Differentiated, rather than shared, strategies for time-coordinated action in social and non-social domains in autistic individuals

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Conflict of interest

The authors declare no conflict of interest.

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Data and code availability

The conditions of our ethics approval do not permit public archiving of pseudonymized study data. Readers seeking access to the data should contact the corresponding author. Access to data that do not breach participant confidentiality will be granted to individuals for scientific purposes in accordance with ethical procedures governing the reuse of clinical data, including completion of a formal data sharing agreement. The scripts used for data acquisition and analysis are available at the Open Science Framework.

Authors' contribution

Carola Bloch: Conceptualization, methodology, investigation, data curation, software, formal analysis, writing - original draft, review & editing, visualization, project administration. **Shivakumar Viswanathan**: Methodology, formal analysis, writing - original draft, review & editing, visualization. **Ralf Tepest**: Software, writing - review & editing. **Mathis Jording**: Conceptualization, funding acquisition, writing - review & editing. **Christine M. Falter-Wagner**: Conceptualization, funding acquisition, supervision, project administration, writing - review & editing. **Kai Vogeley**: Conceptualization, funding acquisition, supervision, project administration, writing - review & editing.

Ethical declaration

All data were acquired with a protocol in accordance with the declaration of Helsinki. The study was approved by the ethics committee of the Faculty of Medicine, University of Cologne. All participants provided written informed consent to participate in the study.

Additional information

Considering the role of the stakeholders is important in the choice of language and terminology about autism. In the present work, we have chosen to use identity-first language when referring to individuals and use the term autism spectrum disorder (ASD) when referring to the group based on the designation in the ICD, which was the basis to define the group. The decision to use identity-first language was based on studies that indicate that a majority of people from the autism community in English-speaking countries prefer this form of expression (Keating et al., 2022; Kenny et al., 2016; Monk et al., 2022). However, we also note that person-first language is endorsed by a non-negligible minority of individuals in the aforementioned studies. Individuals with higher levels of internalized stigma deem identity-first language to be offensive (Bury et al., 2022). Furthermore, linguistic factors may influence preferences, as studies from non-English speaking countries have shown a majority preference for person-first language (Buijsman et al., 2022). Additionally, the perspective of the naming person is an important consideration in clinical research contexts (Kenny et al., 2016; Tepest, 2021).

List of abbreviations

ASD	Autism Spectrum Disorder
TD	Typically-Developed
SMS	Sensorimotor Synchronization
SP	Social Pointing
SCE	Synchronization Error
SCE_{vr}	Within-subject standard deviation of SCE
ITI	Inter-Tap-Interval
ITI_{vr}	Within-subject standard deviation of ITI
MAD	Median Absolute Deviation
IOI	Inter-Onset-Interval
LMM	Linear Mixed Model
GLMM	Generalized Linear Mixed Model
EMM	Estimated Marginal Means
LRT	Likelihood Ratio Test
PCA	Principal Component Analysis

Abstract

Autism spectrum disorder (ASD) is a neurodevelopmental condition with a highly heterogeneous adult phenotype that includes social and non-social behavioral characteristics. The link between the characteristics assignable to the different domains remains unresolved. One possibility is that social and non-social behaviors in autism are modulated by a common underlying deficit. However, here we report evidence supporting an alternative concept that is individual-centered rather than deficit-centered. Individuals are assumed to have a distinctive style in the strategies they adopt to perform social and non-social tasks with these styles presumably being structured differently between autistic individuals and typically-developed individuals. We tested this hypothesis for the execution of time-coordinated (synchronized) actions. Participants performed (i) a social task that required synchronized gaze and pointing actions to interact with another person, and (ii) a non-social task that required finger-tapping actions synchronized to periodic stimuli at different time-scales and sensory modalities. In both tasks, synchronization behavior differed between ASD and TD groups. However, a principal component analysis of individual behaviors across tasks revealed associations between social and non-social features for the TD persons but such cross-domain associations were strikingly absent for autistic individuals. The highly differentiated strategies between domains in ASD are inconsistent with a general synchronization deficit and instead highlight the individualized developmental heterogeneity in the acquisition of domain-specific behaviors in ASD. We propose a cognitive model to help disentangle individual-centered from deficit-centered effects in other domains. Our findings reinforce the importance to identify individually differentiated phenotypes to personalize autism therapies.

Keywords: autism, neurodevelopmental conditions, synchronization, cross-domain, adults

1. Introduction

Autism spectrum disorder (ASD) is a neurodevelopmental condition with an estimated global prevalence of nearly 1/100 (Zeidan et al., 2022). A major obstacle in personalizing therapies to support individuals is the heterogeneity of the individual ASD phenotype (Lord et al., 2022). Although persistent deficits in social behavior and communication are important criteria to diagnose ASD (American Psychiatric Association, 2013), the phenotype also includes non-social characteristics such as low-level sensory atypicalities (Coll et al., 2020; Hannant et al., 2016; Rosen et al., 2021; Thye et al., 2018). However, the relationship between these features from the social and non-social domains has remained elusive (Coll et al., 2020; Thye et al., 2018).

A general suggestion is that the features that differentiate ASD and typically-developed (TD) populations are attributable to common underlying factors that modulate behavior in ASD across domains (Happé, 1999; Plaisted, 2001; Rajendran & Mitchell, 2007; van de Cruys et al., 2014; Wimpory et al., 2002). These common underlying factors in ASD have been hypothesized to include deficits in core capabilities such as temporal processing (Falter & Noreika, 2014; Murat Baldwin et al., 2021; Wimpory et al., 2002) and multisensory integration (Murat Baldwin et al., 2021), which could plausibly impact a broad variety of social and non-social behaviors. However, focusing on explaining inter-population differences disregards *individual-specific* factors that can shape behavior across domains. For instance, when a task, such as using a phone, is performed repeatedly, individuals can integrate their attentional, cognitive, and motor resources into a distinctive information processing strategy or "task-set" to efficiently execute the task (Botvinick & Plaut, 2004; Monsell, 2003; Norman & Shallice, 1986; Sakai, 2008). As a task-set can be used for different tasks, this can potentially lead to characteristic similarities in an individual's behavior across tasks, sometimes referred to as the individual's "cognitive style" (Happé, 1999; Kozhevnikov, 2007; Riding, 1997). Therefore, it is conceivable that autistic individuals might employ a distinctive style across social and non-social domains that modulate their behavior in the different domains. Here, we investigated this possibility for the temporal coordination (i.e., synchronization) of actions.

The ability to synchronize the timing of motor outputs to time-varying sensory inputs is crucial in physical contexts, for example, when catching a moving ball. Social interactions with other persons similarly require the synchronization of social-motor outputs to dynamic multisensory inputs within the interacting person. Notably, action synchronization performance has been shown to distinguish ASD from TD populations both in the social domain (de Marchena & Eigsti, 2010; Georgescu et al., 2020; Koehler et al., 2021; Koehne et al., 2016; Xavier et al., 2018) and in the non-social domain (Hannant et al., 2016; Morimoto et al., 2018; Vishne et al., 2021; Whyatt & Craig, 2013). Based on these shared relationships between the social and non-social domains, we evaluated whether the differing synchronization behaviors of ASD and TD populations in both domains indicate group-specific synchronization styles**.**

Participants performed a social and a non-social task (Figure 1). The non-social task was a classical sensorimotor synchronization (SMS) task (Repp & Su, 2013; Rubia et al., 2003) where participants had to synchronize button-presses to periodic pacing stimuli (Figure 2).

The social task was a novel Social Pointing (SP) task that focuses on the role of *intra*-personal (i.e., within-person) action synchronization in *inter*-personal (i.e., between-person) social interactions (Bloch et al., 2019). The synchronization between interacting persons involves reciprocal processes related to, for example, turn-taking dynamics (Levinson, 2016), mimicry of behavior (Chartrand & Lakin, 2013) and the alignment of nonverbal cues (Delaherche et al., 2012). However, inter-personal interaction is also based on another level of synchronization: each person might produce multiple kinds of actions, for example, gestures, gaze changes, and speech. Therefore, successful interaction relies on each person to synchronize their multimodal actions so that these actions are perceived as an integrated communication signal by the counterpart. Examples of this include the intra-personal synchronization of speech with co-speech gestures (De Jonge-Hoekstra et al., 2021; de Marchena & Eigsti, 2010) and gaze with gestures (Bloch et al., 2022; Cañigueral & Hamilton, 2019; Caruana et al., 2021; Conty et al., 2012; Feldman, 2007; Stukenbrock, 2020). In the SP task (Figure 3), participants had to synchronize their gaze and gestures to communicate the location of a target stimulus to a trained partner.

From each task, we identified synchronization features that differed between ASD and TD groups (schematically illustrated as features F1-F6 in Figure 1). Combining these features provided a profile of each individual's overall synchronization behavior. The individual profiles from each group were subjected to a principal component analysis (PCA) to identify multivariate associations between features from the two domains. We hypothesized that the structuring of these cross-domain associations for the ASD and TD groups would reveal their distinctive synchronization styles.

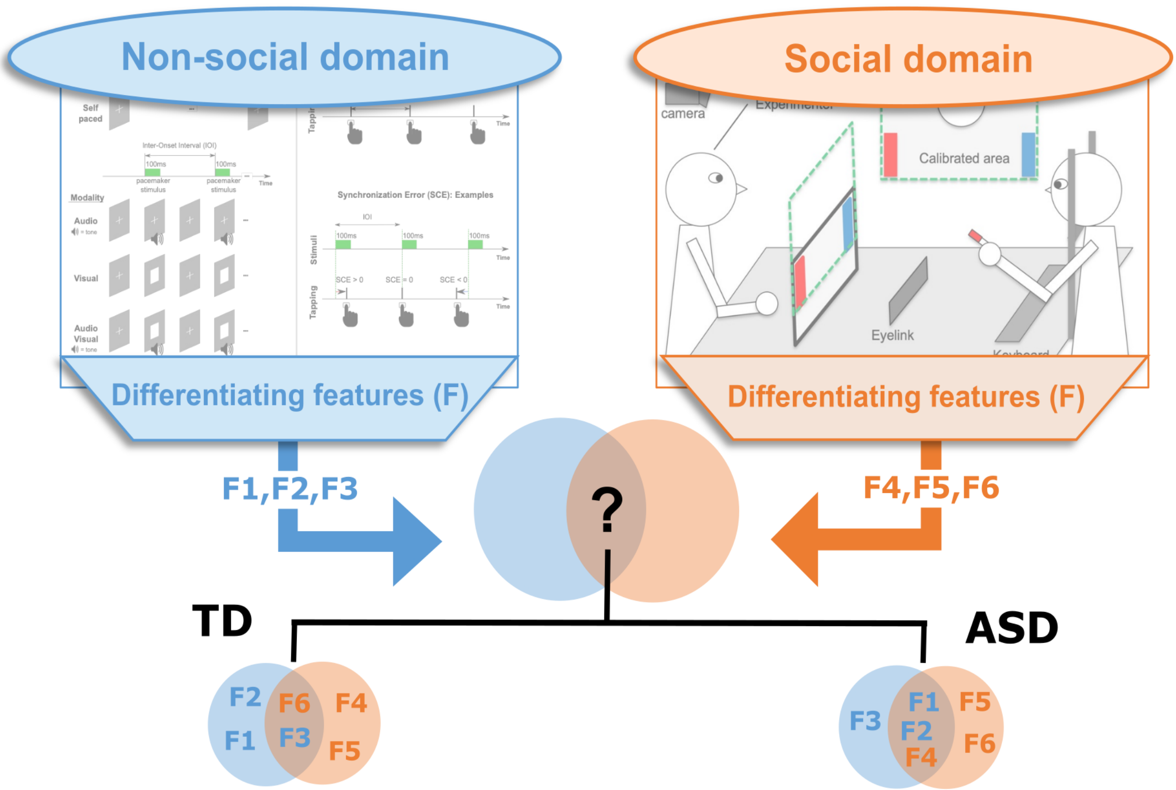

Figure 1. *Schematic of analysis and inference strategy*. We measured synchronization behavior of all participants in a non-social task (sensorimotor synchronization task, expanded version in Figure 2) and a social task (social pointing task, expanded version in Figure 3). We sought to use the synchronization behavior in each domain to extract task features that distinguished the ASD from TD groups. These features were then used to construct each individual's behavioral profile across tasks. The individual profiles were examined separately for each group using principal components analysis (PCA) to identify associations between social and non-social task features. As illustrated by the upper Venn diagram, if the non-social features (blue circle) and social features (orange circle) showed associations (overlapping area "?") then it would be indicative of a generalized synchronization style that modulates behavior across both domains. As illustrated by the lower Venn diagrams, we hypothesized that the cross-domain overlap of features would be different for the ASD and TD groups where, for instance, as schematically illustrated here, the overlap for the TD group involves the non-social feature F3 and social feature F6 for the TD group while the overlap for the ASD group involves non-social features F1 and F2 and social feature F4.

2. Materials and Methods

2.1. Participants

Participants were a group of autistic individuals (N = 24), and a group of TD individuals matched for gender, age and handedness (N = 24). All participants provided their written informed consent before the first (of two) experimental sessions and received financial compensation on completing both experimental sessions. The study protocol was approved by the ethics commission of the medical faculty at the University of Cologne (case number: 16-126) and preregistered in the German register of clinical trials (reference number: DRKS00011271). We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria and whether these were established prior to data analysis, all manipulations, and all measures in the study.

The inclusion/exclusion criteria for all participants were established prior to data analysis and were: age between 18 and 60 years, normal (or corrected-to normal) vision, intact motor capabilities related to arm movements, and no current usage of psychoactive medication (except antidepressants for the ASD group). For inclusion in the ASD group, a confirmed diagnosis of autism according to ICD-10 (World Health Organization, 1993) was required as well as an absence of co-occurring psychiatric or neurological diagnoses with the exception of depression. Due to the high co-occurrence in adult ASD populations (Bloch et al., 2021; Hollocks et al., 2019; Lehnhardt et al., 2013), depression (and the use of antidepressants) was not an exclusion criterion to obtain a representative sample. Participants in the TD group had to be free of psychiatric or neurological diagnoses.

2.2. Sample size justification

Estimating a suitable sample size with a formal power analysis required a quantitative estimate of the expected inter-group difference in synchronization behavior in the SMS and SP tasks. In the absence of prior studies employing this novel combination of tasks (particularly the SP task), we deployed theoretical considerations to derive an effect size estimate from the findings of Falter et al. (2012). In their study, the authors investigated perceptual judgments about event synchrony in autistic adults relative to a control TD group. In their paradigm, participants were presented on each trial with two visual stimuli with variable onset timings and participants judged whether these stimuli appeared at the same time (i.e., simultaneously) or not. Falter et al (2012) found that the simultaneity judgments were suggestive of a higher temporal acuity in the ASD group as compared to the TD group (N = 16 per group). This between-group difference in temporal acuity when judging event synchrony suggested a general relevance to the SMS and SP tasks where multimodal events had to be placed into a synchronized relationship. In the SMS task, a button press has to be timed to coincide with the onset of the pacemaker stimulus. In the SP task, the timing of the gaze onset/offset had to be temporally coordinated with that of the gesture onset/offset.

Based on the centrality of event synchronization in these different tasks, the effect size from the perceptual simultaneity paradigm (Falter et al., 2012) (d = .76) was used as a heuristic estimate of the possible inter-group difference in synchronization performance in the SMS and SP tasks respectively. The required sample size was estimated to be N = 23 (power = 0.8, alpha = 0.05) (Faul et al., 2009). This planned sample size was comparable to other temporal synchrony studies related to ASD (Murat Baldwin et al., 2021).

2.3. Participant recruitment

Autistic participants were recruited at the University Hospital Cologne via the database of the outpatient clinic for autism in adulthood. One participant (aged 18) was recruited via the pediatric outpatient clinic for autism at the University Hospital Cologne. ASD diagnosis was provided by two independent clinicians according to the German national S3 guideline on ASD (Arbeitsgemeinschaft der Wissenschaftlichen Medizinischen Fachgesellschaften, 2016).

28 autistic individuals were initially invited. All individuals had received the diagnosis F84.5. The experimental protocol could not be completed for four (of 28) invited participants: Three participants had ocular particularities that prevented successful eye tracking and one participant decided to terminate the experiment before completion. Therefore, the final ASD sample consisted of

24 individuals (10 identifying as female, 14 identifying as male), aged *M* = 40.84y (min:18y, max: 59y) with handedness (self-reported): left = 3, right = 21.

TD participants from the local population were recruited as pairwise-matches for autistic participants based on age (range ± five years), gender identity, and self-reported handedness. The matched TD group consisted of 24 individuals (10 identifying as female; 14 identifying as male), aged *M* = 37.05y (min: 19y, max: 58y) with an identical number of left/right handers to the ASD group (see Supplementary Material S1 and Supplementary Table S1 for neuropsychological profiles and statistical comparisons).

