



Research article

Reduced precision of motor and perceptual rhythmic timing in autistic adults

Jonathan Cannon^{a,*}, Annie Cardinaux^b, Lindsay Bungert^b, Cindy Li^{b,c}, Pawan Sinha^b

^a Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada

^b Department of Brain & Cognitive Science, MIT, Cambridge, MA, USA

^c McGovern Institute, MIT, Cambridge, MA, USA

A B S T R A C T

Recent results suggest that autistic individuals exhibit reduced accuracy compared to non-autistic peers in temporally coordinating their actions with predictable external cues, e.g., synchronizing finger taps to an auditory metronome. However, it is not yet clear whether these difficulties are driven primarily by motor differences or extend into perceptual rhythmic timing tasks. We recruited autistic and non-autistic participants for an online study testing both finger tapping synchronization and continuation as well as rhythmic time perception (anisochrony detection). We fractionated each participant's synchronization results into parameters representing error correction, motor noise, and internal time-keeper noise, and also investigated error-correcting responses to small metronome timing perturbations. Contrary to previous work, we did not find strong evidence for reduced synchronization error correction. However, we found compelling evidence for noisier internal rhythmic timekeeping in the synchronization, continuation, and perceptual components of the experiment. These results suggest that noisier internal rhythmic timing processes underlie some sensorimotor coordination challenges in autism.

1. Introduction

Autism spectrum disorder (ASD) is defined primarily in terms of a set of functional competencies in social settings [1]. However, it is also observed to be associated with a multiplicity of differences in sensory perception [2] and motor coordination [3–6]. To unify these observations, recent proposals have attempted to trace the defining social function symptomatology back to these more basic perceptual and sensorimotor differences [6–8].

One causal pathway by which sensorimotor differences might develop into social challenges is through impaired interpersonal synchronization. Coordination of one's own actions with others' requires rapid and precise sensorimotor processing, and reduced ability to synchronize could lead to difficulties in social learning, communication, and developing a sense of social connectedness [9]. Accurate interpersonal synchronization does indeed seem to be impaired in autism [10–12], as does synchronization of finger tapping with a simple metronome [13–15] (though see Ref. [16] for negative results), suggesting that nonsocial sensorimotor differences could potentially underlie difficulties in social coordination.

Synchronization with a metronome is also relevant to ASD in light of the hypothesis of “predictive impairment” in autism [8]. Tapping along with a metronome requires temporally precise prediction of each click, expressed through precisely timed movements. A recent systematic review of the literature on ASD and prediction [17] found that the spontaneous predictive engagement of motor processes seems to be impaired in autism. Although synchronized tapping in an experimental setting is not “spontaneous,” the process

* Corresponding author.

E-mail address: cannoj9@mcmaster.ca (J. Cannon).

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of prediction and error correction seems to be at least partially unconscious [18] and may draw on the same mechanisms that incline the human organism toward spontaneous movement to rhythm [19]. Further, synchronized finger tapping requires precise time perception and time interval reproduction, faculties that have been hypothesized to be compromised in autism [20]. A recent systematic review has shown that the literature on time perception in ASD is equivocal with few consistent differences between ASD and NT participants [21], but none of the reviewed studies looked specifically at rhythmic time perception.

Synchronized finger-tapping is generally thought to be divisible into two processes, at least partially distinct from each other: the production of a steady sequence of taps, and the adjustment of motor timing to correct for small timing errors relative to the reference rhythm. A recent pair of studies by Vishne et al. (2021) [14] and Kasten et al. (2023) [15] have provided evidence that error correction is reduced in autistic adults, whereas steadiness of timing appears to be intact. However, the process of synchronization can be further dissected: both of these two processes could be impaired by motor or by non-motor difficulties. Producing a steady sequence of taps is often modeled as the covert internal production of a series of even time intervals that are then expressed as motoric output [22]. Thus,

Table 1
Participant characteristics.

| | NA | ASD | p-value |
|---|--------------|--------------|-----------------------------|
| N | 38 | 43 | — |
| N (usable continuation data) | 34 | 35 | — |
| N (useable phase correction data) | 37 | 38 | — |
| ADHD ^a | 0 (excluded) | 17 | — |
| Age ^a | 31.4 | 30.8 | T-test: $p = 0.74$ |
| IQ (Test My Brain) | 28.3 | 28.8 | T-test: $p = 0.49$ |
| Sex ^b | 18 M, 20 F | 16 M, 27 F | Chi-square test: $p = 0.36$ |
| Gender ^c | 3 GD, 35 Cis | 9 GD, 34 Cis | — |
| Music training (1-6 scale; see Supplementary Information) | 2.58 | 3.98 | T-test: $p = 0.003$ |
| Musical sophistication (1-6 scale; see Supplementary Information) | 2.24 | 2.44 | T-test: $p = 0.39$ |

^a Self-reported

^b Self-reported sex assigned at birth

^c Self-reported gender identity

GD = gender diverse (gender identity incongruent with reported sex)

Cis = cis-gender (gender identity congruent with reported sex)

steady tapping could be impaired by noisy internal timekeeping (“timekeeper noise”) or noisy motor actuation (“motor noise”). Correction of timing errors requires sensory processing of the precise timing of each sound event, followed by adjustments to subsequent motor timing. Thus, error correction could be impaired by poor sensory timing resolution or by difficulty updating ongoing motor programs. It is not yet clear whether differences in synchronization in autistic adults are primarily motoric or are attributable to differences in internal rhythmic timekeeping and time perception.

Here, we build on existing literature on synchronization in ASD by isolating a non-motor component of the synchronization using a purely perceptual timing task, detection of anisochrony (deviation from steadiness in a metronome). We expected that our results would show that tapping error correction was impaired as in previous work [14,15], and preregistered this hypothesis and our planned comparisons online at <https://osf.io/be8fc/>. A group difference in the perceptual task would indicate that these differences stemmed at least partially from a strictly perceptual timing impairment, whereas a lack of group difference would indicate that they were driven primarily by motor or sensorimotor integration challenges.

2. Methods

2.1. Participants

81 adults aged 18–50 years (43 autistic, 38 non-autistic) consented to voluntarily participate in this online research study and were included in the final data analysis. (In this manuscript we primarily employ identity first terminology [i.e. “autistic”] to reflect the preference expressed by many autistic individuals [23].) These participants were derived from an initial pool of 378 adults (310 autistic, 108 non-autistic) that was narrowed down according to the screening criteria listed below and further narrowed by exclusions for poor data quality, as discussed in 2.3.1.3. The screening process and tasks were completed online via each participant’s personal computer. Additional participant characterization details are summarized in Table 1.

