou F, Deliens G, Kissine M (2020): Narrative production in autistic adults: A systematic analysis of the microstructure, macrostructure and internal state language. J Pragmat 164:57–81
- **63.** Koldewyn K, Jiang Y, Weigelt S, Kanwisher N (2013): Global/local processing in autism: Not a disability, but a disinclination. J Autism Dev Disord 43:2329–2340.
- Brieber S, Neufang S, Bruning N, Kamp-Becker I, Remschmidt H, Herpertz-Dahlmann B, et al. (2007): Structural brain abnormalities in adolescents with autism spectrum disorder and patients with attention deficit/hyperactivity disorder. J Child Psychol Psychiatry 48:1251– 1258

- Ke X, Hong S, Tang T, Zou B, Li H, Hang Y, et al. (2008): Voxel-based morphometry study on brain structure in children with high-functioning autism. Neuroreport 19:921–925.
- Libero LE, DeRamus TP, Deshpande HD, Kana RK (2014): Surfacebased morphometry of the cortical architecture of autism spectrum disorders: Volume, thickness, area, and gyrification. Neuropsychologia 62:1–10.
- Boets B, Van Eylen L, Sitek K, Moors P, Noens I, Steyaert J, et al. (2018): Alterations in the inferior longitudinal fasciculus in autism and associations with visual processing: A diffusion-weighted MRI study. Mol Autism 9:10.
- 68. Koldewyn K, Yendiki A, Weigelt S, Gweon H, Julian J, Richardson H, et al. (2014): Differences in the right inferior longitudinal fasciculus but no general disruption of white matter tracts in children with autism spectrum disorder. Proc Natl Acad Sci U S A 111:1981–1986.
- Stolk A, Verhagen L, Schoffelen J-M, Oostenveld R, Blokpoel M, Hagoort P, et al. (2013): Neural mechanisms of communicative innovation. Proc Natl Acad Sci U S A 110:14574–14579.
- Wadge H, Brewer R, Bird G, Toni I, Stolk A (2019): Communicative misalignment in autism spectrum disorder. Cortex 115:15–26.
- Byrge L, Dubois J, Tyszka JM, Adolphs R, Kennedy DP (2015): Idiosyncratic brain activation patterns are associated with poor social comprehension in autism. J Neurosci 35:5837–5850.
- Hahamy A, Behrmann M, Malach R (2015): The idiosyncratic brain: Distortion of spontaneous connectivity patterns in autism spectrum disorder. Nat Neurosci 18:302–309.
- Hasson U, Avidan G, Gelbard H, Vallines I, Harel M, Minshew N, Behrmann M (2009): Shared and idiosyncratic cortical activation patterns in autism revealed under continuous real-life viewing conditions. Autism Res 2:220–231.
- Lyons KM, Stevenson RA, Owen AM, Stojanoski B (2020): Examining the relationship between measures of autistic traits and neural

- synchrony during movies in children with and without autism. Neuroimage Clin 28:102477.
- Nunes AS, Peatfield N, Vakorin V, Doesburg SM (2019): Idiosyncratic organization of cortical networks in autism spectrum disorder. Neuroimage 190:182–190.
- Ou W, Zeng W, Gao W, He J, Meng Y, Fang X, Nie J (2022): Movie events detecting reveals inter-subject synchrony difference of functional brain activity in autism spectrum disorder. Front Comput Neurosci 16:877204.
- Pegado F, Hendriks MHA, Amelynck S, Daniels N, Steyaert J, Boets B,
 Op de Beeck H (2020): Adults with high functioning autism display
 idiosyncratic behavioral patterns, neural representations and con nectivity of the 'Voice Area' while judging the appropriateness of
 emotional vocal reactions. Cortex 125:90–108.
- Salmi J, Roine U, Glerean E, Lahnakoski J, Nieminen-von Wendt T, Tani P, et al. (2013): The brains of high functioning autistic individuals do not synchronize with those of others. NeuroImage Clin 3:489–497.
- Atherton G, Cross L (2018): Seeing more than human: Autism and anthropomorphic theory of mind. Front Psychol 9:528.
- Pellicano E, Burr D (2012): When the world becomes "too real": A Bayesian explanation of autistic perception. Trends Cogn Sci 16:504–510.
- 81. Holroyd CB (2022): Interbrain synchrony: On wavy ground. Trends Neurosci 45:346–357.
- Hasson U, Ghazanfar AA, Galantucci B, Garrod S, Keysers C (2012): Brain-to-Brain coupling: A mechanism for creating and sharing a social world. Trends Cogn Sci 16:114–121.
- Mayo O, Lavidor M, Gordon I (2021): Interpersonal autonomic nervous system synchrony and its association to relationship and performance - A systematic review and meta-analysis. Physiol Behav 235:113391.
- Stolk A (2014): In Sync: Metaphor, mechanism or marker of mutual understanding? J Neurosci 34:5397–5398.