Data quality exclusions resulted in a reduced sample size for single analyses, see Table A1 in the Appendix for an overview.

2.4. Study protocol

Participants completed the experiment in two sessions. The first session consisted of the non-social tasks, namely, a self-paced motor timing task followed by the sensorimotor synchronization (SMS) task (Figure 2). The second session involved the social pointing (SP) task (Figure 3). Participants provided demographic information and completed the clinical questionnaires in the first session and were debriefed after completing the second session. In the second session, participants also performed an unrelated prosody study for a different project (not presented here). The ordering of the social pointing task and the prosody task were counterbalanced across participants to control for any unintended interactions.

The second session was scheduled either on the same day after a minimum break of 30 minutes or on another day. For participants with sessions on two days (n = 16), the median time between the first and second sessions was 6 days (min: 1, max: 30). Due to technical errors during data acquisition, five participants in the TD group had to be re-invited to repeat the non-social tasks. The session ordering was reversed for these individuals. For these five cases repeated measurement took place more than nine months after their first measurement.

2.5. Non-social tasks

2.5.1. Apparatus & Stimuli

The non-social tasks (Figure 2A) were executed using PsychoPy3 (version 3.2.2) (Peirce et al., 2019) implemented in the Python programming language version 3.8 on Windows 10 running on a Lenovo ThinkPad X1 Carbon laptop computer. In the self-paced timing task (Figure 2A, upper), a central fixation cross (0.8° x 0.8° visual angle) was displayed continuously on each block. The sensorimotor synchronization (SMS) task (Figure 2A, lower) involved the presentation of an isochronously paced stream of stimuli (henceforth referred to as pacemakers). In the Auditory modality, the pacemaker was a 256 Hz tone that was presented in stereo with the laptop's two in-built speakers (symmetrically located along the left and right edges). In the Visual modality, the pacemaker stimulus was a white square sized 1.2° x 1.2° visual angle displayed centrally on a grey background on the laptop's LED screen (14 inches [diagonal], resolution: 2560 pixels x 1440 pixels). Finally, in the combined Audiovisual modality, the visual and auditory pacemaker stimuli were presented simultaneously. In all modalities, the pacemaker stimuli were presented for 100ms. The fixation cross was displayed between consecutive stimuli in the Visual and Audiovisual modalities and was displayed continuously in the Auditory modality. Tapping responses were recorded by key-presses on the laptop's space bar.

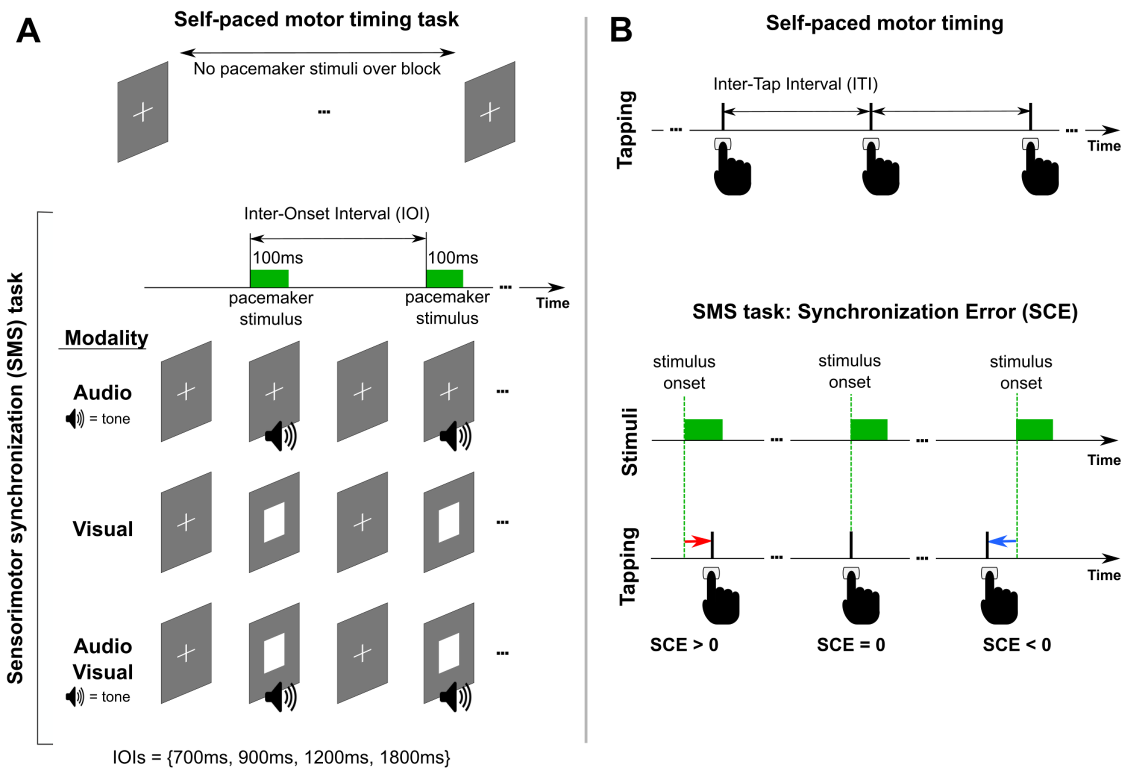

Figure 2. *Schematic of stimulus and response organization in the non-social tasks*. (**A**) **Stimuli**. In each block of the self-paced motor timing task (upper row), a fixation cross was continuously displayed on the screen without additional stimuli. In the sensorimotor synchronization (SMS) task (bottom rows), each block involved brief presentations of pacemaker stimuli separated by a fixed inter-onset interval (IOI). Each SMS block was defined by the sensory modality of the pacemaker stimulus (either Audio, Visual, or Audiovisual) and the IOIs (either 700ms, 900ms, 1200ms, or 1800ms). (**B**) **Responses**. In the self-paced task (upper row), the pacing of the finger taps was quantified by the inter-tap interval (ITI) between consecutive tapping responses. In the SMS task (bottom rows), the synchronization error (SCE) linked to the given stimulus was defined as the difference in timing between the stimulus onset and the associated tapping response. As shown schematically, the SCE could be positive (response follows onset, red arrow), zero (response coincides with onset) or negative (response precedes onset, blue arrow).

2.5.2. Task design

The SMS task assessed the ability to synchronize a simple action (i.e., an index finger movement) to a predictable external stimulus (i.e., the pacemakers) (Figure 2A lower). Before assessing performance on this stimulus-paced sensorimotor task, the general ability to establish and maintain a motor rhythm was tested in a self-paced task (Figure 2A, upper). All conditions required participants to press a designated button with the index finger of the dominant hand. The details of the two tasks are described below.

2.5.2.1. Self-paced motor timing task

Participants were instructed to repeatedly press the designated button with a freely chosen pacing frequency that they could steadily maintain over a longer duration. To reduce the ambiguity in performing this unconstrained task, participants were explicitly instructed that the block would end when 81 button presses were completed independently of their selected response pacing. This ending criterion was used (rather than a block with a fixed duration) to ensure that all participants would produce an equal and sufficiently large number of button-presses. Participants performed two blocks of this task separated by a short break of 10 seconds minimum.

2.5.2.2. Sensorimotor synchronization (SMS) task

The SMS task (Figure 2A lower) was organized into blocks where each block consisted of 60 presentations of the pacemaker stimulus with a constant isochronous inter-onset interval (IOI). Each block was defined by the sensory modality of the pacemaker (Visual, Auditory, Audiovisual) and the pacemaker's IOI (700 ms, 900 ms, 1200 ms, 1800 ms). The IOI parameters of the SMS task were based on Rubia et al. (Rubia et al., 2003). A non-uniform sample of IOIs was used to test a broader range of timescales beyond and above one second. Participants were instructed to press the designated button with the index finger of their dominant hand to coincide with each stimulus onset, while they rested their non-dominant hand on the table. Blocks with the same sensory modality were presented sequentially. The order of the sensory modalities was randomized as well as the order of IOIs within modalities. A short break of at least 10 seconds separated consecutive blocks within modalities. At each modality change, participants were informed with written instructions that the pacemaker's sensory modality was now changing, and the pacemaker stimulus would be presented to them once to allow familiarization. During the task, participants were seated in front of a computer screen and were instructed to fixate on the centrally displayed cross or stimulus at all times during a task block.

2.5.3. Analysis

2.5.3.1. Self-paced motor timing data

The dependent variable was the inter-tap-interval (ITI), that is, the time span between consecutive button presses (Figure 2B, upper panel). For each participant 80 ITI were recorded per block. The mean ITI was used as the index of individually preferred motor tempo and its within-subject *SD* (ITI_{vr}) per block as an index of variability.

Although participants were free to select their response pacing, we excluded ITIs with extreme values. 4 erroneous trials in the whole data set with ITI > 10 seconds were excluded. Additionally, extreme outliers were defined subject-wise per block as ITIs that were less or more than 6 MADs from the median ITI, where MAD refers to the Median Absolute Deviation which has been shown to be robust measure of dispersion (Leys et al., 2013, 2019). On average there were M = 78.88 (min = 64) observations per person per block in the ASD group and M = 79.44 (min = 76) observations per person per block in the TD group left for analysis for the analysis of ITI. For all participants observations from both blocks were available for the analysis of variability (i.e., ITI_{vr}).

2.5.3.2. Sensorimotor synchronization (SMS) data

The dependent variables in the SMS task were the synchronization error (SCE) (Figure 2B, lower panels) and its within-subject *SD* (SCE_{vr}). The SCE on each trial was calculated as the time span between stimulus onset and tapping response. One trial was defined in the temporal domain as the stimulus onset $\pm$ 40% IOI (Binder et al., 2014). The SCE was negative if the tap preceded the stimulus onset. Since the IOI on each block was revealed only after two stimulus presentations, the first two trials of each block were excluded. For a remaining trial to be valid, one tapping response had to be logged within the trial window (i.e., stimulus onset ± 40% IOI). (See Supplementary Table S2 for number and percentages of trial exclusions per group.) We additionally excluded blocks with less than 25% valid trials (see Supplementary Table S3).

After trial-wise and block-wise exclusions, we excluded participants with more than one block missing in one or more modalities. Consequently, one participant from the ASD group (one female) and three participants from the TD group (one female, two males) were excluded from analysis of the SMS task. The group comparisons in Supplementary Table S1 were conducted with the cleaned sample (N = 44). Six values from two TD individuals with block-wise exclusions were imputed for the PCA analysis (see **Statistical analysis**, section 2.7.). On average there remained *M* = 56.7 (*min* = 16) observations per person per block in the ASD group, and *M* = 56.0 (*min* = 15) observations per person per block in the TD group for the analysis of SCE.

2.6. Social task

The social pointing (SP) task (introduced in Bloch et al., 2022), required participants to engage in a real-life, non-verbal communicative interaction with the experimenter who served as a trained interaction partner (Figure 3). Using only directed gaze and deictic pointing gestures, participants had to communicate the spatial location of a target stimulus to their interaction partner on each trial as described below.

2.6.1. Apparatus & Stimuli

The task was conducted in a quiet, windowless room with stable lighting conditions and air conditioning. Participants and the interaction partner were positioned as shown in Figure 3A. The trial structure of the task was implemented using PsychoPy2 version 1.90.3 (Peirce et al., 2019) in the Python programming language version 2.7.11 in Windows 7 running on a HP desktop computer.

Stimuli were presented on an LED monitor (HP EliteDisplay E241i, size: 515 mm x 320 mm; resolution: 1920 pixels x 1200 pixels) that was placed between the interaction partners to face participants at a distance of 94 cm. The stimuli on each trial were two simultaneously displayed bars that were colored red and blue respectively. The bars (width: 2.9º visual angle; height: 9.6º visual angle) were symmetrically displayed on the left and right border of the screen (12.3° visual angle from the center). The red bar was the target stimulus and its position (i.e., left or right) varied randomly from trial to trial. The hygiene requirements due to the SARS-Cov2 pandemic made it necessary to modify the setup for some participants (see Supplementary Material S2).

Monocular gaze movements were recorded at a sampling rate of 1000 Hz using an Eyelink 1000 Plus System (SR Research®) in a desktop-mounted configuration. The Eyelink online-parser was used to detect gaze events. Saccades were defined as movements with a velocity greater than 30°/s and an acceleration greater than $8000°/s^2$. Participants used a chin-rest with a head restraint while performing the task.

Gesture onsets were captured by key-release times and integrated as events into the gaze data stream using functions from the PyLink module version 27 (SR Research®). To obtain gesture trajectories for each trial, the participant's actions were continuously recorded by a video camera (Logitech C270, frame rate: 30/s) that was positioned outside the participant's line of sight to the interaction partner (60° relative to the horizontal). A colored finger cap was placed on the participant's index finger and served as a marker to automatically read out gesture trajectories from the video recording (see **Social pointing (SP) data,** section 2.6.4.1.).

2.6.2. Task design

The SP task required the participant to engage in a real-life, non-verbal interaction with a trained interaction partner. The experimenter who also instructed participants about the task served as the interaction partner, rather than another participant. When performing the task, the participant and interaction partner sat facing each other as shown in Figure 3A. The monitor was positioned so that the participant could see the screen but the interaction partner (i.e., the experimenter) could not.

The structuring of each trial's timeline is shown schematically in Figure 3B. The start of the trial was indicated by a tone. At this time, the participant had to establish mutual eye-contact with the interaction partner to signal readiness for the trial and to continuously press a designated key on the keyboard (space bar) with the index finger of their dominant hand. When eye-contact was established, the experimenter pressed a separate button that triggered the appearance of the stimuli (red and blue bars) on the monitor facing the participant. The target stimulus (red bar) had a variable location on each trial (i.e., left or right of screen) that was not visible to the experimenter. The participant had to communicate the position of the target to the interaction partner by (i) shifting their gaze to the target and (ii) releasing the pressed button to point to the target with their index finger (Figure 3B). Following the participant's actions, the interaction partner acknowledged the communicated target position by looking downward to note the indicated target position. This signaled the end of the trial, and the participant had to return their gaze and index finger to the home position.

Each participant performed four blocks of 30 trials each resulting in a total of 120 (4 x 30) trials. In each block, the target appeared to the left and to the right on an equal number of trials in a randomized order.

2.6.3. Instructions

Before performing the task, each participant was informed by the experimenter that they would serve as the participant's interaction partner for the task. Participants received written instructions and also viewed an instruction video explaining the task and showing the experimenter performing four trials. Participants performed 10 practice trials to familiarize themselves with the task. Specifically, the interaction protocol at the start of each trial (e.g., making eye-contact with the experimenter, pressing the button) and at the end of the trial (e.g., experimenter would look down to make a note). Participants were explicitly informed that the interaction partner could not see the screen or the target stimulus on each trial.

Importantly, the instructions emphasized that the task was to convey the information about the target's location by only using a combination of a pointing gesture and gaze but *without speech*. It was emphasized both gaze and gesture were to be used but there were no explicit instructions on how the gaze and gesture actions were to be coordinated.

Before receiving instructions and performing the SP task, participants also performed a separate minimally constrained version of the SP task (same stimuli, setup, block structure) to assess their spontaneous communication strategies using, for example, speech, gaze, or gesture. This free response task was not the focus of the current investigation (see Bloch et al. 2022) and is described here only for completeness.