The 43 autistic participants all had a clinical diagnosis of autism spectrum disorder. Autistic (ASD) participants were recruited through the Simons Foundation Powering Autism Research database [24] through a multi-step screening process. Participants were first identified as eligible through SPARK’s existing characterization measures based on a clinical diagnosis of ASD, plus the criteria listed below. The SPARK database has been confirmed to have a high degree of diagnostic validity [25]. All ASD participants were located in the United States.

The 38 non-autistic (NA) participants were recruited through Prolific (<https://prolific.com>), an online portal to recruit and screen participants for online research. NA participants were recruited from the United States.

Potential participants were first filtered using pre-screening characteristics via SPARK or Prolific, based on data they had provided upon registering with either platform. Interested participants who were eligible based on the pre-screening filtering then completed a study eligibility screening questionnaire that determined their final eligibility for the study. If eligible, they were invited to continue with the experiments. Exclusion criteria for both groups included self-report of any history of head trauma (resulting in concussion), seizures, hearing conditions, color-blindness, and prematurity. Only participants who self-reported English as their native language (including bilingual or multilingual individuals) were included. Additional exclusion criteria for the ASD group included a self-reported set of possible ASD diagnostic confounds: schizophrenia, cognitive fetal alcohol syndrome, brain infections like encephalitis or meningitis, insufficient oxygen at birth with NICU stay, and any developmental delays or impairment due to another medical condition or exposure. Additional exclusion criteria for the NA group included a self-report of any history of diagnosis of psychiatric,

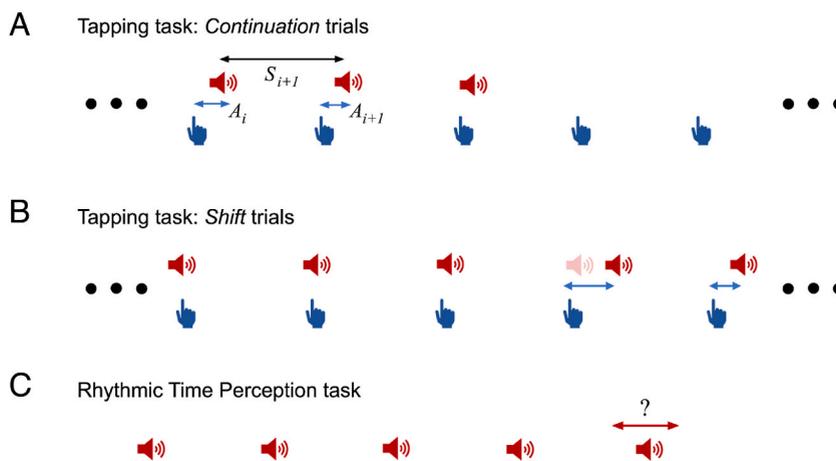


Fig. 1. Illustration of tasks. A) In *Continuation* trials of the Tapping task, participants were asked to tap in synchrony with a steady metronome, then continue a steady rhythm after the metronome ended. Inter-stimulus intervals S_i and tap/tone asynchronies A_i are illustrated. B) In *Shift* trials of the Tapping task, participants tapped with a metronome with interspersed timing irregularities (“shifts”). The asynchrony at each shift was compared to the asynchrony immediately following the shift as a measure of error correction. C) In the Rhythmic Time Perception task, participants listened to short metronomes with the last tone shifted in time, and reported whether the last tone was early or late.

mood, or learning disorder, or medications to treat these conditions, including any antipsychotic medication. All participants completed the Test My Brain matrix reasoning subtest [26], a validated and normed measure of nonverbal intellectual ability comparable to other standardized measures of nonverbal IQ. In the matrix reasoning subtest, participants must identify the image that completes an incomplete matrix based on a logical rule. Test My Brain matrix reasoning scores are referred to below as “IQ” for easy interpretation. Only individuals who achieved a score of 20 or above on the matrix reasoning subtest (i.e. within ~ 2.75 standard deviations below the mean of 28.8) were included in the study.

The research study was approved by the MIT Committee On the Use of Humans as Experimental Subjects (COUHES), in accordance with the ethical standards in the Declaration of Helsinki. Participants could opt out of the study at any time and were compensated for the portion of the study that they completed. Compensation was not linked to accuracy of task performance.

2.2. Setup

Tasks described below were built and presented via the online experiment interface Gorilla (<https://gorilla.sc>). Screening and characterization questionnaire responses were collected via Qualtrics (<https://www.qualtrics.com>). Participants were instructed to complete the experimental session online using a laptop computer in a quiet, distraction-free environment. They were asked *not* to use headphones due to the requirements of the finger-tapping system described below. Task instructions were delivered to participants through on-screen text and concurrent audio.

2.3. Experiments and analysis

During the online testing session, participants completed two experimental tasks, 1) Tapping (Fig. 1A and B) and 2) Rhythmic Time Perception (Fig. 1C).

2.3.1. Tapping task

Recording System. Finger-tapping data was collected and analyzed using the REPP system – see Ref. [27] for complete details. The principle of the REPP tap recording system is to play a stimulus through the participant’s laptop speakers, record their tapping with the laptop onboard microphone, and simultaneously record the stimulus, including an initial and final marker sound, to align it with the taps. This tap recording system allowed us to circumvent any keystroke-logging jitter that might have posed a problem in a key-tapping task, and ideally to record taps with zero latency relative to the stimuli. In practice, we found that some participant recordings were slightly longer or shorter than the intended duration of the stimuli, presumably due to slight browser-related discrepancies in playback or recording rate. We dealt with these as described below in 2.3.2 (Audio Recording Analysis).

Calibration. Participants were first asked to set their laptop speaker volume so that the beeps were “loud, but not uncomfortably loud.” They were then guided through a process of playing sample stimuli and tapping along as their microphone recorded. They were asked to listen to the resulting recordings to ensure that marker sounds and taps were clearly audible and there was no interfering noise. Based on personal communications with the REPP creators, we were able to anticipate and address potential data quality issues in participants’ recordings resulting from the need for simultaneous playback and recording. However, this did not eliminate all data quality issues. During later stages of recruitment, participants were immediately excluded if they reported problems with their recordings, resulting in fewer post-hoc exclusions. (The criteria used to exclude datasets are described in 2.3.3.)