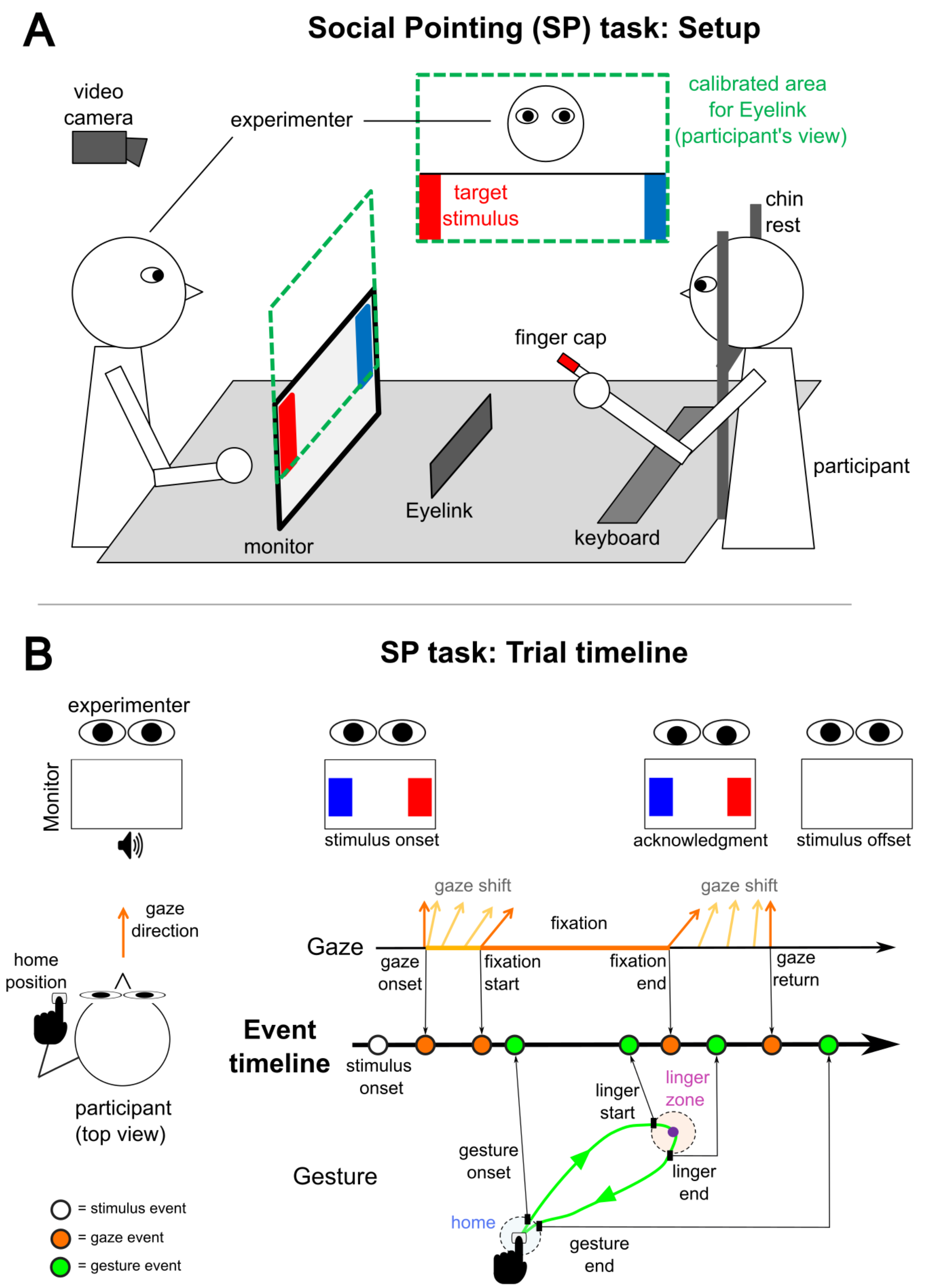

Figure 3. *Schematic of setup and trial timeline in the Social Pointing (SP) task.* (**A**) **Schematic of setup (side-view)**. The participant with head in a chin-rest (right) faced the experimenter (left), who was the interaction partner for the task. The monitor displaying the stimuli (red/blue bars) faced the

participant. The Eyelink system was positioned and calibrated to track the participant's gaze directed at points inside a rectangular area containing the stimuli and the experimenter's head (green dotted line). A video camera (above experimenter) recorded the participant's pointing movements. The recordings were used to track the participant's index finger, which was identified in the video by the red finger cap (see text). (**B**) **Trial timeline.** At the start of each trial, a tone alerted participants to establish eye-contact with the experimenter (orange arrow) while pressing a key with their pointing (i.e., index) finger. Following stimulus onset, participants had to locate the target (red bar) and communicate its location (left or right) to the experimenter by gazing and gesturing towards the target. The experimenter acknowledged the communicated location by looking down to make a note. The event timeline on each trial (large bold font) sets events from different sources into a temporal context and was defined by the stimulus onset (white dot) and multiple gaze-related events (orange dots) and gesture-related events (green dots). *Gaze:* As illustrated by the changing orientation of the gaze direction (orange arrows), the key gaze events were the initiation of a gaze shift from the experimenter to the target (shift start) followed by an extended fixation of the target (fixation start/end) and then another gaze shift, e.g., back to the experimenter (gaze return). *Gesture:* As illustrated by the index finger's movement trajectory (thick green line), the key gesture events were the initiation of a movement (gesture start) away from the home zone (shaded blue disc) to a self-chosen communicative position closer to the target (filled purple dot). After lingering briefly (linger start/end) around this location (linger zone, shaded purple disc), the finger was returned to the home location (gesture end).

2.6.4. Analysis

2.6.4.1. Social pointing (SP) data

The data obtained from eye-tracking and gestures were used to the construct the event timeline for each individual trial (as shown schematically in Figure 3B).

The gaze onset that depicted social disengagement and visual re-orientation towards the target (Figure 3B) were selected per trial deploying a selection algorithm in R (RCoreTeam, 2019). This algorithm applied several exclusion criteria to the gaze data to select behavior that was in alignment with the instructions and to ensure high data quality (see Supplementary Material S3 and Supplementary Table S4 for all criteria and respective exclusion counts). On average *M* = 92.7 (*min* = 37) trials in the ASD group, and *M* = 96.2 (*min* = 32) trials in the TD group were available for analysis. For each selected trial, the following parameters were extracted from the Eyelink data: Stimulus onset, gaze shift onset, target fixation start, target fixation end, fixation duration, dwell time on the target, and pointing onset (by time-stamps from external device).

A second data stream was extracted from the video recordings with a customized frame-differencing algorithm implemented in Matlab (R2017b supplemented with the Image Processing Toolbox). The algorithm filtered the colored area of the pointing finger by RGB value analysis at each pixel and reduced the area of interest to one representative data point per frame. The outputs were two-dimensional coordinates of the finger position sequences that were stringed together to obtain motion trajectories for each trial. Using custom scripts in R, the trajectories were smoothed to suppress noise by the technical equipment with a kernel (width: 10). A distance threshold (10 pixels) was then applied to the trajectory at the start (i.e., home) location to identify the gesture onset and its termination (Figure 3B). The point on the trajectory furthest from the home location was treated as the putative location where the pointing finger was held (i.e., lingered) in a communicative position (violet point in green trajectory in bottom row of Figure 3B). A circular threshold area was applied around this extreme point to define a *linger zone* with a corresponding linger start and end. For each trial, the following temporal parameters were extracted from the video data per trial: Gesture onset, linger start, linger end, and gesture end.

One outlier participant in the ASD group for whom the fixation of the target ended before gesture onset was excluded in the analysis of the synchronization of signal terminations and before running PCA.

2.6.4.2. Coordination analysis

For the coordination analyses, we assume that the gaze changes (involving oculomotor movements) and gesturing (involving hand/arm actions) that follow stimulus onset are coordinated to achieve a common goal of communicating the target location to the interaction partner. To uncover these temporal coordination strategies, we explored the relative timing of gaze-related events and gesture-related events. As illustrated in the hypothetical event timeline in Figure 3B, we treat gaze and gesture events as having a comparable structure related to initiation, movement to the target, time spent at the target, and the return to the home position. Based on this structure, we assessed whether there were systematic regularities in the coordination *"rules"* linking gaze to gesture events during the initiation of the action and the termination of the target-directed orientation.

For the gaze and gesture events involved during action initiation, we investigated whether these events were temporally ordered based on a serial *fixate-then-point* coordination rule, in which pointing was initiated only *after* the acquisition of a foveal representation of the target, i.e., target fixation. This simplistic coordination rule yielded two testable predictions. Firstly, gesture onsets should follow the start of target fixation. Secondly, the timing of the gesture onset (relative to the fixation onset) should be independent of pre-fixation processes (e.g., the duration of gaze shifts), since the gesture was expected to be initiated only *after* the successful fixation of the target regardless of the time taken to achieve the fixation. A violation of this second prediction in particular would support an alternative possibility that the planning and execution of the gesture and gaze initiation occurred in parallel following stimulus onset.

Mirroring this rationale at initiation, we examined the coordination rules that might govern the ordering of gaze/gesture events when the target-oriented positioning of gaze and gesture were terminated, i.e., the start of the home-directed gaze and gesture actions. These home-directed actions depend on when participants believed that the target position had been successfully signaled to the interaction partner. Because this termination criterion could take different forms, we examined the synchronization of gaze and gesture events after normalizing their timing relative to the total duration of the hand movement (from the home position to the target and back).

2.7. Statistical analysis

Data preprocessing and analysis were performed in the programming language R (RCoreTeam, 2019) version 4.0.3 using the RStudio environment (RStudioTeam, 2020), version 1.4.1103 with the package library *tidyverse* (Wickham et al., 2019). The analyses were not officially preregistered.

2.7.1. Mixed effects models

Statistical tests of factorial effects were evaluated using Linear Mixed Effects Models (LMM) on non-aggregated (i.e., trial-wise) data as LMMs have been shown to handle missing and unbalanced data well (Barr et al., 2013; Bates et al., 2015; Brauer & Curtin, 2018; Brown, 2021; Cumming et al., 2014; Singmann & Kellen, 2019). Model assumptions, namely homoscedasticity [residuals-predicted values scatter plot], normality of residuals [Q-Q-plot], and lack of multicollinearity [variance inflation factor (VIF)] were inspected using the check_model() function from the *performance* package (Lüdecke et al., 2021). If these assumptions were violated, Generalized Linear Mixed Effects Models (GLMM) were fit for the non-negative, skewed data with a Gamma distribution and log link function. See Supplementary Table S5 for all fitted models in *lme4* grammar (Bates et al., 2015). To test whether a factor in question explained variance above chance level, likelihood ratio tests (LRT) were conducted against an alpha level of 0.05 using the mixed() function from the *afex* package (Singmann et al., 2021). Differences between factor levels were assessed using Holm-adjusted post-hoc pairwise comparison tests with the *emmeans* package (Lenth et al., 2022). Specifically, estimated marginal means (EMM) for specified factor levels (averaged over other factor levels) were retrieved from the model and compared with *z*-tests. Unless specified otherwise, error bars of factorial designs in all plots indicate the within-subject standard error of the mean (Cousineau & O'Brien, 2014), estimated using the afex_plot() function from the *afex* package.

2.7.2. Non-factorial tests

Non-factorial exploratory tests on subject-wise aggregated data were assessed with a *t*-test if all, homogeneity of variances [Levene test, non- significant tests at α = .05], and normality of data [Shapiro-Wilk test; non- significant tests at α = .05] were confirmed, otherwise a non-parametric Wilcox test was used. Deviations of a distribution from unimodality were tested using the excess mass test as implemented in the *multimode* package (Ameijeiras-Alonso et al., 2021, 2019).

2.7.3. Correlograms

The association between parameters (after subject-wise aggregation) were assessed with the Pearson's correlation coefficient. Correlograms were used to visualize the conjoint associations between multiple parameters. To identify groups of variables that were more correlated to each other than to other variables (i.e., modules), correlograms were clustered to maximize modularity using the Louvain method (Blondel et al., 2008) as implemented in the Community Detection Toolbox (Kehagias, 2021).

2.7.4. Principal Component Analysis (PCA)

Each individual's unique behavioral profile across the social and non-social domains was defined by a set of parameters that revealed inter-group differences in the SMS task (six parameters) and SP task (six parameters) (see **Results**, section 3.). The individual behavioral profiles were submitted to a Principal Components Analysis (PCA) to assess the structure of the multivariate associations between parameters belonging to different domains. The PCA was performed separately for each group. Since the included parameters were selected based on group differences, we specifically sought to assess whether the obtained multivariate associations would differ between groups.

The PCA was performed on subject-wise aggregated, centered, and scaled data separately per group with the *FactoMineR* package (Lê et al., 2008). Missing values for parameters from the SMS task were imputed before running the PCA using the PCA model (Josse & Husson, 2016). To select suitable components, scree plots were used to visualize the cumulative variance explanation per additional component. Besides visual inspection of scree plots, Horn's parallel analysis (Horn, 1965) was used to decide how many components to keep before using Varimax orthogonal rotation to retrieve rotated component loadings. Scree plots were created with the *factoextra* package (Kassambara; & Mundt, 2016), Horn's analysis was performed using the *paran* package (Dinno, 2012), and the Varimax rotation using the *psych* package (Revelle, 2022).

Bartlett's tests of sphericity confirmed that data were suitable for multivariate analysis [TD: $X^2(66) = 516.49$, p < .001; ASD: $X^2(66) = 508.71$, p < .001]. The Kaiser-Meyer-Olkin (KMO) tests (Kaiser, 1970) indicated a relatively high proportion of shared variance among the selected parameters for both groups (TD: KMO = .38; ASD: KMO = .44). We did not consider these low KMO values as a critical concern due to our restricted focus on evaluating whether the same variables would contribute to component loadings in both groups.

2.7.5. Bootstrapped confidence intervals

We report bootstrapped confidence intervals (Davison & Hinkley, 1997) for the key population-level effects to provide an indicator of the sample-related uncertainty associated with the effects. Specifically, we report the bootstrapped effects (i.e., bootstrapped estimated marginal means differences ($DIFF_{BT}$); correlation coefficients (r_{BT})) together with the bootstrapped 95% confidence interval (CI_{BT}). Bootstrapped confidence intervals were calculated using the bias-corrected and accelerated bootstrap interval (BCA) method as recommended by (Carpenter & Bithell, 2000; Efron, 1987). Resampling iterations were fixed at 1000. For the bootstrapping procedures, the functionality of the *parameters* (Lüdecke et al., 2020) and *boot* (Canty & Ripley, 2022; Davison & Hinkley, 1997) packages were used.

3. Results

3.1. Non-social tasks

3.1.1. Speed and variability of self-paced motor timing are comparable between ASD and TD

In the sensorimotor synchronization (SMS) task participants had to produce periodic actions that coincide with external pacing stimuli. Therefore, a first precondition was to assess how individuals produce periodic actions in the *absence* of external stimuli, that is, based on an internally defined pacing. When producing self-paced tapping actions, the preferred inter-tap interval (ITI) (averaged across blocks) was in the sub-second (≤ 1s) range for the majority of individuals in both the TD group (87.5%) (Figure 4A, left) and ASD group (79.2%) (Figure 4A, right) with large inter-individual differences within each group (TD: 354.66ms – 1682.29ms; ASD: 162.09ms – 1788.10ms). The ITIs were similar for both groups (TD: *M* = 742.44ms, *SD* = 324.22ms; ASD: *M* = 758.96ms, *SD* = 411.73ms; GLMM LRT: Group: $\chi^2(1) = 0.03$, $p = .854$). The variability of the inter-tap intervals (ITI_{vr}) over the duration of the task (averaged across blocks) was also comparable between both groups (TD: *M* = 47.96ms, *SD* = 34.63ms; ASD: *M* = 50.13ms, *SD* = 33.32ms; GLMM LRT: Group: $\chi^2(1) = 0.01$, $p = .919$).

The similarity in self-paced timing between groups validated the ability of autistic participants to generate periodic actions comparable to TD individuals. This similarity further implies that when actions have to be synchronized to *external* pacemakers, any observed inter-group differences cannot be solely attributed to differences in basic motor timing mechanisms.

3.1.2. Sensory modality and IOI have differing influences on synchronization in ASD [1]

In the SMS task (Figure 2), the demand to synchronize the finger tap with the onset of the pacemaker stimulus was the same for pacemakers of all sensory modalities (Visual, Auditory, Audiovisual) and IOI (700ms, 900ms, 1200ms, 1800ms). Therefore, the synchronization error (SCE) as

[1] For the SMS task, due to data quality exclusions (see **Materials and Method,** section 2.), the TD group included n = 21 (of 24) participants and the ASD group included n = 23 (of 24).

the temporal delay between responses and pacemaker onsets provided a common measure to compare synchronization behavior across conditions and groups.

Participants in both groups exhibited behavior consistent with sensorimotor synchronization across all conditions (Figures 4B) with a concentration of the SCE between ≈ -70ms (i.e., slightly before stimulus onset) to ≈ +60ms (i.e., slightly after onset) for both groups (see Supplementary Figure S1 and S2 for full individual SCE data). Nevertheless, the conjoint influence of modality and IOI on SCE manifested differently in the TD and AS groups [LMM LRT: modality*IOI*group: $\chi^2(6) = 134.48$, $p < .001$] (see Supplementary Table S6 for full listing of effects). As qualitatively evident in both panels of Figure 4B, for both groups the SCE increased with increasing IOI for all modalities. However, the SCE were concentrated below 0ms for the Auditory modality, while being marginally above 0ms for the Visual modality. Importantly, synchronization in the Audiovisual modality exhibited a qualitatively different pattern between groups where the SCEs were more similar to the Auditory than to the Visual modality in the TD group (Figure 4B, left) but were between the Auditory and Visual modalities in the ASD group (Figure 4B, right). We confirmed these distinct effects of modality and IOI on synchronization by fitting separate LMMs for the two groups.