Stimuli. On each trial, participants listened to a ~ 1 min stimulus consisting of a sequence of beeps (1000Hz, 50 ms duration, 5 ms ramp-up and ramp-down) and tapped along with the beeps on a solid, flat surface on their laptop outside the trackpad and keyboard areas. Participants listened and tapped along to five stimulus sequence types (*Practice*, *Continuation*, and three kinds of *Shift* sequences). Each stimulus was accompanied by a visual timer showing how long the trial would last and when the participant could stop tapping. The *Continuation* stimulus (Fig. 1A) consisted of 56 beeps with a constant inter-beep interval of 700 ms, followed by 15 s during which participants were instructed to continue tapping steadily. The *Practice* stimulus was a shorter version of the same. The three *Shift* stimuli (Fig. 1B) each consisted of a sequence in which beeps occurred metronomically with a constant inter-beep interval of 700 ms except for eight perturbed intervals: perturbations of size -50 ms, -25 ms, $+25$ ms, and $+50$ ms (where negative numbers reflect early beeps and positive numbers reflect late beeps) were each repeated twice. In each of the three *Shift* stimuli, these perturbed intervals occurred in a random order, preceded by 7–9 beeps and separated from each other by 5–7 beeps. The stimuli were presented in the following order:

Practice, *Continuation*, *Shift1*, *Shift2*, *Shift3*, (short break), *Shift1*, *Continuation*, *Shift2*, *Shift3*, (short break), *Shift1*, *Shift2*, *Shift3*, *Continuation*.

This order was chosen so that each of the four main stimuli – *Continuation*, *Shift1*, *Shift2*, and *Shift3* – was presented three times for a total of 12 trials, no stimulus occurred twice in a row, and we could compare a *Continuation* trial at the beginning and end to detect any systematic changes over the course of the experiment.

2.3.2. Tapping task analysis

Audio Recording Analysis. Trial recordings were reviewed for data quality issues and excluded according to the procedures described in the next paragraph. Participants with more than one excluded trial were excluded from further analysis. This resulted in the exclusion of 53 participants in the ASD group and 29 participants in the NA group. The high number of exclusions was expected based on the experiences of the REPP development team (N. Jacoby and M. Anglada-Tort, personal communication, March 3, 2022).

Recordings were analyzed according to the basic protocol for REPP recording analysis [27], updated with a progressive

threshold-lowering procedure to maximize the number of useable data sets. Each recording was analyzed by first extracting tap times and marker times based on first threshold-crossing times. The amplitude threshold for marker sounds was progressively lowered until all of the marker sounds could be detected unambiguously; the amplitude threshold for taps was then progressively lowered until a sufficient number of taps was detected (56 taps for *Shift* stimuli, 60 taps for *Continuation* stimuli). If the threshold-lowering procedure was not successful in identifying all marker sounds and an appropriate number of taps, presumably due to hardware or software problems with the playback/recording setup, the trial was excluded from further analysis.

The length of the recording was compared to the length of the original stimulus. If the time separation between the initial and final marker sounds was more than 100 ms longer or shorter than the corresponding separation in the original stimulus (indicating dropped recording frames or other irregularities during recording), the trial was excluded. Otherwise, any deviation between the original stimulus duration and the recorded stimulus duration was compensated for by linearly scaling the tap time sequence to align the beginning and ending markers with those of the original stimulus. In principle, the timing irregularities that gave rise to this slight stretching could have accumulated nonlinearly, leading to drift in the asynchrony time series; we applied high-pass filtering to the asynchrony time series to remove drift in order to evaluate this as a possible source of group differences (see Results 3.1.1).

Synchronization Analysis. Every beep time t_{beep} in the synchronization phase of the Tapping trials following the *Practice* trial was paired with its nearest tap time t_{tap} . Beeps whose nearest taps preceded or followed them by more than 200 ms were excluded from this analysis because they could not be unambiguously associated with a tap. For all other tap times, the “asynchrony” A was defined as $t_{tap} - t_{beep}$. A mean asynchrony μ_A and a standard deviation of asynchronies σ_A was calculated for each trial, and then averaged over all trials for each participant. Asynchrony standard deviation σ_A was log transformed for comparison between groups to adjust for the skewed, strictly positive distribution of the standard deviations.

The series of asynchronies for each trial was shifted to zero mean on each trial by subtracting off the mean asynchrony μ_A for that trial. Then it was used to fit an error correction model in which each asynchrony was produced as a linear correction of the previous asynchrony plus motor and timekeeper noise, as described in Ref. [28]:

$$A_{i+1} = (1 - \alpha)A_i + T_i - S_{i+1} + M_{i+1} - M_i$$

where α is a parameter representing the thoroughness of the ongoing error correction process (“ongoing error correction”), S_{i+1} is the $i + 1$ inter-beep interval, T_i is a time interval generated by an internal timekeeper with standard deviation σ_{ST} (“synchronization timekeeper noise”), and M_i is the execution time with standard deviation σ_{SM} (“synchronization motor noise”). Model fitting was performed using the bounded general least squares method detailed in Ref. [28], omitting missing asynchronies from the model fit. Noise terms were log transformed for comparison between groups to adjust for skewed, strictly positive distributions.

Continuation Analysis. Statistics for inter-tap intervals during continuation were calculated for each participant in which five or more continuation taps were detected for each *Continuation* trial. This left groups of size $N = 34$ (NA) and $N = 35$ (ASD). Only inter-tap intervals between 400 ms and 1000 ms were included in the analysis in order to exclude situations where taps were not detected or were mistaken for two taps in rapid succession. We calculated the mean continuation interval μ_C and the standard deviation of these intervals σ_C (“continuation noise”) for each *Continuation* trial, and then took the means of these values across trials to calculate a value of μ_C and σ_C for each participant.

Perturbation Correction Analysis. Phase correction responses (PCRs) were calculated as follows. Tapping responses to time shifts of each of the four shift sizes were pooled across all 9 *Shift* trials. Responses were included in the analysis if the beeps preceding,

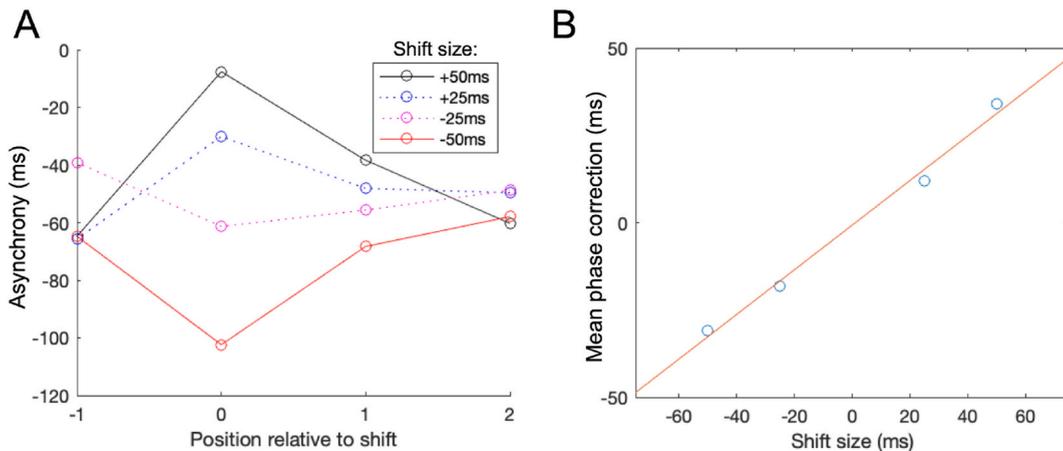


Fig. 2. Calculating phase correction response to phase shift perturbations (illustrated for an example participant). A) Mean asynchronies for each shift size, immediately preceding, coinciding with, and following perturbations for an example participant from the ASD group. B) For each perturbation, we found the difference between the asynchrony at the perturbation and the asynchrony immediately following it, which defined the phase correction. We fit a line to the mean phase corrections for each perturbation size; the slope of this line was a_{PCR} , the “perturbation error correction”.