In the TD group, the SCE was modulated by sensory modality, IOI, and their interaction [LMM LRT: modality*IOI: $\chi^2(6) = 94.99$, $p < .001$; modality: $\chi^2(2) = 10.57$, $p = .005$; IOI: $\chi^2(3) = 13.37$, $p = .004$]. Figure 4C (left) shows the relationship between the SCE in the different modalities (averaged across IOI). Even though the Audiovisual modality involved the simultaneous presentation of the auditory and visual pacemaker stimuli, the auditory pacemaker was seemingly the dominant stimulus for the TD group. The estimated marginal mean (EMM) SCE in the Auditory modality (EMM = -41.0ms, SE = 15.1ms) and Visual modality (EMM = 30.2ms, SE = 16.6ms) were substantially different [$DIFF_{BT}$ = 73.1ms, CI_{BT} [31.6, 114.5], $z = -3.43$, $p = .002$]. However, the SCE in the Audiovisual modality (EMM = -21.8ms, SE = 16.1ms) was highly similar to the Auditory modality [$DIFF_{BT}$ = -21.1ms, CI_{BT} [-47.5, 5.4], $z = 1.40$, $p = .343$] as compared to the Visual modality [$DIFF_{BT}$ = 52.8ms, CI_{BT} [20.0, 82.2], $z = -3.33$, $p = .003$].

For the ASD group, the SCE was likewise affected by modality, IOI, and their interaction [LRT: modality*IOI: $\chi^2(6) = 90.67$, $p < .001$; modality: $\chi^2(2) = 15.46$, $p < .001$, IOI: $\chi^2(3) = 15.23$, $p = .002$]. However, the relationship between the modalities showed a different pattern than in the TD group (Figure 4C, right). As in the TD group, the SCE in the Auditory modality (EMM = -34.1ms, SE = 12.8ms) and the Visual modality (EMM = 29.9ms, SE = 16.6ms) were comparably different [$DIFF_{BT}$ = 62.3ms, CI_{BT} [34.9, 89.8], $z = -4.24$; $p < .001$]. However, unlike the TD group, the SCE in the Audiovisual modality (EMM = -6.8ms, SE = 9.2ms) showed a prominent difference to the Auditory modality [$DIFF_{BT}$ = -26.9ms, CI_{BT} [-48.9, -7.3], $z = -2.64$; $p = .023$] while being only marginally different to the Visual modality [$DIFF_{BT}$ = 35.8ms, CI_{BT} [5.6, 67.3], $z = -2.25$; $p = .064$].

The SCE patterns above revealed the presence of different synchronization strategies across sensory modalities and IOI for the ASD and TD groups. Next, we targeted the possibility that these inter-modal and inter-timescale differences might be attributable to corresponding differences in variability.

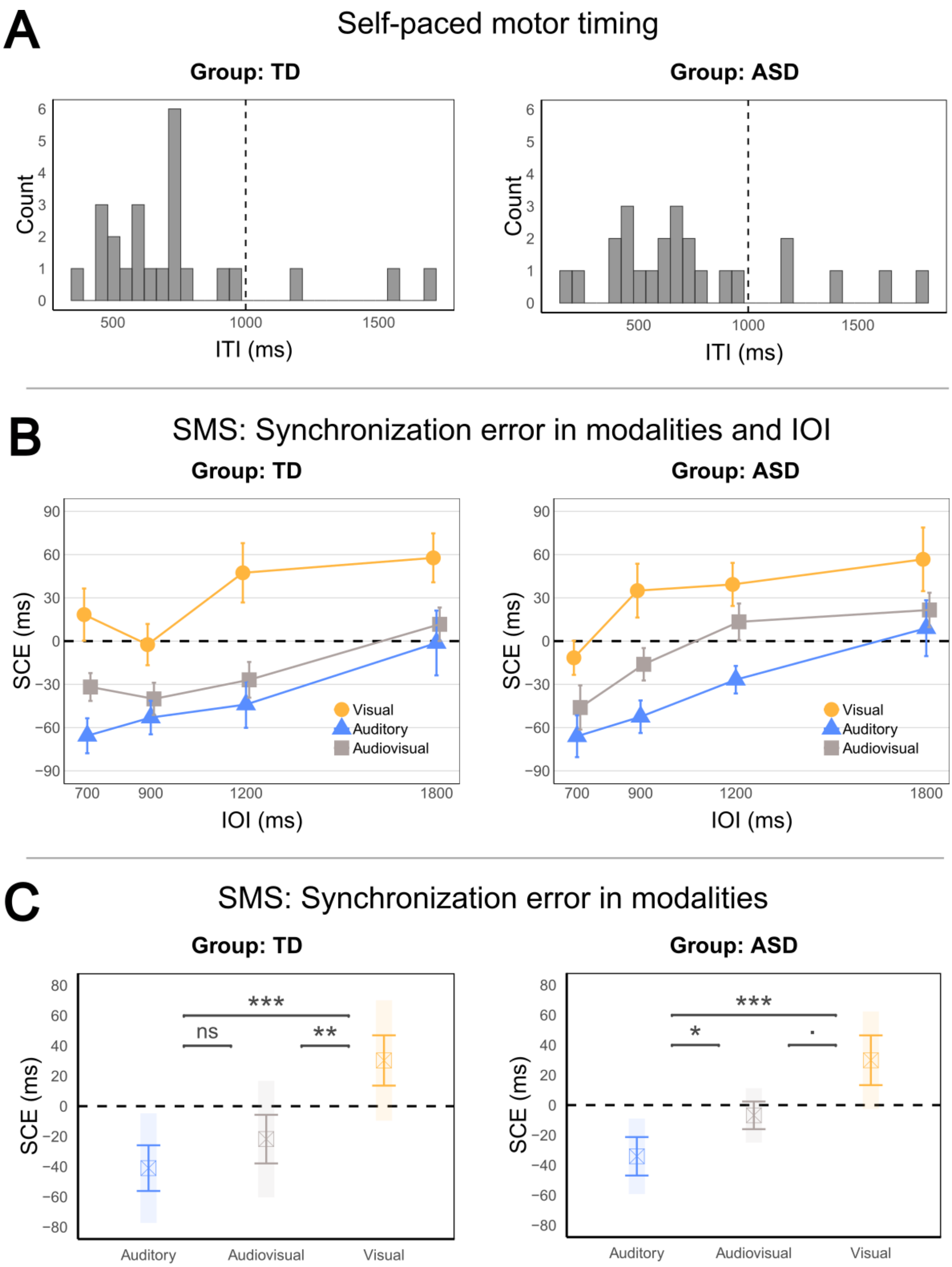

Figure 4. *Inter-tap intervals (ITI) in self-paced motor timing task and synchronization errors (SCE) in SMS task*. (**A**) Histogram of individual mean inter-tap-intervals (ITI) in self-paced motor timing task in the TD group (left) and ASD group (right). In both groups, more individuals had a mean ITI in the

subsecond (< 1000ms) range (left of black dashed line) than in the suprasecond range (right of dashed line). (**B**) Change in synchronization error (SCE) [estimated marginal mean] with pacemaker inter-onset-interval (IOI) in each modality for the TD group (left; n= 21) and the ASD group (right; n = 23). The black dashed line indicates the idealized SCE if responses were perfectly synchronized with the stimulus onset (i.e., SCE = 0). Error bars: within-subject standard error of the mean (Cousineau & O'Brien, 2014). (**C**) Change in SCE [estimated marginal mean] with modality pooled across IOIs in the TD group (left; n= 21) and ASD group (right; n = 23). Error bars: within-subject standard error of the mean. Light colored rectangles indicate the 95% confidence intervals. (ns: not significant; *: .01 ≤ p < .05; **: .001 ≤ p < .01; ***: p < .001).

3.1.3. Increased variability of synchronization in visual modality and with increasing timescales

Synchronizing an action to the onset of an upcoming pacemaker stimulus requires an accurate prediction of when this upcoming onset would occur. The within-subject variability of the SCE (SCE_{vr}) measured in the SMS task (Figure 2) provided a simple indicator of the stability of these predictions from stimulus to stimulus under different conditions.

Unlike the SCE (see previous section), the SCE_{vr} was modulated by modality and IOI in a similar manner for both the TD (Figure 5A, left) and ASD groups (Figure 5A, right) [GLMM LRT: modality*IOI*group: $\chi^2(6) = 2.89$, $p = .823$; modality*IOI: $\chi^2(6) = 13.26$, $p < .039$; modality: $\chi^2(2) = 135.30$, $p < .001$; IOI: $\chi^2(3) = 251.43$, $p < .001$; group: $\chi^2(1) = 0.00$, $p = .993$] (see Supplementary Table S7 for full listing of effects, and Supplementary Figures S3 and S4 for full individual SCE_{vr} data). For all modalities, variability increased with IOI where the supra-second interval of 1800ms had a variability that was almost double that of the sub-second 700ms interval. However, across IOI and groups, the variability in the Visual modality (EMM = 88.8ms, SE = 5.58ms) was substantially larger than in the Auditory modality (EMM = 63.5ms, SE = 4.0ms) [$z = -10.6$, $p < .001$] and the Audiovisual modality (EMM = 63.3ms, SE = 4.0ms) [$z = -10.6$, $p < .001$]. Notably, the Auditory and Audiovisual modalities did not differ in variability [$z = -0.1$, $p = .994$].

As with the SCE, the SCE_{vr} increased with increasing IOIs and variability was larger for the Visual modality than for the Auditory and Audiovisual modalities. However, the variability in the Auditory and Audiovisual modalities was closely matched for both the TD and ASD groups. This absence of modality-related differences in variability between the groups suggests that differences in SCE variability were not the main sources of the group differences in SCE.

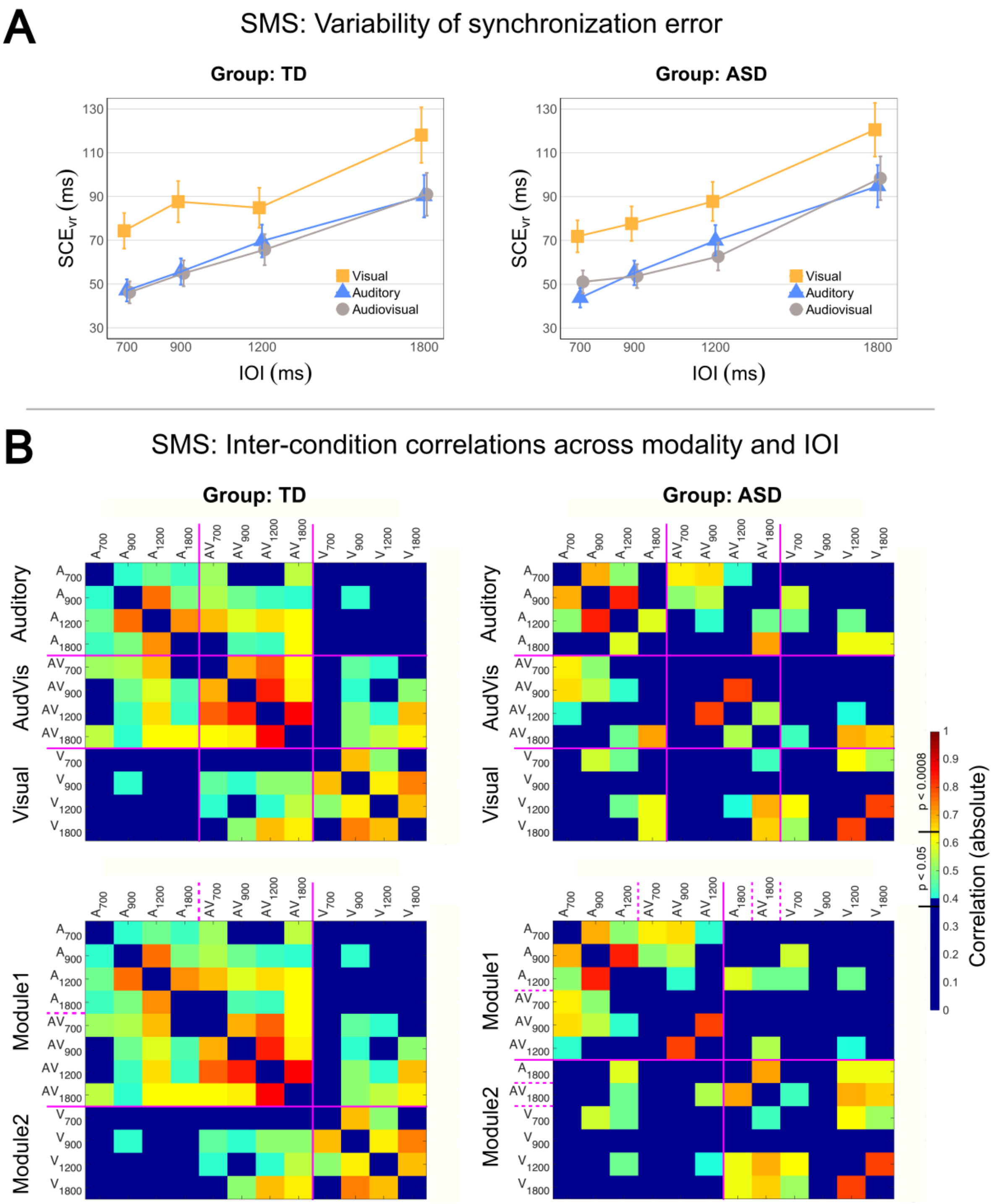

Figure 5. *Intra-condition variability (SCE$_{vr}$) and inter-condition correlation in synchronization error (SCE).* (**A**) Change in variability of synchronization error (SCE$_{vr}$) [estimated marginal mean] with pacemaker inter-onset-interval (IOI) in each modality for the TD group (left; n= 21) and the ASD group (right; n = 23). Error bars: within-subject standard error of the mean. (**B**) Correlogram summary of the (absolute) correlations in individual synchronization error (SCE) between conditions for the TD group (left; n = 21) and ASD group (right; n = 23). The color of the pixel indicates the strength of the correlation between the SCEs. Only Pearson's correlation coefficients with $|r| > 0.4$ are shown. The

critical $|r|$ thresholds for $p < 0.05$ were .37 (TD group) and .35 (ASD group), and for $p < 0.0008$ (=0.05/66, Bonferroni-corrected) were 0.64 (TD group) and .62 (ASD group). Correlations of a condition to itself (along the diagonal) are set to zero. In the upper row, the correlograms are clustered by modality (clusters separated by thick purple lines). In the lower row, the correlograms are clustered by correlation strength into modules, where correlations between conditions within a module are stronger than between conditions in different modules. Within each module, the dashed purple lines mark the boundary between conditions of the same modality. For the TD group, the correlograms clustered by modality (left upper) and by correlation strength (left lower) were identical but this was not the case for the ASD group (right upper, right lower).

3.1.4. Non-social synchronization styles in TD individuals are dominantly shaped by sensory modality but not in autistic individuals

Each modality and IOI combination in the SMS task (Figure 2) involved a unique set of demands. To assess whether individuals have a characteristic non-social synchronization style across modalities and timescales in the SMS task, we investigated correlations of SCE across different SMS settings.

Figures 5B is a correlogram summary of the linear (absolute) correlations between the individual SCE in each modality and IOI to the SCE in each of the other modality x IOI combinations. The focus was on the pattern of SCE relationships across conditions and not to identify key correlations, therefore, all correlations with $|r| > 0.4$ are shown without correction for multiple comparisons. The critical $|r|$ thresholds for $p < 0.05$ were .37 (TD group) and .35 (ASD group), and for $p < 0.0008$ (=0.05/66, Bonferroni-corrected) were 0.64 (TD group) and .62 (ASD group).

Clustering the conditions by modality (Figure 5B, upper row) revealed marked within-modality correlations across IOI for both groups (TD: left panels, ASD, right panels). However, there were also important differences: For the TD group (Figure 5B, left upper), there was a low correlation between individual SCEs in the Auditory and Visual modalities across IOI. The Audiovisual modality showed a high correlation to both the Auditory and the Visual conditions, although with a higher correlation to the Auditory condition. This was confirmed by performing modularity clustering where conditions were clustered based on the strength of the correlations (Figure 5B, left lower). The Auditory and Audiovisual conditions were clustered together into a single module (Module 1), while the Visual conditions were designated as a distinct module (Module 2).

In comparison, the correlations were less coherently organized for the ASD group when the conditions were clustered by modality (Figure 5B, right upper). This was confirmed by modularity clustering (Figure 5B, right lower). Specifically, modularity clustering resulted in a clustering of Auditory and Audiovisual modalities for the sub-second IOIs and for the 1200ms IOI (Module 1). However, the supra-second 1800ms IOI for the Auditory and Audiovisual condition was clustered with the Visual conditions (all IOIs) into a separate module (Module 2). Unlike the dominant role of modality for the TD group, the individual styles in the ASD group were determined by both modality and IOI, particularly in the supra-second domain.

3.2. Social pointing (SP) task

3.2.1. Separate timing of gaze and gesture events are comparable between ASD and TD

Before considering the intrapersonal coordination of gaze and gesture actions, we first analyzed their timing parameters independently to assess the presence of gaze-specific and gesture-specific temporal deviations between groups. Table 1 is a summary of the key temporal parameters related to the initiation and termination of gesture and gaze respectively for the TD and ASD groups (see Supplementary Figure S5 for individual SP data profiles of participants in both groups). The values of all the timing parameters considered were similar between groups, without any statistically significant differences.

Table 1. *Descriptive statistics and group comparisons of gaze-specific and gesture-specific temporal parameters in the Social Pointing (SP) task (see Figure 3B).*

		TD		ASD				
	parameters	*M* (ms)	*SD* (ms)	*M* (ms)	*SD* (ms)	*statistic*	*p*	*effsize*
Gaze	onset	278.77	73.68	251.65	72.79	*U* = 228	.222	*r* = .179
	shift duration	130.32	32.42	136.29	36.76	*U* = 322	.493	*r* =.101
	fixation duration	1160.26	573.55	1092.63	473.74	*U* = 279	.862	*r* =.027
Gesture	onset	484.54	90.24	515.09	132.25	*U* = 329	.407	*r* =.122
	onset -> linger onset	542.77	115.42	503.10	96.12	*t* = -1.29	.202	*d* = -0.37
	linger duration	450.20	293.79	447.27	270.44	*U* = 293	.927	*r* =.015
	Linger end -> offset	600.83	138.53	559.48	162.23	*t* = -0.95	.347	*d* = -0.27

Note. Group differences were assessed with two-sided Students *t*-tests with effect size Cohen's *d*, if the following assumptions were satisfied: normality of data (Shapiro-Wilk tests) and homogeneity of variances (Levene tests). When these assumptions were violated, Wilcox tests (*U* statistic) are reported with effect size *r*. For all tests, *df* = 23. Data was aggregated for participants and for target sides.

3.2.2. Larger delay between post-stimulus gaze and gesture onsets in ASD

The onset of the target stimulus required the initiation of appropriately directed gaze and gesture actions from the home position of the eye and hand to the target (see Figure 3B). The mean timing onset of the gaze typically preceded the gesture onset for both groups (see Table 1 & Supplementary Table S4). However, the magnitude of this delay between the gaze and gesture onsets was modulated by group and target side [LMM, LRT: group*side: $\chi^2(1) = 0.32$, $p = .572$; group: $\chi^2(1) = 5.53$, $p = .019$, $EMM_{BT} = 58.7$ms, CI_{BT} [11.1, 110.0]; side: $\chi^2(1) = 7.36$, $p = .007$, $EMM_{BT} = 14.8$ms, CI_{BT} [3.8, 24.7]] [2]. The mean delay (averaged across sides) for the ASD group (*M* = 263.44ms, *SD* = 103.13ms) was nearly 60ms larger than for the TD group (*M* = 205.77ms, *SD* = 59.52ms). The mean delay for the left targets (collapsed across groups) (*M* = 242.05ms, *SD* = 97.32ms) was marginally larger by ~15ms as compared to the right targets (*M* = 227.16ms, *SD* = 82.99ms). A small lateral difference exists similarly in both groups as indicated by a non-significant interaction of side*group.

[2] The group effect has been previously reported in Bloch et al. (2022) and is reported here for completeness.

The differential synchronization of the gaze/gesture onsets between ASD and TD was notable as neither the gaze onset nor the gesture onset on its own differed between the TD and ASD groups (Table 1). Due to the relatively small difference between the left and right sided actions, the measures computed for left/right sides actions were averaged together for all the following analyses. We next assessed whether the gaze-gesture delay might have an origin in a specific coordination strategy.

3.2.3. Serial gaze-gesture dependence at initiation in ASD but not TD

In the Social Pointing (SP) task (Figure 3) individuals had to relocate their gaze and pointing fingers towards a target. The initiation of the gaze shift to the target was typically completed rapidly (~130ms, see Table 1). This raised the possibility that the start of the target fixation might serve as a coordinating event to execute the pointing gesture where the gesture is initiated only after the successful target fixation, i.e., a serial *fixate-then-point* strategy. A first prediction of such a serial fixate-then-point strategy was, that the mean onset of the pointing gesture followed *after* successful target fixation. This was indeed found for both, the TD group [M = 75.44ms, SD = 69.26ms; $t(23) = 5.34$, p < .001] and the ASD group [M = 127.14ms, SD = 99.40; $t(23) = 6.27$, p < .001]. This delay between the gesture onset and the start of target fixation was marginally larger for the ASD group as compared to the TD group [$t(46) = -2.09$, p = .042]. However, the delay between fixation and gesture onset was not sufficient evidence of a serial dependence between gaze and gesture.

For a serial fixation-then-point strategy, the successful fixation of the target would be a necessary event to initiate the pointing gesture. Consequently, a second prediction of a serial fixate-then-point strategy was, that the gesture onset should be independent of the duration of the pre-fixation process of shifting the gaze from the home position to the target, since the gesture was expected to be initiated only *after* the target fixation regardless of the time taken to achieve the fixation. In line with this prediction, for the ASD group (Figure 6A, right), the gesture onset relative to the start of target fixation was uncorrelated of the time taken for the gaze shift to the target [$r(23) = -.073$, $p = .736$; $r_{BT} = -.073$, CI_{BT} [-.533, .479]]. That is, the gesture onset and gaze shift duration were effectively independent. By contrast, for the TD group (Figure 6A, left), the gesture onset was correlated with the gaze shift duration, where longer gaze shift durations were associated with shorter gesture onset times [$r(23) = -.513$, $p = .010$; $r_{BT} = -.513$, CI_{BT} [-.696, -.153]]. This difference between the groups was particularly striking since the mean gaze shift durations did not differ between the groups (see Table 1).

In summary, the behavior of the ASD group, but not the TD group, was consistent with a serial fixate-then-point strategy. However, the apparent dependence between gesture onset and gaze shift duration for the TD group was instead suggestive of a strategy where the gaze and gesture actions were planned and executed *in parallel* after target onset.

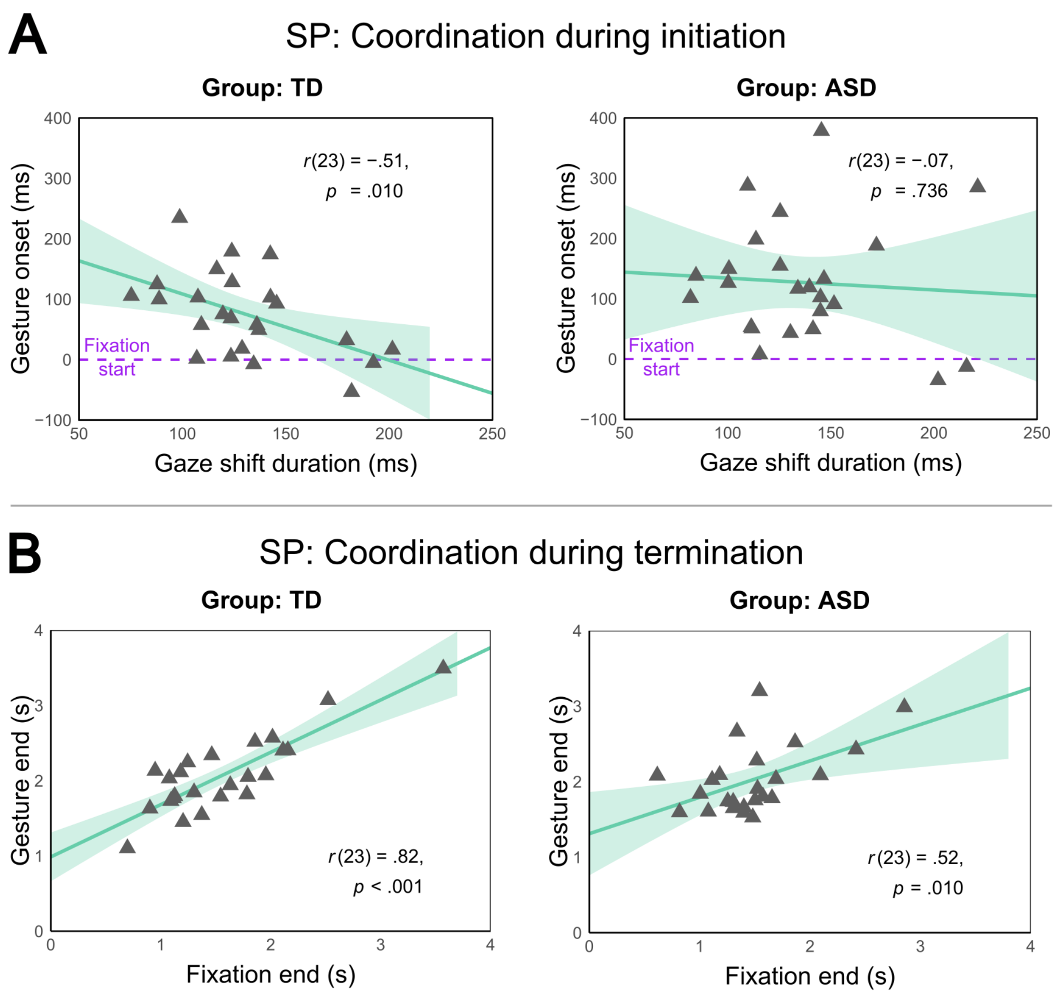

Figure 6. *Coordination of gaze/gesture initiation and termination in social pointing (SP) task*. (**A**) Correlation between gesture onset times (relative to fixation start) (y-axis) and gaze shift durations at initiation (x-axis) for the TD group (left) and ASD group (right). The dotted purple line denotes idealized gesture onsets (= 0) that perfectly coincide with the start of the fixation. Each grey triangle denotes data from a single participant. The linear regression lines with confidence bands are presented in green. Insets report Pearson's correlation coefficients (*r*) and *p* values (alpha = .05). (**B**) Correlation between gesture end times (y-axis) and fixation end times (x-axis) for the TD group (left) and ASD group (right). Plotting conventions are as in (**A**).

3.2.4. Differing gaze-gesture dependence at termination between ASD and TD

After achieving the target-directed communicative position of the gaze and hand, participants had to terminate the action by relocating their gaze and hand to the home position (Figure 3B). These termination actions depended on when participants believed that they successfully signaled the target to the partner. We assessed whether there was a coordinated ordering of the home-directed gaze and gesture actions (as was observed for action initiation (previous section)).

A first indicator of the coordination between the home-directed gaze and gesture actions was the correlation between the timing of the fixation termination and the termination of the hand movements (both relative to target onset). This correlation was considerably stronger for the TD group (Figure 6B, left) [$r(23) = .824$, $p < .001$; $r_{BT} = .848$, CI_{BT} [.598, .940]] than for the ASD group (Figure 6B, right) [$r(23) = .515$, $p = .010$; $r_{BT} = .515$, CI_{BT} [.168, .835]]. To better characterize this differing strength of correlation, we evaluated the distribution of individual preferences in the fixation termination relative to the key events for the hand actions.

For the TD group (Figure 7A, upper), relative to the normalized movement duration, the start of the linger period (blue colored histogram, median: 35.63%) and its end (green colored histogram, median = 60.78%) showed a high consistency across participants. However, the distribution of individual fixation terminations (orange colored histogram) revealed a striking bimodal distribution. One major sub-group (45.8% of the TD group) terminated the fixation immediately after the start of the linger period, while the other major sub-group (50% of the TD group) terminated their fixation after the linger period ended. The deviation from unimodality of the fixation termination times was confirmed with an excess mass test [*excess mass* = 0.19, $p = .008$].

The ASD group showed a linger pattern similar to the TD group (Figure 7B, lower), with the start (blue colored histogram, median: 34.58%) and end of the linger period (green colored histogram, median = 61.49%) having a relatively high consistency across participants. However, unlike the TD group, the individual fixation terminations exhibited a skewed but approximately unimodal distribution [*excess mass* = 0.11, *p* = .804]. The majority of individuals (54.2% ASD group) had fixation termination times that followed after the linger period while 33.3% of the group had fixation terminations during the linger period, and 12.5% of the group had a fixation termination even before the linger period. A comparison of these distributions for the TD and ASD groups are shown using kernel density estimations in Figure 7B.

In summary, the pointing-related termination events (i.e., onset and end of linger times) were consistent between groups. However, the coordination of fixation terminations relative to the hand's position at the target revealed a systematic structuring of inter-individual differences that indicated differing strategies in how the target position was signaled to the interaction partner. Crucially, these preferred strategies differed between the ASD and TD groups.

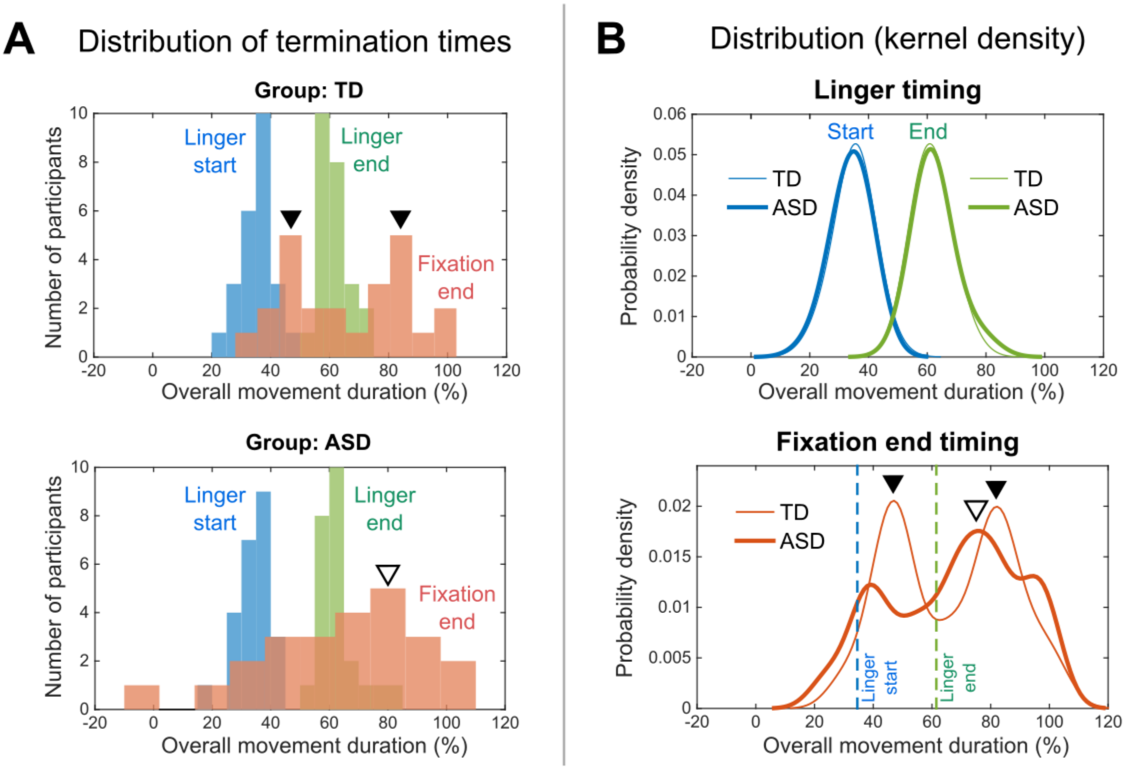

Figure 7. *Distributional analysis of temporal coordination during action termination*. (**A**) Histograms of the timing of the fixation end (orange), linger start (blue) and linger end (green) for the TD group (upper) and ASD group (lower). All times per individual were normalized relative to the individual's mean overall movement duration from gesture start (departure from home position) until gesture end (return to home position). In both groups, the linger start times were concentrated around a single value (i.e., one mode). This was also true for the longer end times. However, for the TD group, the fixation end times (orange) exhibited two distinct modes (black triangles): one between the typical linger start and end times and the second after the typical linger end times. For the ASD group, only one mode was identifiable after the linger end times (white triangle). (**B**) Upper panel: Kernel density plots of the linger start (blue) and end (green) time distributions for the TD group (thin lines, n = 24) and ASD group (thick lines, n=23). Lower panel: Kernel density plots of the fixation end time distribution (orange) for the TD group (thin line, n = 24) and ASD group (thick line, n = 23) with mean linger start and end times shown as dashed vertical lines. As in Figure (A), two modes were evident for the TD group (black triangles) while only one prominent mode was evident for the ASD group (white triangle).

3.3. Evidence for cross-domain synchronization styles for TD individuals but not for autistic individuals

Differences based on TD and AS groups could be identified for both social and non-social tasks. However, these group differences could be domain-specific, i.e., independent of each other, and thus they do not provide a clear indication of a synchronization style across domains. To target this possibility, we pooled together the above findings from the social and non-social domains to examine whether and how an individual's behaviors in one domain were informative about behaviors in the other domain. Such a cross-domain relationship would provide key evidence of synchronization styles across social and non-social domains.