coinciding with, and following the time shifted beep were all successfully paired with a tap within ± 350 ms. (Note that we did not use the more stringent ± 200 ms criterion for this analysis in order to preserve as much data as possible.) Mean asynchronies preceding and following each shift size for an example participant are plotted in Fig. 2A. We verified that all participants produced valid data for at least 9 out of 18 shifts for each of the four shift sizes. For each shift response at beep index i , the “phase correction” was defined as the difference $A_{i+1} - A_i$. A mean phase correction was calculated for each of the four shift sizes and plotted as a function of shift size

Table 2
Group differences across original and balanced groups.

| | Original groups | Naive matching | Genetic matching with replacement |
|--|--|--|---|
| N | NA: 38 ASD: 43 | NA: 19 ASD: 27 | — |
| Asynchrony standard deviation σ_A^a | NA: 47.6ms ASD: 59.2ms $p = 0.10$ | NA: 39.1ms ASD: 69.9ms $p < 0.001$ | NA: 41.4ms ASD: 59.8ms $p < 0.001$ |
| Synchronization timekeeper noise $\sigma_{ST}^{* a,b}$ | NA: 23.4ms ASD: 27.1ms $p = 0.013$ | NA: 22.6ms ASD: 28.0ms $p = 0.004$ | NA: 23.3ms ASD: 29.2ms $p < 0.001$ |
| Perceptual noise $\sigma_p^{* a}$ | NA: 46.6ms ASD: 61.6ms $p = 0.022$ | NA: 44.3ms ASD: 68.9ms $p = 0.012$ | NA: 46.1ms ASD: 64.7ms $p < 0.001$ |
| Continuation noise σ_C^a | NA: 28.2ms (N=34) ASD: 35.8ms (N=35) $p = 0.009$ | NA: 27.5ms (N=16) ASD: 37.0ms (N=23) $p = 0.013$ | — (not available for matched groups due to exclusions) |
| Ongoing error correction $\alpha^{* b}$ | NA: 0.42 ASD: 0.42 $p = 0.79$ | NA: 0.44 ASD: 0.38 $p = 0.09$ | NA: 0.46 ASD: 0.46 $p = 0.99$ |
| Perturbation error correction α_{PCR}^* | NA: 0.64 ASD: 0.55 $p = 0.06$ | NA: 0.65 ASD: 0.54 $p = 0.12$ | NA: 0.68 ASD: 0.53 $p < 0.001$ |

Cells are shaded by group difference significance as measured by t-test p-value, where darker cells indicate lower p values.

* Variable pre-registered for comparison

^a T-tests performed on log of variable due to asymmetric distribution

^b Based on fitting an error correction model

(Fig. 2B). The error correction factor α_{PCR} (“perturbation error correction”) was calculated as the slope of a regression line fit to these four points.

2.3.3. Rhythmic time perception task

A second experiment performed with the same participants evaluated the ability to discern precise relative timing of rhythmic auditory events. For each stimulus, participants were asked to judge whether the last beep in a sequence was early or late, and answer by selecting one of four options: “Early (confident)”, “Early (uncertain)”, “Late (uncertain)”, or “Late (confident)” (Fig. 1C).

Stimuli. Stimuli used the same beeps and base inter-onset interval (700 ms) as the tapping experiment. Stimuli consisted of 4, 5, or 6 “lead-in” beeps; this variety was intended to avoid the participant knowing a priori which beep would be last, and thus to avoid measuring the participants’ ability to direct attention toward a known final beep. The lead-in beeps were followed by a final beep shifted from isochrony by either -150 ms, -100 ms, -60 ms, -30 ms, -15 ms, 0 ms, 15 ms, 30 ms, 60 ms, 100 ms, or 150 ms. Each shift was paired with each number of lead-in beeps three times, plus an additional pairing for the 5 lead-in beep condition, for a total of 10 stimuli per shift condition (110 stimuli total). The order of stimuli was pseudorandomized, with the same order for all participants.

2.3.4. Rhythmic timing experiment analysis

We first checked that participants understood the task by comparing the “early” response rate for the two largest negative (early) shifts and the two largest positive (late) shifts. If the “early” rate for large early shifts did not exceed the “early” rate for large late shifts by at least 0.3, indicating understanding of the task and some capacity and intent to perform it accurately, the participant was excluded from analysis. This led to the exclusion of 1 NT participant and 12 ASD participants. This difference in exclusion rates is addressed in Results and Discussion below.

For each participant, the fraction of “early” responses E for each shift value s was fit with a logistic curve:

$$E = \frac{1}{1 + e^{-(k+\beta s)}}$$

Logistic curves were fit using logistic regression with ridge regularization ($\lambda = 0.001$) to avoid extreme outliers by penalizing very large parameters. The “point of subjective isochrony” (PSI) was defined as the shift value s for which $E = 1/2$, and was calculated as

$$PSI = -\frac{k}{\beta}.$$

Finally, we used β to estimate the imprecision of internally-produced time intervals. We assumed that individuals produced early/late responses by measuring the final time intervals in each sequence relative to an internally produced time interval generated according to a Gaussian distribution with mean equal to the individual’s PSI and standard deviation σ_p (“perceptual timing noise”). According to these assumptions, the slope β would be directly determined by σ_p according to the relation $\beta = \frac{4}{\sigma_p \sqrt{2\pi}}$. Thus, we could estimate σ_p for each individual based on their measured psychometric curve: $\sigma_p = \frac{4}{\beta \sqrt{2\pi}}$.

2.3.5. Additional data collected

In addition to taking the Test My Brain matrix reasoning subtest as discussed above, all participants answered a set of questions quantifying their musical experience and sophistication adapted from the Goldsmith Musical Sophistication Index [29] and the Ollen Musical Sophistication Index [30,31], including years of musical training and self-designated musical sophistication on scales of 1–6. Results are reported in Table 1. All questions are included in the Supplementary Information.