Each individual's unique behavioral profile across the social and non-social domains was defined by the following twelve parameters (six per domain) that revealed group-specific synchronization strategies. In the social domain (SP task), we selected parameters that revealed inter-group differences in gaze/gesture coordination strategies during action initiation (three parameters) and termination (three parameters). The initiation-related parameters (Figure 6A) were the delay between gaze and gesture onsets relative to stimulus onset ($\Delta Gz(0)_{on}Gs(0)_{on}$), gaze shift duration ($\Delta Gz(0)_{on}Gz(fix)_{on}$), and the delay between the gesture onset and fixation onset ($\Delta Gz(fix)_{on}Gs(0)_{on}$). The termination-related parameters (Figure 7) were the normalized end time of the fixation ($Gz(fix)_{end}$), the delay between the fixation end and the start of the linger period ($\Delta Gz(fix)_{end}Gs(Lg)_{on}$), and the delay between the fixation end and linger end ($\Delta Gz(fix)_{end}Gs(Lg)_{end}$). In the non-social domain (SMS task), we selected parameters that revealed inter-group differences in the influence of modality on SCE (three parameters) and the conjoint influence of modality and pacemaker time-scale on SCE (three parameters) (Figures 4A & 5B). Specifically, these parameters were the SCEs in the three sensory modalities collapsed across IOIs (SCE_A, SCE_{AV}, SCE_V) and the difference between the SCEs for the 700ms and the 1800ms IOIs in the three modalities (ΔSCE_A, ΔSCE_{AV}, ΔSCE_V).

Figure 8 is a graphical summary of the bivariate correlations between each pair of these 12 parameters for the TD group (N = 21; left panel) and the ASD group (N = 22; right panel). In both groups, there were strong positive correlations for related clusters of parameters *within* the social domain and *within* the non-social domain (along the diagonal). However, there was a qualitative difference in the relationship of parameters *between* the two domains (i.e., off-diagonal zones). The correlations *between* domains were dominantly positive (i.e., yellow-red) for the TD group but were dominantly negative (i.e., green-blue) for the ASD group.

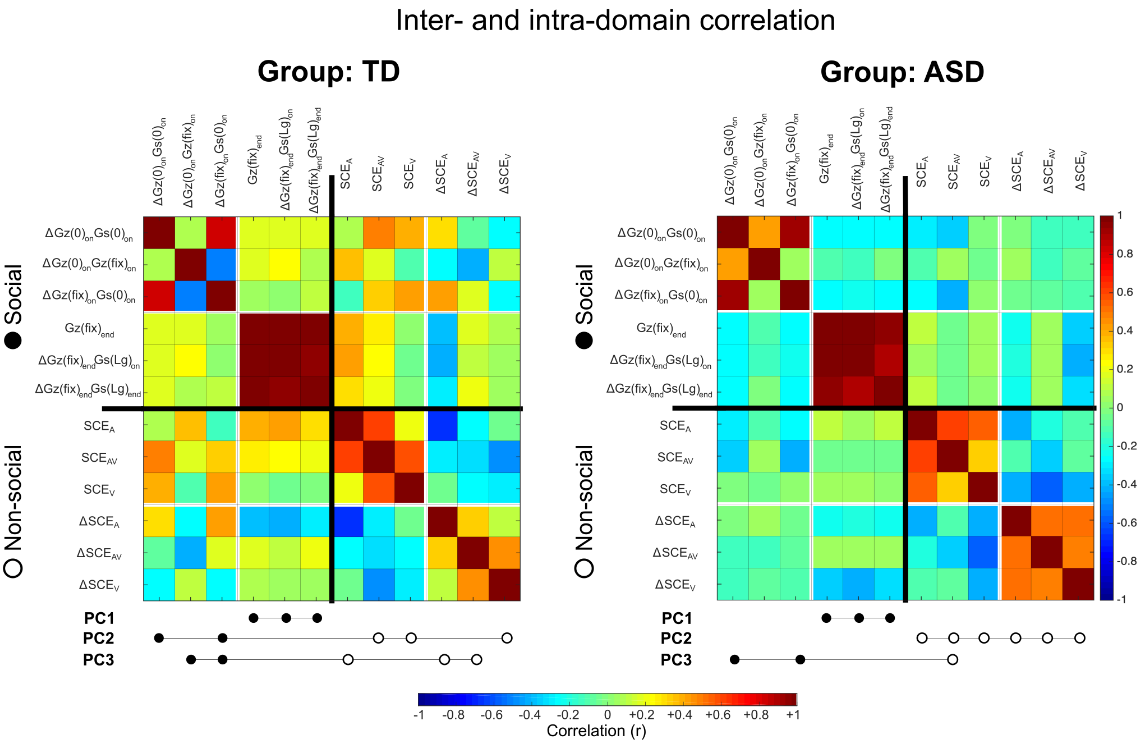

Figure 8. *Correlations of task parameters within and between domains*. Correlogram summary of bivariate correlations between selected task parameters (see text) from the social domain (rows/columns 1-6) and the non-social domain (rows/columns 7-12) for the TD group (N = 21; left) and the ASD group (N = 22; right). The color of the pixel at row *i* and column *j*, indicates the value of the Pearson correlation coefficient between the parameters associated with rows *i* and column *j*. Parameters were clustered by domain (separated by thick black line) and by clusters of related parameters within each domain (separated by thick white lines). Within-domain correlations lie along the diagonal (social domain in upper left quadrant; non-social domain in lower right quadrant) while between-domains correlations are located away from the diagonal (lower left and upper right quadrants). Correlations between domains (i.e., off-diagonal) were dominantly positive for the TD group (yellow-red) but were dominantly negative for the ASD group (green-blue). For each group, the three principal components identified by PCA are summarized below the correlograms (see Table 2). Parameters that load on each component are shown as dots below the corresponding columns of the correlogram (black: social variables; white: non-social variables).

To obtain an integrated multivariate characterization of the cross-domain relationships, the individual behavioral profiles in each group were submitted to a PCA. As summarized in Table 2, the PCA (after parallel analysis) yielded three principal components for both groups (see Supplementary Figure S6). These three components (PC1, PC2, PC3) explained 73.9% of the total variance in the TD group and 71.5% variance in the ASD group. The total explained variance was divided among the three components in a similar manner in both groups. In both groups, the first component (PC1) involved loadings from the three termination-related parameters from the social domain (only loadings > 0.50 are reported). However, the parameters that loaded on PC2 and PC3 differed markedly between the groups.

In the TD group, both PC2 and PC3 yielded loadings of a mixture of parameters from the social domain and non-social domain. The mixed loadings of parameters from the social and non-social domains in the TD group were consistent with the cross-domain behavioral dependencies that might be expected for a cross-domain synchronization style.

By contrast, in the ASD group, PC2 and PC3 showed parameter loadings that were far less mixed regarding their relation to the two domains. PC2 had a parameter loading consisting of all six parameters from the non-social domain and none from the social domain, while the primary parameter loadings of PC3 were from the social domain with a single weaker loading from the non-social domain. This strikingly limited role of cross-domain parameter loadings in the ASD group provides evidence for the absence of cross-domain synchronization styles for individuals with ASD.

Table 2. *Results of Principal Component Analysis (PCA).*

	Parameters		TD			ASD		
			PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Social parameters	Initiation	$\Delta Gz(0)_{on}Gs(0)_{on}$		0.75				0.93
		$\Delta Gz(0)_{on}Gz(fix)_{on}$			-0.65			
		$\Delta Gz(fix)_{on}Gs(0)_{on}$		0.69	0.66			0.88
	Termin.	$Gz(fix)_{end}$	0.98			0.97		
		$\Delta Gz(fix)_{end}Gs(Lg)_{on}$	0.96			0.96		
		$\Delta Gz(fix)_{end}Gs(Lg)_{end}$	0.97			0.94		
Non-social parameters	Modality	SCE_{A}			-0.67		0.63	
		SCE_{AV}		0.80			0.53	-0.59
		SCE_{V}		0.74			0.82	
	Modality x IOI	ΔSCE_{A}			0.79		-0.71	
		ΔSCE_{AV}			0.64		-0.82	
		ΔSCE_{V}		-0.64			-0.62	
	Variance exp. (%)		31.4	23.2	19.3	30.3	22.2	19.0

Note. Principal components (PC) and standardized parameter loadings based upon correlation matrices are shown for each group (TD group: left columns; ASD group: right columns). PCs are ordered in descending order of percentage variance explained (indicated by shading). PCs were selected by means of parallel analysis. Component loadings for all parameters are shown after varimax rotation. Only component loadings > .50 are reported.

4. Discussion

In this study we investigated whether time-coordinated behavior in the social and non-social domains in ASD was modulated by a common synchronization style. For that, we evaluated individual synchronization behavior across domains for multivariate associations, using Principal Component Analysis (PCA). Consistent with the assumption of a characteristic synchronization style, individual synchronization behavior showed associations across domains in TD individuals. Strikingly, in the ASD group there were no comparable associations indicative of *any* synchronization style, thus suggesting an increased differentiation of individual synchronization strategies between domains in ASD.

4.1. Within-domain synchronization

Time-coordinated actions have been found to elicit ASD-related differences both in social and non-social tasks (de Marchena & Eigsti, 2010; Georgescu et al., 2020; Hannant et al., 2016; Koehler et al., 2021; Vishne et al., 2021; Xavier et al., 2018). Similarly, we found group-level synchronization differences within both tasks but these were consistent with differences in strategies rather than abilities.

4.1.1. Synchronization in the non-social domain

Prior studies have reported inconsistent findings about SMS performance in ASD (Edey et al., 2019; Isaksson et al., 2018; Morimoto et al., 2018; Morrison et al., 2018; Tryfon et al., 2017; Vishne et al., 2021). We therefore assessed SMS performance across a range of conditions that included sub-second and supra-second timescales and pacemaker stimuli in multiple modalities. Autistic and non-autistic individuals successfully performed the synchronization required by these different conditions. As in prior studies, synchronization responses preceded pacemaker stimuli in auditory sub-second conditions (Aschersleben, 2002), and the variability was larger for visual stimuli relative to auditory stimuli (Hove et al., 2013; Lorås et al., 2012).

Despite the fact that individuals in the two groups did not differ in synchronization abilities, two key findings highlight that their strategies to achieve sensorimotor synchronization differed.

As such, groups differed in the priorization of timing sources for the audiovisual stimuli (Figure 4B). In the TD group the auditory modality was decisive for synchronization. This finding is compatible with a higher temporal resolution of the auditory system (Comstock et al., 2018; Holcombe, 2009; Mu et al., 2018; Shi et al., 2013). However, this prioritization was less evident for autistic individuals. Possibly, the choice of optimal timing source during audiovisual SMS was modulated by the increased visual temporal resolution in ASD (Blaser et al., 2014; Falter et al., 2012). Secondly, exploratory correlation analysis revealed that the synchronization strategies across conditions showed consistencies that were highly structured by sensory modalities in the TD group but by a mixture of modality *and* time-scale in the ASD group (Figure 5B).

Importantly, these strategy differences between groups are not attributable to altered basic motor timing mechanisms in ASD, as indicated by the similarity in timing and variability during self-paced tapping in both groups (Figure 4A), where the preferred pacing was in sub-second range (~750 ms) in both groups consistent with previous findings (Hammerschmidt et al., 2021).

4.1.2. Synchronization in the social domain

Individuals with ASD and TD individuals successfully met the communicative goal of the social pointing task. However, our results reveal differences in the temporal conjunction of gaze and gesture events that imply differences in the underlying coordination strategies between groups.

A serial *fixate-then-point* strategy has been demonstrated for eye-hand coordination during object manipulation (de Brouwer et al., 2021; Johansson et al., 2001). However, deviating from this, there was no precise target to be grasped or touched in our task. Therefore, the use of this coordination rule in ASD (Figure 6A) might implicate an increased tendency to engage in low-level structured or stereotype behavior. In contrast, a parallel execution of manual and oculomotor movements at the onset of the stimulus could lead to flexible gesture executions relative to gaze in comparison to a serial strategy in which the execution of the gesture is bound to a post-stimulus gaze event (i.e., fixation start). Furthermore, it is possible that coordination strategies differed in autistic individuals due to a preference to avoid direct eye-contact with others (Madipakkam et al., 2017; Tanaka & Sung, 2016). During joint-attention, after fixating the object, another gaze shift to the interaction partner can occur as a reassurance of the successful initiation of joint attention (Emery, 2000; Jording et al., 2019; Pfeiffer et al., 2012; Shteynberg, 2015). Our results suggest that TD individuals were divided into two subgroups based on whether or not they exhibited reassuring gaze after linger onset (Figure 7B). However, for autistic individuals, strategies with a gaze shift to the partner were not comparably evident and there was a relative preference to terminate the fixation and gesture together.

Our results are consistent with the assumption that communication characteristics are not categorically different in ASD (i.e., attenuated communication behavior) but are associated with fine-tuning of event timing (Georgescu et al., 2020; Noel et al., 2018).

4.2. Synchronization across domains

We did not have prior predictions about specific multivariate associations that might be identified by the PCA, so the component loadings are not interpreted here. Rather, we sought to assess whether the cross-domain associations (interpreted as evidence of a synchronization style) would differ between the TD and ASD groups (see schematic Venn-diagrams in Figure 1). Our finding of highly differentiated strategies in ASD (Figure 8, Table 2) seemingly contradicts the existence of ASD-specific cross-domain factors. However, on closer consideration, the evidence for such factors might be difficult to identify due to the possible consequences of these factors for developmental variation. It is possible that employing an individual-centered perspective might enable nuanced inferences about factors that determine the phenotype of ASD. To help guide these inferences, we propose a simplified explanatory model.

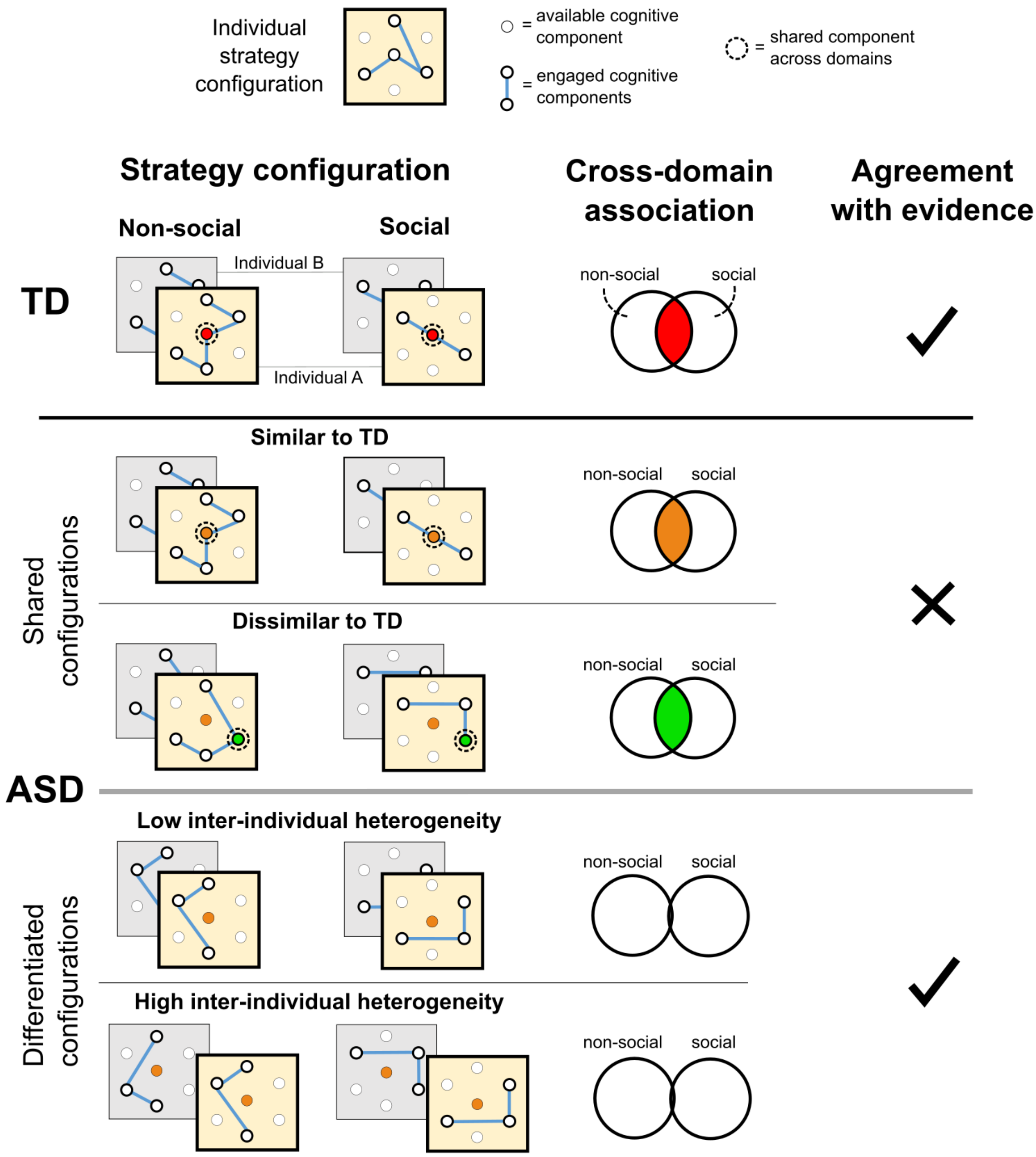

Figure 9. *Explanatory model for individual-level inferences*. Yellow and grey squares depict different individuals. Nodes within squares represent cognitive components that may be engaged in a task. The blue edges connecting the nodes represent different strategies. If similar cognitive components are engaged in social and non-social strategies, a cross-domain association is depicted as overlapping circles in the Venn-diagram, with the overlap area colored by the color of the component that caused the intersection. For all ASD scenarios (rows 2-5) the orange node represents an ASD-specific component that may cause shared configurations (rows 2 & 3) or differentiated configurations of components (rows 4 & 5). The right column depicts which scenarios are supported by our data (i.e., the TD scenario and the differentiated configurations scenarios for ASD).

In our simplified model (Figure 9), an individual strategy (or task-set) is treated as a particular configuration of cognitive components that are jointly used to perform a task. For illustrative purposes, a strategy is schematically represented as a graph that is defined by how different cognitive components (nodes) are connected (blue edges). Consider the scenario for TD individuals (top row) where the strategies for the non-social task (left) and the social task (right) crucially involve the same cognitive component (red node). This engagement of a shared cognitive component across tasks could produce a cross-domain association in task-behavior suggestive of a synchronization style (overlapping circles in the Venn diagram).

Suppose the shared cognitive component in TD individuals (red node) is functionally different in ASD due to neurodevelopmental factors (orange node in rows 2-5). For simplicity, the potential impact of such a functional difference on strategy organization could be divided into two broad categories: *shared* and *differentiated configurations*.

Shared configurations are depicted in rows 2 and 3. In one scenario (row 2), similar strategies could be engaged in autistic individuals as with the TD individuals. However, the difference in the ASD-specific component (orange node) could produce a functional deficit that might lead to decreased task performance. Crucially, hypothetically assuming a common engagement of this affected component in the social and non-social tasks would still produce a cross-domain association as with the TD individuals. A related scenario (row 3) is when the strategies are assumed to be reconfigured (e.g., over development) to recruit an alternative cognitive component (green node) to bypass the functionally different component (orange node) in both domains. This alternative configuration would still produce a cross-domain association. Neither of these two scenarios was supported by our findings.

In contrast, our data are seemingly in greater agreement with scenarios where the strategies in both domains involve *differentiated configurations* (illustrated in the bottom two rows). In these scenarios the functionally distinct components (orange nodes) are bypassed by individuals employing specialized strategies for each task with a limited overlap of cognitive components (row 4). This might be further compounded by a high inter-individual heterogeneity in the adopted strategies (row 5). Both scenarios would be predicted to yield limited cross-domain associations in task behavior. Specifically, these scenarios emphasize an individual-centered rather than a general deficit-centered view of the ASD phenotype. They assign a crucial role to individual heterogeneity where the individual's unique developmental history has an essential role in shaping the individual phenotype over and above any ASD-specific common factors that might be present. Our findings suggest that these differentiated scenarios might be of relevance for understanding the observed cross-domain heterogeneity in synchronization behavior in ASD.

Importantly, all these hypothetical ASD-related scenarios considered here would entail population-level differences between the ASD and TD groups in the social and non-social domains. However, the above scenarios emphasize that these population-differences alone would be insufficient to distinguish the structure of the cross-domain relationships. Our model, although simplistic, provides a means to translate population-level differences into differentiated individual-centered inference and could serve as a guide for future research in the direction of individualized analyses.

We examined a sample of autistic adults in this study. However, autism could be considered here as an example and the implications of the model are theoretically applicable to other neurodevelopmental conditions. This is because other neurodevelopmental conditions (e.g., ADHD) are likewise associated with early onsets and concurrent with distinct cognitive abilities and individual resources to cope with situational demands. For example, early-onset differences in time processing in developmental conditions could have cascading effects on cognitive functioning by influencing developmental trajectories (Falter & Noreika, 2014). Thus, in adulthood, it seems essential to consider the effects of alternative developmental trajectories on behavioral observations.

4.3. Limitations and future directions

The sample size planning in the current study was limited by the absence of directly comparable prior studies in autistic adults. Consequently, the power analysis was guided by a study on the visual perception of event synchronization in a comparable sample (Falter et al., 2012) (**Sample size justification**, section 2.2.). Although the perception of event simultaneity can be assumed to have a key role in the tasks investigated here study, both the SMS and SP tasks involved (i) events from multiple sensory modalities (rather than only vision) as well as (ii) a major additional role for motor control processes to adjust behavior to achieve synchronization. Therefore, the sample size based on these inter-task comparability assumptions might have limited the detection of smaller true effects in each of the domain-specific tasks, and is a key issue to be addressed by subsequent confirmatory and replication studies.

As noted in section 2.1. (**Participants**), in our tested sample, depression was associated with ASD but not with TD. Although this increased the representativeness of the sample for the adult ASD population (Bloch et al., 2021; Hollocks et al., 2019; Lehnhardt et al., 2013), we cannot exclude the confounding of the results reported here by depression-related factors.

As suggested by our simplistic model to identify cross-domain relationships within the individual (Figure 9), testing cross-domain relationships of behavior in autistic and non-autistic children and longitudinal studies over the lifetime would be of high relevance in order to investigate a potential change of the relation between domains over ontogeny. In the present study, a repeated-measures design was used in both tasks, allowing participants to become familiar with the task requirements across trials. This familiarity factor should also be considered in future studies. Baseline differences in the use of specific communication channels, especially in childhood, (LeBarton & Iverson, 2016; Manwaring et al., 2018; Mastrogiuseppe et al., 2015; Murillo et al., 2021; Shumway & Wetherby, 2009) could systematically confound cross-domain correlations. Tasks should therefore be chosen that are equally experienced by all participants in terms of familiarity and difficulty.

In addition, more studies should conduct individual-level cross-domain linkages to better describe ASD phenotypes in adulthood. For example, combinations of predictive coding (van de Cruys et al., 2014), perceptual simultaneity (Falter et al., 2012, 2013; Menassa et al., 2018), temporal binding (Brock et al., 2002; Foss-Feig et al., 2010; Stevenson et al., 2014), or executive functions (Chmielewski & Beste, 2015; Ozonoff et al., 1991) tasks with social interaction tasks would be conceivable.

5. Conclusion

The defining features of ASD have an early onset in life, which is why it is considered a developmental condition. They persistently shape cognitive processes over the lifespan and underlie the heterogeneity that is frequently observed in adult samples. Our findings reinforce the view that heterogeneity is not just a side effect but a defining characteristic of adult ASD populations (Georgiades et al., 2013; Keles et al., 2022; Mottron & Bzdok, 2020). Our study inspires a research agenda on neurodiversity that combines population-level with individual-centered observations to incorporate the crucial role of individual developmental pathways. While it is important to continue to strive for unification in the context of the heterogeneity, our results point to individual specialization within domains. This spectrum of unification and specialization of behavior is essential to consider for individualizing treatments in the context of precision psychiatry (Fernandes et al., 2017).

Appendix

	Planned sample size	**Non-social tasks**		**Social (SP) task**			**Cross-domain**
		Self-paced	*SMS task*	*Unimodal*	*Initiation*	*Termination*	*Within-group PCA*
ASD	*23*	*24*	***23***	*24*	*24*	***23***	***22***
TD	*23*	*24*	***21***	*24*	*24*	*24*	***21***

Table A1. *Sample size in different analyses*. Power analysis led to a planned sample size of 23 per group to detect between-group differences. The final sample size was 24 per group. Analyses in which the sample size was reduced due to data quality exclusions are printed in bold. One ASD and three TD participants had to be excluded for the SMS task analysis. For the gaze-gesture termination analysis one ASD participant had to be excluded. For the PCA, which was conducted within each group, only full datasets were included so that two ASD and three TD participants were not included.

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SUPPLEMENTARY MATERIAL

Manuscript title: Differentiated, rather than shared, strategies for time-coordinated action in social and non-social domains in autistic individuals

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Supplementary Material S1. *Neuropsychological profiles*

S1.1 Clinical measures

With regard to autism screening measures, German versions of the Autism Quotient (Baron-Cohen et al., 2001), Empathy Quotient (Baron-Cohen & Wheelwright, 2004), and Systemizing Quotient (Baron-Cohen et al., 2003) were raised as indices of the manifestation of traits that are typically ascribed to autism. Current depression was assessed with Becks Depression Inventory (Beck et al., 1961). The Adult Developmental Co-ordination Disorders/ Dyspraxia Checklist (Kirby et al., 2010) assessed motor coordination difficulties. Group scores as well as results of group comparisons are depicted in Supplementary Table 1.

S1.2 Control measures

Concentration abilities were measured with D2 (Brickenkamp, 1981). The Wechsler adult intelligence scale third edition (von Aster et al., 2006) was used to assess IQ scores, as well as the ‚Wortschatztest' (Schmidt & Metzler, 1992). The Sensory Perception Quotient (Tavassoli et al., 2014) was raised to measure sensory sensitivity. All tests were on hand as German versions. Group scores as well as results of group comparisons are depicted in Supplementary Table 1.

Supplementary Material S2. *Setup modifications due to hygiene requirements.*

The hygiene requirements due to the SARS-Cov2 pandemic made it necessary to modify the Social Pointing (SP) task setup for some participants. A glass panel was positioned between the participant and the interaction partner and an anti-reflection foil was applied on this panel to minimize reflections affecting visibility. To further improve stimulus visibility, the screen background color for the stimuli was changed from grey to white. This modified setup was used for 14 (of 24) participants with ASD and 17 (of 24) TD participants.

Supplementary Material S3. *Gaze selection algorithm.*

Orienting gaze shifts were defined as starting in the social gaze region (i.e., face area of interaction partner) and ending in the correct target region. Three different gaze pathways were identified: direct saccades, or segmented gaze shifts with an intermittent fixation of the social gaze region or a random gaze region (i.e., not social or left or right target regions). For segmented gaze shifts, those saccades were selected that defined social detachment and visual reorienting to the target. This tolerance for segmented gaze shifts took into consideration that eye movements are spatially inaccurate to a certain degree (i.e., hypo- and hypermetric). Further exclusion criteria for orienting gaze shifts were applied:

1. First trials of each block were excluded due to recommendations of the eye-tracking system.
2. Blinks < 100 ms before stimulus onset.
3. Saccade latency was too short (< 75 ms).
4. Gesture onset preceded saccade onsets.
5. Gaze was not in the social gaze region at stimulus onset.
6. Gaze shifts to wrong target.
7. No orienting gaze shifts (no fixation of the target at all or > 1 intermitted fixation).

Supplementary Table S1. *Sample characteristics and group comparisons.*

Measure	M_{ASD}	SD_{ASD}	M_{TD}	SD_{TD}	**statistic**	p	**eff. size**
AQ	41.50	3.81	14.61	5.87	t = 18.55[ab]	< .001	d = 5.44
EQ	11.96	5.38	47.96	10.79	t = -14.38[ab]	< .001	d = -4.22
SQ	44.83	13.75	20.61	10.34	U = 500[c]	< .001	r = 0.70
ADC	51.00	12.83	22.35	12.41	U = 516[cb]	< .001	r = 0.75
BDI	15.88	10.73	5.50	5.48	U = 448[c]	< .001	r = 0.48
SPQ	59.92	17.48	60.04	17.22	t = -0.03[b]	.980	d = -0.01
D2	103.83	9.50	100.04	7.79	t = 1.51	.137	d = 0.44
WST	111.46	11.74	110.67	8.35	t = 0.27	.789	d = 0.08
IQ	114.38	16.48	108.50	13.07	t = 1.37	.178	d = 0.40
PIQ	110.67	17.65	102.38	13.66	t = 1.82	.080	d = 0.53
VIQ	115.00	15.95	112.17	12.61	t = 0.68	.498	d = 0.20
Age	40.84	12.12	37.05	12.66	t = 1.06	.296	d = 0.31

Note. AQ = Autism Quotient; EQ = Empathy Quotient; SQ = Systemizing Quotient; ADC = Adult Dyspraxia Checklist; BDI = Becks Depression Inventory; SPQ = Sensory Perception Quotient; WST = ‘Wortschatztest’; IQ = Intelligence Quotient; PIQ = Performance-based Intelligence Quotient; VIQ = Verbal Intelligence Quotient.

Means (*M*) with standard deviations (*SD*) in ASD group and TD group with results of Student’s *t*-test (α = .05) and Cohens *d* as effect sizes. *df* of all tests = 23.

[a] Bartlett test revealed heterogeneous variances and results of Welchs two-sample *t*-test are reported.

[b] Data from one control participant missing.

[c] Shapiro-Wilk test revealed non-normality of data in groups and results of Mann-Whitney test with effect size *r* are reported.

Supplementary Table S2. *Number and percentage of excluded trials per exclusion criterion (EC) in modality conditions of the sensorimotor synchronization (SMS) task in both groups.*

		EC1	**EC2**	**EC3**	**EC4**	**EC5**	**EC6**
		n (%)	n (%)	n (%)	n (%)	n (%)	n (%)
ASD	**V**	192 (3.33)	38 (0.66)	5 (0.09)	54 (0.94)	315 (5.47)	0 (0)
	A	192 (3.33)	4 (0.07)	10 (0.17)	27 (0.47)	283 (4.91)	0 (0)
	AV	192 (3.33)	9 (0.16)	3 (0.05)	12 (0.21)	251 (4.36)	0 (0)
TD	**V**	192 (3.33)	58 (1.01)	7 (0.12)	67 (1.16)	220 (3.82)	27 (0.47)
	A	192 (3.33)	32 (0.06)	7 (0.12)	52 (0.92)	268 (4.65)	0 (0)
	AV	192 (3.33)	31 (0.54)	7 (0.12)	64 (1.11)	478 (8.30)	27 (0.47)

Note. **EC1**: First two trials; **EC2**: Missed taps; **EC3**: Double taps (after correction [a]); **EC4**: IOI cutoff; **EC5**: System error; **EC6**: < 25% valid trials. Percentage is given in relation to all possible trials per modality per group. V = visual; A = auditory, AV = audiovisual.

[a] The exclusion of double responses was preceded by an identification double tapping responses with too short intervals in between taps (< 200 ms) that were most likely technical issues. 21 observations of double tap occurrences fell into this criterion and first tapping responses were included as valid trials in analysis.

Supplementary Table S3. *Number of excluded blocks per modality and IOI conditions of the sensorimotor synchronization (SMS) task in both groups.*

	Auditory				**Audiovisual**				**Visual**				**total**	**in *n***
	700	**900**	**1200**	**1800**	**700**	**900**	**1200**	**1800**	**700**	**900**	**1200**	**1800**	**missing**	**subjects**
ASD	1	1	1	1	1	1	1	1	1	1	0	1	11	1
TD	0	1	1	1	3	2	1	2	2	0	0	0	13	5

Note. One subjects from the ASD group and three subjects from the TD group were excluded from analysis due to > 1 block missing in at least one modality.

Supplementary Table S4. *Number and percentage of excluded trials in different exclusion criteria (EC) for orienting gaze shifts per group in Social Pointing (SP) task.*

	EC1	**EC2**	**EC3**	**EC4**	**EC5**	**EC6**	**EC7**	**total**
	n (%)	n (%)	n (%)	n (%)	n (%)	n (%)	n (%)	n (%)
ASD	96 (3.3)	5 (0.2)	59 (2.1)	63 (2.2)	117 (4.1)	58 (2.0)	247 (8.6)	645 (22.4)
TD	96 (3.3)	16 (0.6)	11 (0.4)	177 (6.2)	52 (1.8)	29 (1.0)	170 (5.9)	551 (19.1)

Note. **EC1:** First trials; **EC2:** Blinks; **EC3:** Low saccade latencies; **EC4:** Pointing preceded gaze; **EC5:** Gaze was not in facial region of partner at stimulus onset; **EC6:** Direct saccades to wrong target; **EC7:** > 1 fixation before gaze landed on target or no fixation of target at all.

Percentage is given in relation to all possible trials per group.