2.3.6. Analysis of group differences

We preregistered an analysis plan of comparing performance between groups using ANOVAs. However, our samples turned out to be seriously imbalanced in years of musical training (as measured on a 1–6 scale: see Supplementary Information), with significantly more musical training in the ASD group. Therefore, we applied two approaches to balancing the two groups. We first produced “naively balanced” groups by limiting our sample to individuals with between 2 and 9 years of music training; this produced groups that were well-matched in age, IQ, musical training, and self-designated musical sophistication. We next produced “matched” groups using multivariate matching on age, IQ, and music training via the genetic matching algorithm in the R package `Matching` [32]. Since the matching package provided weighted t -test results, we departed from our preregistered ANOVA plan and instead reported t -test results for all group comparisons. Standard deviations measures were necessarily positive and therefore formed skewed distributions over participants, so these were subjected to t -tests after a log transform except where otherwise noted. All comparisons are reported in Table 2. In the text, we report the results of the simple t -test on the original groups (described in Table 1) except where otherwise specified.

3. Results

3.1. Tapping task

3.1.1. Synchronization

The ASD group showed a slightly but not significantly larger standard deviation of asynchronies (NA: 47.6 ms, ASD: 59.2 ms, $p =$

0.10) (Fig. 3A). In order to separate possible sources of asynchrony variability (which may be large due to timekeeper noise, motor noise, or weak ongoing correction of tapping errors), we fit an error-correction model to each trial of each participant using the bGLS method as described above and in our preregistration, producing estimates of ongoing error correction α , synchronization timekeeper noise σ_{ST} , and synchronization motor noise σ_{SM} for each trial and then averaging them to produce average estimates for each participant (Fig. 3B, C, and 3D). Ongoing error correction α did not differ significantly between groups (NA: 0.42, ASD: 0.42, $p = 0.79$). Synchronization motor noise σ_{SM} was marginally higher in the ASD group (NA: 4.98 ms, ASD: 6.65 ms, $p = 0.07$, no log transform due to zero values). However, the ASD group showed significantly greater synchronization timekeeper noise σ_{ST} (NA: 23.4 ms, ASD: 27.1 ms, $p = 0.013$).

Fitting a simpler error correction model with only a single combined noise term using simple regression (as described in Supplementary Information) produced similar results: error correction did not significantly differ between groups (NA: 0.41, ASD: 0.41, $p = 0.85$), but the ASD group showed significantly greater noise (NA: 30.3 ms, ASD: 35.7 ms, $p = 0.008$).

To ensure that any group differences were not attributable to drift in the mean asynchrony, which could have represented an

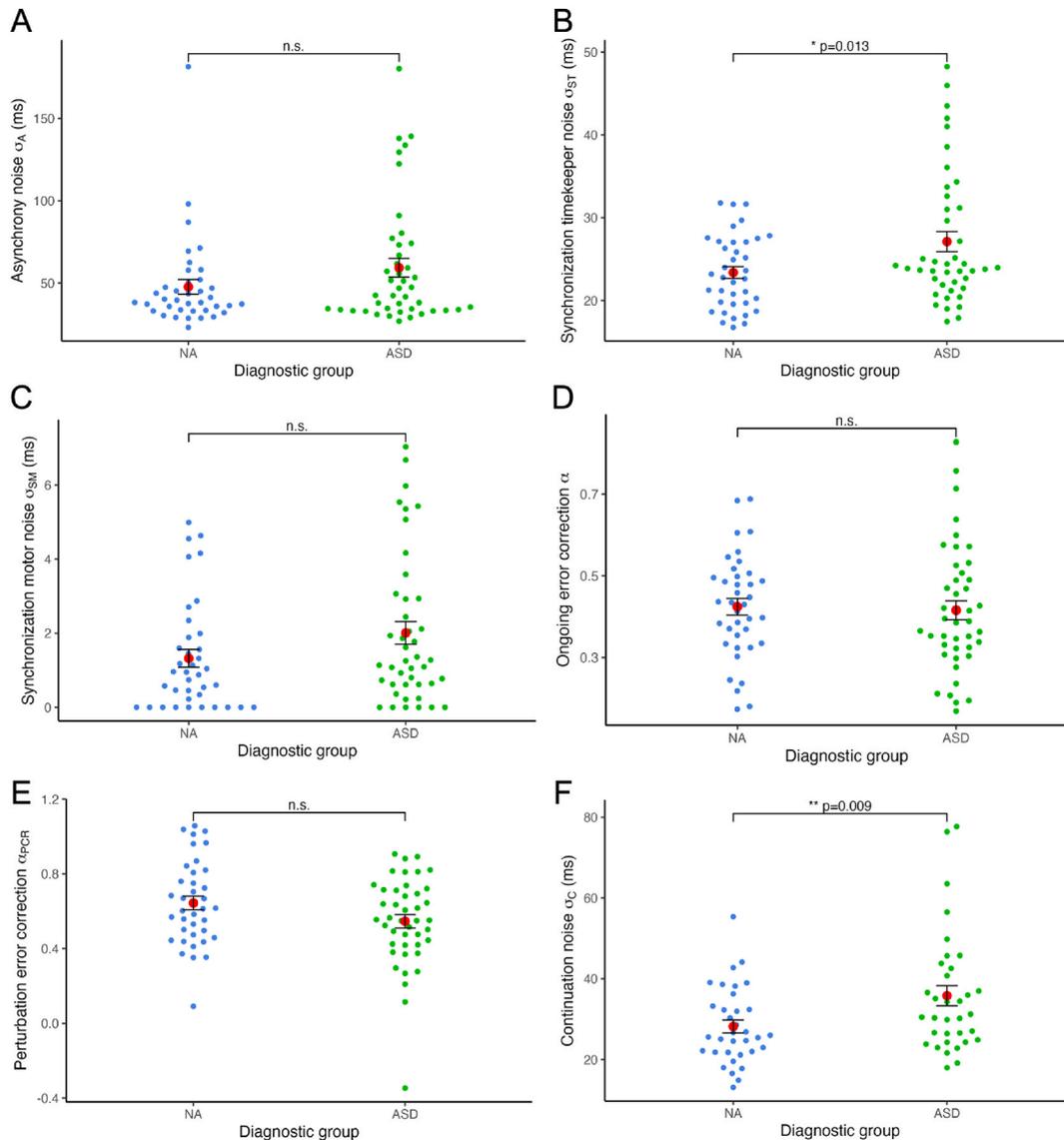


Fig. 3. Tapping task results (Shift and Continuation trials). A) Standard deviations of tap/tone asynchronies σ_A (both trial types) did not differ significantly between groups. B) Synchronization timekeeper noise σ_{ST} (based on model fit, both trial types) was significantly higher in the ASD group. C) Synchronization motor noise σ_{SM} (based on model fit, both trial types) was marginally but not significantly higher in the ASD group. D) Ongoing error correction α (based on model fit, both trial types) did not differ significantly between groups. E) Correction of perturbation-induced errors (Shift trials only) was marginally but not significantly weaker in the ASD group. F) Continuation noise σ_C (Continuation trials only) was significantly higher in the ASD group.

unmodeled sensorimotor drift process or might have been introduced in the data by nonlinear accumulation of timing discrepancies in recording or playback, we high-pass filtered the asynchrony time series to remove drift. We first interpolated missing taps in each asynchrony time series, then applied a high-pass filter with cut-off 1 cycle per 20 taps, and finally fit the full model. The results were once again similar (see Supplementary Information): error correction did not significantly differ between groups (NA: 0.81, ASD: 0.83, $p = 0.54$), but the ASD group showed significantly greater synchronization timekeeper noise (NA: 22.9 ms, ASD: 26.2 ms, $p = 0.02$).