Supplementary Table S5. *List of multilevel models in lme4 grammar*.

model	**DV**	**FF**	**RS**	**RI**
GLMM	ITI	group	block	ID
GLMM	*SD* of ITI	group		ID
LMM	SCE	modality*IOI*group	modality + IOI	ID
LMM (ASD)	SCE	modality*IOI	modality + IOI	ID
LMM (TD)	SCE	modality*IOI	modality + IOI	ID
GLMM	SCE_{vr}	modality*IOI*group		ID
LMM	Onset delay	group*target_side	target_side	ID

Note. All mixed models were fit with BOBYQA optimizer. DV = Dependent Variable; FF = Fixed Factors; RS = Random Slopes; RI = Random Intercepts; GLMM = Generalized Linear Mixed effects Model with gamma distribution and log-link function; LMM = Linear Mixed effects Model; ITI = Inter-Tap-Interval; SCE = Synchronization Error

Supplementary Table S6. *Results of likelihood ratio tests of all effects in a linear mixed effects model predicting synchronization errors (SCE).*

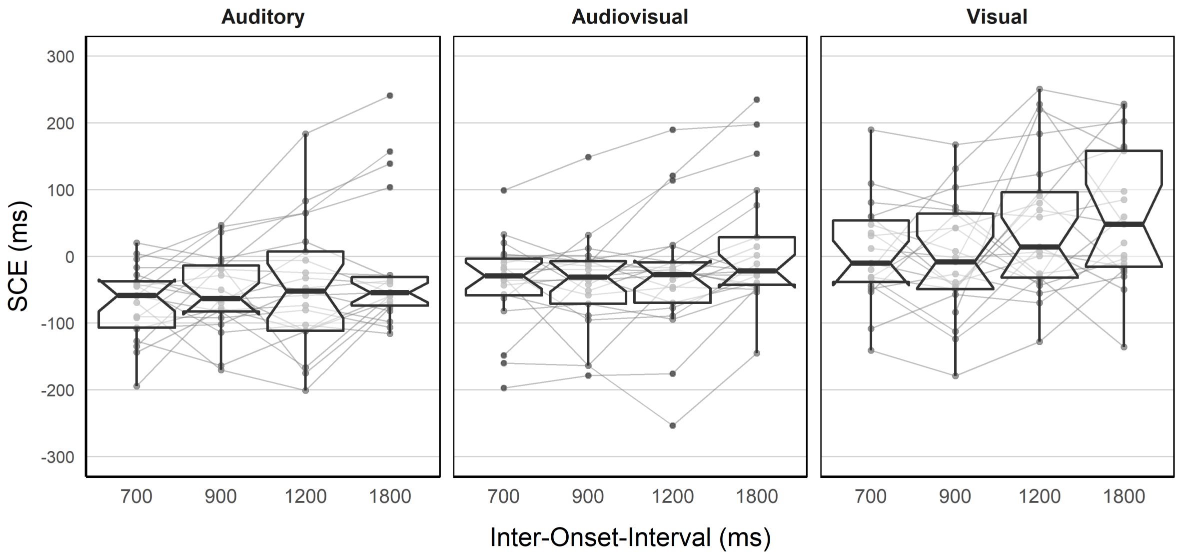
Effect	**Test statistc (χ^2)**	**Df**	**p**
Group	0.21	1	.648
Modality	22.79	2	<.001
IOI	17.56	3	<.001
*Group*Modality*	0.60	2	.740
*Group*IOI*	8.24	3	.041
*Modality*IOI*	51.83	6	<.001
*Group*Modality*IOI*	134.48	6	<.001

Note. Results were obtained by the mixed() function from the *afex* package (version 1.0-1) in R.

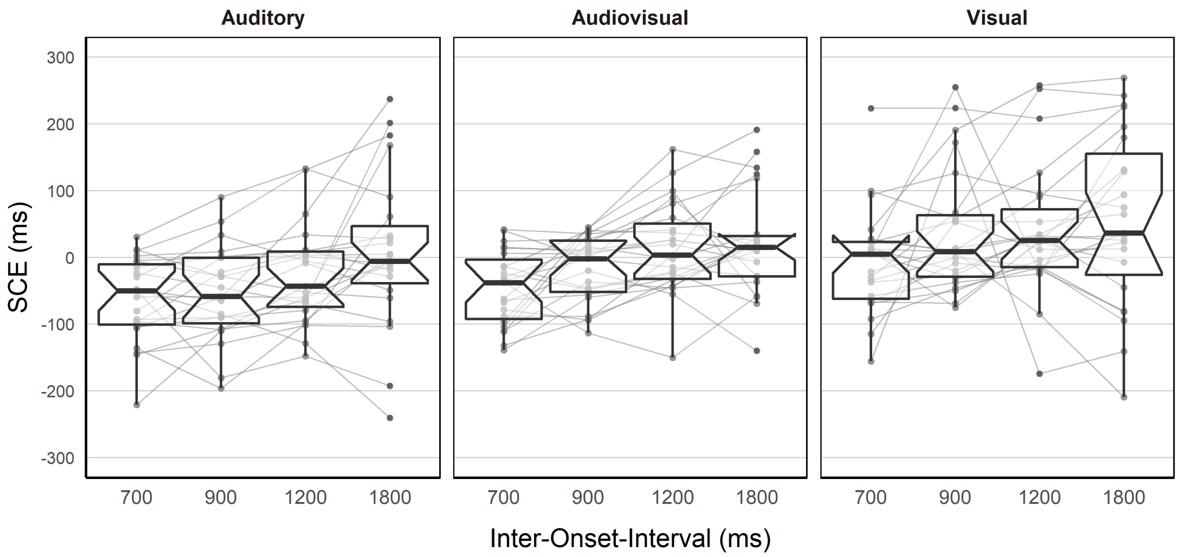
Supplementary Table S7. *Results of likelihood ratio tests of all effects in a generalized linear mixed effects model predicting variability of synchronization errors (SCE_{vr}).*

Effect	**Test statistc (χ^2)**	**Df**	**p**
Group	0.00	1	.993
Modality	135.30	2	< .001
IOI	251.43	3	< .001
*Group*Modality*	0.69	2	.709
*Group*IOI*	1.90	3	.594
*Modality*IOI*	13.26	6	.039
*Group*Modality*IOI*	2.89	6	.823

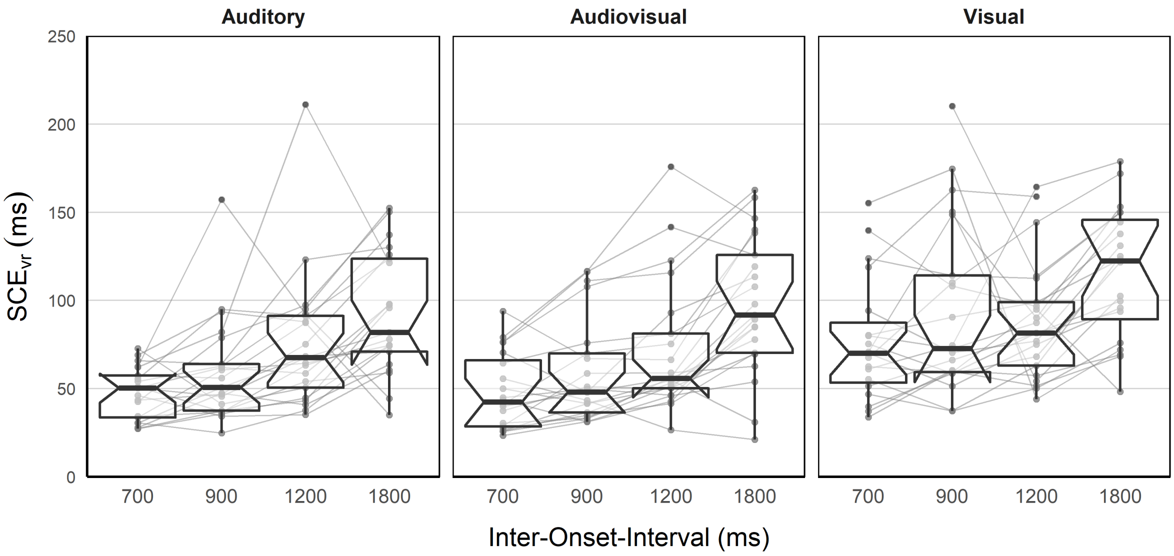
Note. Results were obtained by the mixed() function from the *afex* package (version 1.0-1) in R.



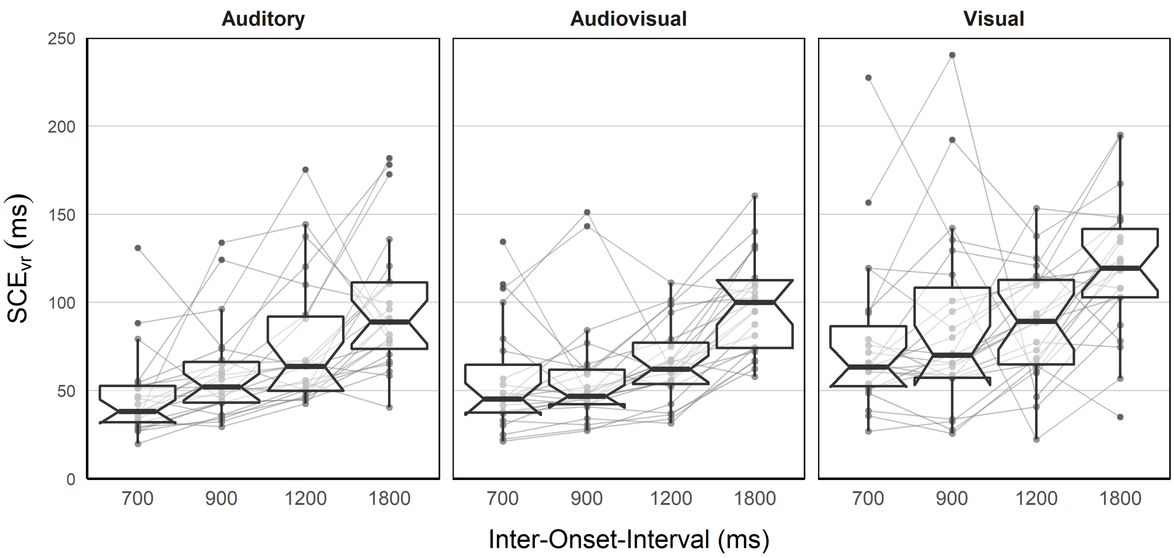
Supplementary Figure S1. *Synchronization errors (SCE) across different pacemaker Inter-Onset-Intervals (IOI) in three modalities in the TD group*. Individual values across IOIs are displayed as connected dots in three different modalities (Auditory left; Audiovisual middle; Visual right). Boxplots display distribution of values in different IOI x modality combinations.



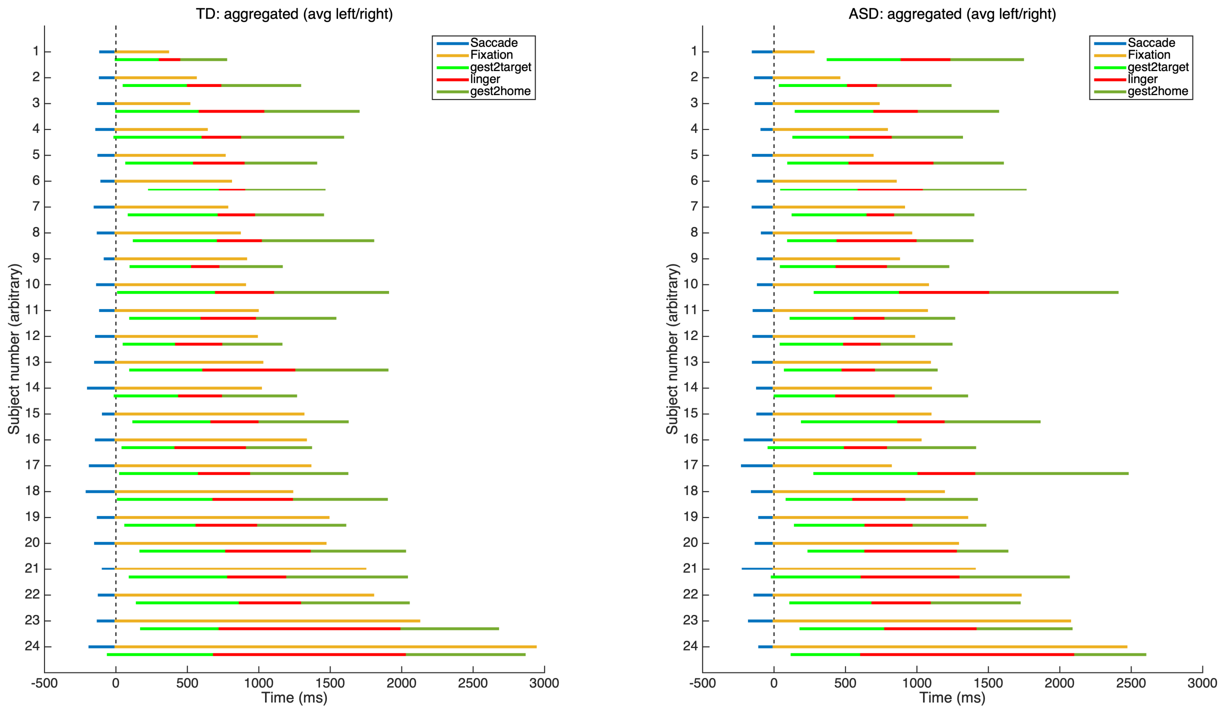
Supplementary Figure S2. *Synchronization errors (SCE) across different pacemaker Inter-Onset-Intervals (IOI) in three modalities in the ASD group*. Individual values across IOIs are displayed as connected dots in three different modalities (Auditory left; Audiovisual middle; Visual right). Boxplots display distribution of values in different IOI x modality combinations.



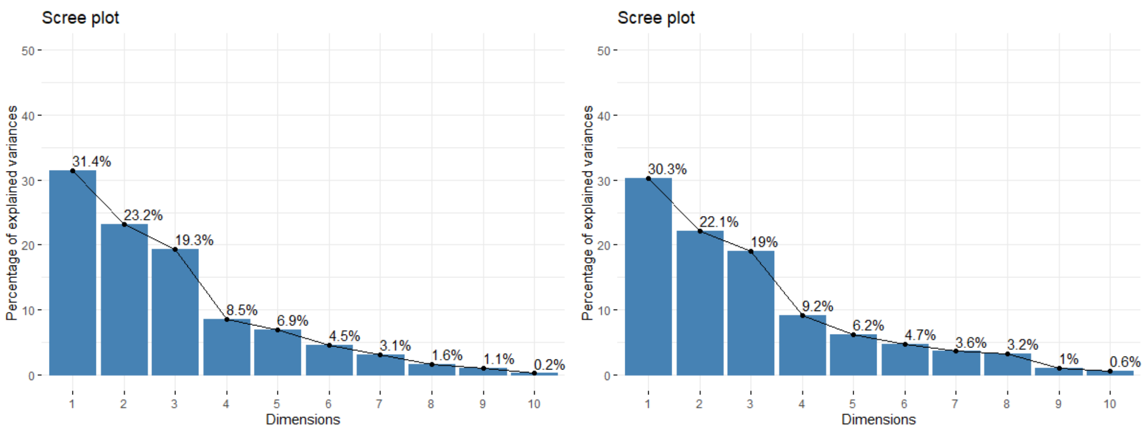
Supplementary Figure S3. *Variability of Synchronization errors (SCE$_{vr}$) across different pacemaker Inter-Onset-Intervals (IOI) in three modalities in the TD group*. Individual values across IOIs are displayed as connected dots in three different modalities (Auditory left; Audiovisual middle; Visual right). Boxplots display distribution of values in different IOI x modality combinations.



Supplementary Figure S4. *Variability of Synchronization errors (SCE$_{vr}$) across different pacemaker Inter-Onset-Intervals (IOI) in three modalities in the ASD group*. Individual values across IOIs are displayed as connected dots in three different modalities (Auditory left; Audiovisual middle; Visual right). Boxplots display distribution of values in different IOI x modality combinations.



Supplementary Figure S5. *Individual Social Pointing (SP) task data profiles in TD group (left) and ASD group (right).* Data was aggregated across valid trials per subject and averaged for target position. Colored lines display mean durations of key stages of the gesture and gaze actions. Two line levels are assigned to each individual: Upper lines (blue and yellow) display gaze actions; lower lines (light green, red, and dark green) depict gesture actions. Blue lines depicts saccades that are followed by target fixations as yellow lines. Light green lines display the initiation duration of the pointing gestures (i.e., from onset until linger position), red lines depict linger durations, and dark green lines display gesture termination durations (i.e., from linger end until gesture end). The event structure is displayed on a shared timeline centered to the fixation onset/end of saccades. Individual data is ordered ascending by the size of the average fixation duration.



Supplementary Figure S6. *Scree plots of components retrieved from Principal Component Analysis (PCA) in TD group (left) and ASD group (right).* The bars display the percentage of explained variance of components that were derived from Principal Component Analysis (PCA) per group. The bars are ordered in descending order according to the proportion of variance explained.