To ensure that there were no substantial practice or boredom effects on the measures of interest, we performed an exploratory analysis of the change in synchronization timekeeper noise σ_{ST} and ongoing error correction α from the first to the last *Continuation* trial for all participants who provided good data for both (37 NA, 35 ASD). One-sample t-tests in the ASD group found no significant change over the course of the experiment in synchronization timekeeper noise (mean pre-post $\Delta\sigma_{ST} = +0.047$, $t(34) = 0.020$, $p = 0.98$) or ongoing error correction (mean pre-post $\Delta\alpha = -0.046$, $t(34) = -1.33$, $p = 0.19$). The same analysis in the NA group similarly showed no significant change in synchronization timekeeper noise (mean pre-post $\Delta\sigma_{ST} = +0.62$, $t(36) = 0.54$, $p = 0.59$) or ongoing error correction (mean pre-post $\Delta\alpha = +0.009$, $t(36) = 0.21$, $p = 0.84$). Neither pre-post change differed significantly between groups (α : $t(68.3) = 1.01$, $p = 0.31$) ($\Delta\sigma_{ST}$: $t(68.3) = 0.25$, $p = 0.80$).

3.1.2. Perturbation error correction analysis

We calculated the strength of the error correction response following timing perturbations as described in 2.3.2 (Perturbation Correction Analysis). Perturbation error correction α_{PCR} was noticeably weaker (i.e., smaller correction to the tap following a perturbation) in the ASD group, but the difference did not rise to the level of statistical significance (NA: 0.63, ASD: 0.55, $p = 0.061$) (Fig. 3E).

3.1.3. Continuation Analysis

Using only the *Continuation* trials, and including only participants with sufficient useable continuation data (34 NA, 35 ASD), we compared the noise in continuation interval production across groups. The ASD group showed significantly higher continuation noise σ_C (NA: 28.2 ms, ASD: 35.8 ms, $p = 0.009$) (Fig. 3F).

3.2. Rhythmic time perception task

We next compared anisochrony detection between the two groups. The ASD group made fewer correct perceptual judgments of deviation from isochrony, but the difference did not rise to the level of significance (NA: 0.75, ASD: 0.72, $p = 0.068$). When we averaged responses over the population for each group at each degree of anisochrony, the group-level psychometric curve was less steep for the ASD group, indicating less perceptual sensitivity to anisochrony (Fig. 4A). We fit sigmoidal psychometric curves to each individual's average response as a function of shift magnitude to calculate their point of subjective isochrony (PSI) and their perceptual timing noise σ_P (a measure of anisochrony judgement imprecision) as described in 2.3.4 above. We found that PSI did not differ significantly between groups (NA: 9.3 ms, ASD: 13.5 ms, $p = 0.43$), but that the ASD group showed significantly higher perceptual timing noise σ_P (NA: 46.6 ms, ASD: 61.6 ms, $p = 0.02$) (Fig. 4B). This difference was partially driven by two individuals in the ASD group with exceptionally high perceptual timing noise; without these individuals, the difference only trended toward significance ($p = 0.07$). However, note that the substantial difference in performance-related exclusion between the two groups has the effect of reducing this group difference; without these exclusions, the difference would be even more pronounced.

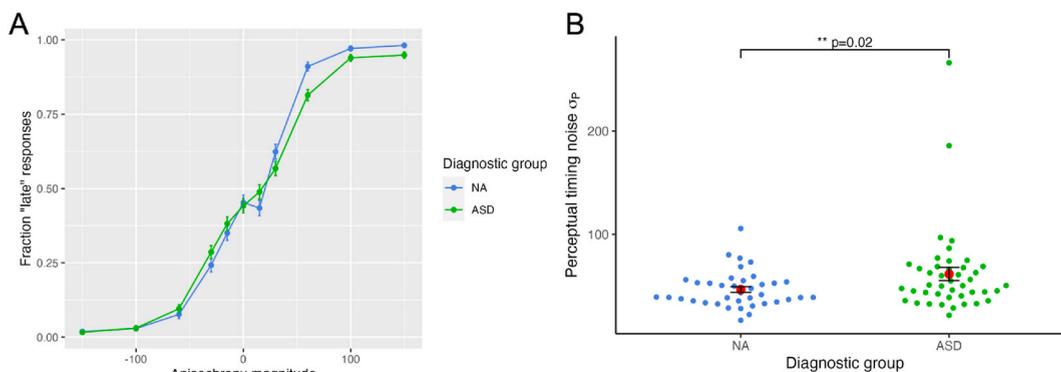


Fig. 4. Rhythmic Time Perception task results. A) The psychometric curve for each group's pooled data was sigmoidal. The ASD group's sigmoid showed a noticeably shallower slope (less precise discrimination of earliness vs. lateness), which translated into a higher degree of perceptual timing noise σ_P . B) Perceptual timing noise σ_P was significantly higher in the ASD group; after excluding two apparent outliers, perceptual timing noise trended higher for the ASD group but did not reach significance.

3.3. Group balancing

Musical training is known to be a predictor of sensorimotor synchronization accuracy [33,34]. We were therefore concerned to find a significant group difference in musical training, with the ASD group reporting more musical training than the NA group. As described in Methods (2.3.4 Analysis of group differences), we took two approaches to rebalancing the groups: we produced “naively balanced” groups by excluding individuals at the two extremes of musical training, and “matched” groups using a multivariate matching that reweighted the influence of different individuals in order to balance the groups on age, IQ, musical training, and self-designated musical sophistication.

We subsequently compared our key variables of interest across the newly balanced groups. The results are shown in Table 2. The group differences in asynchrony standard deviation σ_A , synchronization timekeeper noise σ_{ST} , continuation noise σ_C , and perceptual timing noise σ_P all increased in the newly balanced groups, and in most cases the p-values dropped substantially. The matched groups also showed a highly significant difference in perturbation error correction α_{PCR} , though this difference did not show up in the naively balanced groups.

3.4. Cross-task analysis

Given the apparent group differences in synchronization tapping timekeeper noise and in precision of anisochrony detection, we sought to investigate whether the two differences could stem from the same cause, a greater degree of noise in internal production of isochronous time intervals. We therefore compared perceptual timing noise σ_P to synchronization timekeeper noise σ_{ST} . After log transforming both variables to adjust for positive skew, we found a significant Pearson correlation between perceptual timing noise σ_P and synchronization timekeeper noise σ_{ST} within the ASD group ($R = 0.4$, $p = 0.008$), though not in the NA group ($R = 0.095$, $p = 0.57$) (Fig. 5A).

We were also interested to see whether the group differences in synchronization timekeeper noise σ_{ST} and continuation noise σ_C were similarly linked. We found that the log continuation noise σ_C was very strongly correlated across individuals with the log synchronization timekeeper noise σ_{ST} in both the ASD group ($R = 0.78$, $p < 0.00001$) and the NA group ($R = 0.8$, $p < 0.00001$) (Fig. 5B).

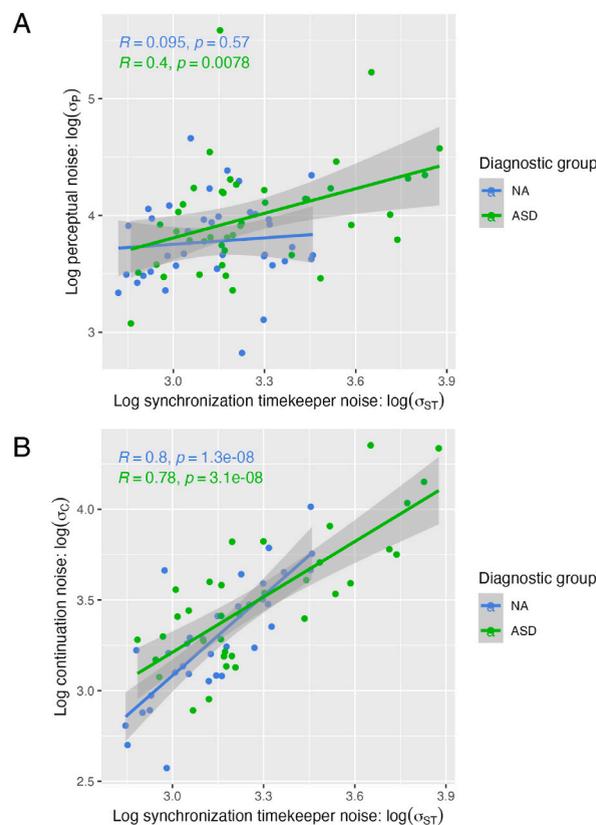


Fig. 5. Relationships among different measures of timing noise. A) Significant correlation within the ASD group between log perceptual timing noise (in the Rhythmic Time Perception task) and log synchronization timekeeper noise (in the Tapping task) suggests that the ASD-linked differences in these two measures may stem from the same underlying group difference. B) A very strong correlation between log synchronization timekeeper noise and log continuation noise in the Tapping task in both groups suggested that these measures might represent the same underlying source of tap timing noise.

4. Discussion

In this set of experiments, autistic and non-autistic individuals completed both a Rhythmic Time Perception task and a synchronization/continuation Tapping task in order to better understand the bases of the reported temporal coordination difficulties in autistic individuals. In agreement with some previous work, we found that the ASD group was less precise in their synchronization to a metronome as measured by standard deviation of asynchronies, though this result was not statistically significant. Two previous reports found that noisier synchronization in ASD groups was attributable to weaker error correction, while measures of tapping noise did not differ between groups [14,15]. By contrast, we found a significant group difference in the noisiness of internal timekeeping during synchronization tapping. This finding was corroborated by significantly noisier continuation tapping in the ASD group, which was strongly correlated with timekeeper noise. Our Rhythmic Time Perception results showed less perceptual timing precision in the ASD group, further reinforcing the conclusion that the ASD group was less precise in rhythmic timing processes. Overall, these results suggest that autistic individuals tend to show broad differences in the production and perception of metronomic regularity, which may have implications for the perception of regular timing in the world as well as interpersonal coordination.

Group differences in measures of motor and perceptual timing noise were partially masked by the fact that our sample of ASD participants was more musically trained than our NA sample. When we balanced the groups by two different approaches, these group differences were, on the whole, accentuated. We did not initially find significant group differences in tapping error correction by either a model-fitting measure or a PCR measure; however, PCR-based error correction was weaker in the ASD group with marginal significance, and emerged as highly significant when the groups were balanced by music training, so we cannot reject the possibility that systematic differences exist in error correction as well. Such differences could be understood as slow integration of sensory information into motor plans, or more generally as slow updating of “internal models,” as discussed in Ref. [14].

A very strong correlation between continuation tapping noise and synchronization tapping timekeeper noise during synchronization in both groups suggests that these measures are quantifying the same source of underlying noise in time interval production. Further, imprecise rhythmic time perception was correlated with synchronization tapping timekeeper noise within the ASD group, suggesting that the ASD-linked differences in perceptual and motor timing we observed may stem from the same underlying source.

Our synchronization results stand in contrast to recent findings [14,15]. On the one hand, our results do not strongly refute previous findings of weaker synchronization error correction in autism: we found a group difference in perturbation error correction in the same direction that rose to the level of significance when groups were matched by music experience. Further, differences in error correction may be more apparent when participants adjust to tempo changes rather than to single interval perturbations. On the other hand, our significant group differences across all three measures of timing noise, including both motor and perceptual measures, are surprising in light of a previous lack of group differences in timing noise during tapping synchronization and continuation.

The discrepancy between the two studies' results could be due to the compositions of our samples of autistic and non-autistic participants. However, it is not clear what type of sample bias could account for the difference between their results and ours by eliminating error correction differences and introducing timekeeper differences. They only recruited participants with little musical training, whereas we had no such exclusion criterion; however, when we balanced our groups to account for group differences in musical training, our multiple group differences in timing noise grew stronger.

One notable difference between our experiment and its predecessor was our online format. Perceptual performance and motor regularity might have been impaired due to distractions in the home environment, and attentional issues might have selectively compromised performance in the ASD group; however, group differences in the three key measures of timing noise persist when all 17 ADHD participants are excluded from the ASD group (see Supplementary Information). Group differences in performance also might have been affected by differences in the number of data-related exclusions in each group. More members of the ASD group were excluded due to extremely poor performance on the perceptual task; including these participants would have made the apparent group difference in perceptual noise even more extreme. Finally, since we were unable to observe participants in their home environments, they may have moved along with the rhythm in the Rhythmic Time Perception task in spite of being instructed not to. Since rhythmic movement improves precision of anisochrony detection in a task similar to the Rhythmic Time Perception task [35], a difference in movement between groups could have contributed to the group difference in these results.

Might there have been subtle differences in the computer systems used by our NA and ASD groups? More ASD participants were excluded due to problems parsing their sound recordings to extract tap times; this might indicate that the ASD group's computer recording setups were on average older or less reliable than those of the NA group, who were drawn from a Prolific-using population experienced in online experiments, but it is not clear how the exclusion of individuals with inadequate technology could bias our results in a specific direction. After our data quality check had screened out any participants with significant disruptions in their tapping sound recordings, there were no obvious differences in the browsers or operating systems used by the two groups. Gorilla. sc pre-loads audio and videos to prevent connection-related delays, and audio playback is designed to be temporally smooth and precise [36]. Further, only systematic irregularities in sound playback could give rise to the group differences observed in perceptual timing noise, whereas only systematic irregularities in sound recording could give rise to the group differences observed in tapping continuation noise; thus, no single technological difference between groups could produce the full spectrum of differences in timing noise that we observed.

These results represent a fundamental, previously unreported difference in auditory rhythmic temporal processing in ASD that manifests in both perceptual and motor timing tasks. A recent meta-analysis shows that most aspects of time perception on the sub-second timescale seem to be intact in autistic adults [21]; however, none of the reviewed literature looked specifically at rhythmic timing, which is known to draw on different neural mechanisms than interval timing [37]. Since our findings run contrary to the general trend of no impairment in sub-second time perception in autism and to the results in two previous tapping studies, it is

important that these results be replicated before they can be taken as authoritative.

We propose two possible explanations for the group differences in rhythmic timing noise we observed (should they prove to be replicable). First, the brain processes that provide a cyclic internal clock may, on average, be noisier in individuals with ASD. This could stem from higher levels of neural variability that have been hypothesized to characterize autism [38,39], although this hypothesis has received mixed experimental support [40,41]. Second, autistic brains may introduce more variable delays in the early stages of auditory event processing. This could also stem from greater neural noise, and would be in keeping with reports of increased intra-participant variability in the latency of EEG sensory evoked potentials [42,43]. However, we would expect such a difference to show up consistently as a group difference in other auditory timing paradigms, which it does not. An experiment manipulating the tempo of auditory cues could discern between these possibilities: in the first case, group differences would increase as tempo slowed, whereas in the second they would not.

Noisier rhythmic timing could underlie certain neural imaging results in autism. Reductions in neural habituation to isochronously repeating auditory stimuli [44,45] could be explained, at least in part, if these stimuli do not *sound* perfectly isochronous to autistic participants but instead seem to repeat at slightly irregular intervals. Similarly, widely-reported reductions in the mismatch negativity potential (MMN) in autism [46], i.e., reductions in the difference between the brain's response to a standard and a deviant (typically pitch- or sound-tone based) auditory stimulus in an isochronous sequence, might be explained by the impression of temporal unpredictability even in regular trains of sounds.

Further research is needed to elucidate the relationship between noisier rhythmic timing and the diagnostic features of autism. However, we can speculate that noisier rhythmic timing might contribute to the emergence of the characteristic symptoms of autism during development. If even temporally regular sequences and other predictable environmental rhythms (including, perhaps, speech rhythms) seem irregular to autistic individuals, this might contribute to difficulty learning predictive models of the physical and social world, leading to social avoidance and/or seeking out of more familiar and predictable conditions [8]. Thus, while our results may not have direct implications for therapies or interventions, they contribute to a better understanding of the brain processes that give rise to difficulties in the lives of people with autism, understanding which may point the way to improvements in quality of life. Our findings highlight the merit of further investigations into rhythmic timing in autistic populations, its possible mechanisms and relationship to the varied characteristics of the autism phenotype, and implications for the provision of effective clinical supports.

5. Limitations of the study

The main limitation of our study is the online format, adopted due to the COVID-19 pandemic. Although we did not observe evidence for failure points in our chain of data collection and analysis, online studies offer limited control over participants' environment, and introduce more potential for unknown variables that could compromise the results. A second limitation is our recruitment approach, which allowed ADHD only in the ASD group (given its common occurrence in this population), and did not exclude on the basis of music training; we have accounted for these factors by comparing the groups after excluding ADHD participants in the ASD group, and by taking several approaches to rebalance the groups by music training. More research using different approaches to participant recruitment and characterization, and ideally conducted in the laboratory is necessary to determine whether our conclusions can be reproduced or generalized.

Interpretation of our results are limited by the fact that even the measures that showed statistically significant group differences overlapped substantially between the two groups. The difference in perceptual timing noise in particular seemed to be accentuated by a few ASD participants with unusually high perceptual timing noise, while most individuals in both groups showed perceptual timing noise in the same range. This is in keeping with the general tendency toward heterogeneity within autistic experimental groups [47, 48], which may be driven by a diversity of genetic subtypes [49,50]. Thus, we cannot make any claims about all individuals with ASD; our results represent only population-level tendencies.

Finally, interpretation of our results in terms of the social differences that characterize autism must be limited by our focus on sequences of timed auditory events and discretely timed movements: social coordination between individuals can be supported by visual or by more complex auditory stimuli, and can be expressed through more continuous and complex movement. Further, participants were aware that they were not synchronizing with another individual, so our tasks were not entirely analogous to true interpersonal interaction. Indeed, research suggests that individuals with autism may interact more easily with machines than humans [51]. Future research should investigate similar tasks with human partners to separate general sensorimotor impairment from difficulties specific to social interactions.

Declarations

This work has not been published or accepted for publication, nor is it under consideration at another journal. Moreover, I would like to declare on behalf of the authors that there are no ethical, financial nor other conflicts of interests and that all authors have seen and approved the manuscript.

Ethics and consent

This study was approved by the MIT Committee On the Use of Humans as Experimental Subjects (COUHES), in accordance with the ethical standards in the Declaration of Helsinki, approval #2009000232. All participants provided consent via online form.

Data accessibility statement

Data and code for stimulus creation and data analysis are available at <https://osf.io/be8fc/>.

CRedit authorship contribution statement

Jonathan Cannon: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Annie Cardinaux:** Writing – review & editing, Writing – original draft, Resources, Project administration, Conceptualization. **Lindsay Bungert:** Writing – review & editing, Writing – original draft, Resources, Project administration. **Cindy Li:** Resources, Project administration. **Pawan Sinha:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pawan Sinha reports financial support was provided by Simons Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.heliyon.2024.e34261>.

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