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Interpersonal synchrony in autism

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Structured Abstract

Purpose of review: We review evidence for the presence, quality, and correlates of interpersonal synchrony in autism spectrum disorder (ASD) across four domains: motor, conversational, physiological, and neural. We also propose cognitive and neural mechanisms for the disruption of interpersonal synchrony and investigate synchrony as a mechanism of intervention in ASD.

Recent findings: Across domains, synchrony is present but reduced or atypical in individuals with ASD during interactions with individuals with typical development (TD). Atypical synchrony may reflect the contribution of both intra-personal mechanisms, such as atypical motor timing, and inter-personal mechanisms, such as atypical inter-individual coupling. Research suggests evidence for synchrony interventions leading to improvements in some aspects of social behavior.

Summary: Understanding synchrony in ASD has the potential to lead to biomarkers and interventions to support social functioning. However, further research should clarify mechanisms of atypical synchrony in ASD including taking features of the dyad into account.

Introduction

Interpersonal synchrony, defined here as time- and form-aligned behaviors that occur in social interactions, naturally emerges in a variety of social contexts. Pairs of individuals in rocking chairs tend to align their rocks to each other [1]; conversation partners match their gestures, expressions, and language in time while communicating [2]; and mothers and infants synchronize their heart rates during social exchanges [3]. This interpersonal synchrony has important social consequences, as moving in synchrony with a social partner leads to increased liking, empathy, and prosocial behavior towards that partner [4–7]. Further, synchrony in communication is associated with improved problem-solving outcomes [8], and physiological and neural synchrony are related to empathy, rapport, and engagement in the social unit [9–11].

Because autism spectrum disorder (ASD) is characterized by differences in social interaction, research has begun to explore interpersonal synchrony in ASD, both as a marker of social interaction quality and as a mechanism of promoting more successful interactions [12–15]. Here we aim to characterize the occurrence of interpersonal synchrony in individuals with ASD, to propose potential mechanisms for the disruption of synchrony in ASD, and to explore the role of synchrony as a mechanism of intervention for improving social interactions.

Occurrence of Interpersonal Synchrony in ASD

Interpersonal synchrony can involve the coordination of a variety of behaviors, from body movements to speech to nervous system activity. Here we divide synchrony into four broad categories—motor synchrony, conversational synchrony, physiological synchrony, and neural synchrony—to explore how these forms of synchrony may be affected in ASD (Table 1).

Motor Synchrony

Motor synchrony, the time- and form-aligned movements of individuals in a social interaction, has been investigated in a variety of ways, from entrainment of pendulum swings with a partner to alignment of full body movement in conversations. Across a variety of tasks and quantification systems, motor synchrony between individuals with ASD and interactive partners with typical development (TD) is present but reduced relative to the synchrony seen in interactions of pairs of individuals with TD [16–23]. In motor tasks performed with their parents, including pendulum swinging and chair rocking, children with ASD tend to show spontaneous entrainment but at reduced levels compared to children with TD [16,17]. Similarly, when instructed to synchronize, children with ASD spend less time entrained with an experimenter while drumming, clapping, and marching than children with TD [18], and their tapping movements cohere less with an experimenter's [19]. These reductions in interpersonal synchrony are not just seen in explicitly rhythmic activities such as rocking and drumming; children with ASD also show reduced motor synchrony compared to children with TD in neuropsychological testing sessions and conversations with clinicians [20]. Yet there is still evidence that children with ASD exhibit synchrony with social partners: children with ASD demonstrate instances of high movement coherence with actors during theatre games [24] and above-chance coherence in conversations with clinicians [25]. Notably, in tasks with fewer social-interactive demands, individuals with ASD show similar levels of motor synchrony to peers with TD. For example, when individuals with ASD were asked to coordinate their movements with computer avatars believed to be human partners, they performed comparably to individuals with TD [26,27].

In ASD, increased motor synchrony with a social partner is associated with reduced symptom severity, in terms of both reduced restricted interests and repetitive behaviors [25,28]

and improved social performance [29–31]. Children who displayed greater levels of full-body motor coherence with a clinician during a conversation had lower levels of clinician-rated restricted interests and repetitive behaviors [25]. Similarly, children who showed increased hand movement coherence during a hand clapping game with an experimenter had reduced levels of repetitive behaviors [28]. Interpersonal motor synchrony also correlates with social performance, although it has been suggested that different forms of motor synchrony have different consequences. Specifically, intentional synchrony (synchrony that occurs when the goal of the activity is explicitly defined as synchronization) and spontaneous synchrony (synchrony that occurs without any task instruction) may uniquely correlate with different aspects of social performance in ASD [30]. Increased spontaneous synchrony during a hand clapping game with an experimenter correlated with improved performance in responding to joint attention, while increased intentional synchrony during an instructed social motor tapping task correlated with improved performance in initiating joint attention [30]. These findings underscore the associations between motor synchrony and social behavior, but also highlight potential differences in the mechanisms and correlates of intentional and spontaneous synchrony.

Conversational Synchrony

Synchrony in ASD has also been investigated in the context of the linguistic and conceptual alignment that occurs over the course of a conversation. This conversational synchrony is proposed to be associated with affiliation and facilitation of communication [2], and increased alignment of communicative acts is associated with improved performance on communication tasks [8]. One way to investigate linguistic alignment is by presenting structured tasks in which the experimenter uses a certain phrasing or label and then assesses the child's later use of that phrasing or label. In these tasks, children with ASD align their sentence structures to

those of adult experimenters [32,33]. Similarly, children with ASD engage in typical levels of lexical alignment by using similar names as an experimenter to refer to an object, even if that object could have multiple names (e.g. bunny, rabbit) [34]. Consistent with this evidence for typical syntactic and lexical alignment in children with ASD, adults with Asperger's syndrome used typical levels of syntactic and lexical alignment and also aligned their frame of reference when describing object locations to a confederate [35].

In contrast to the typical levels of alignment seen in these structured tasks, results from less structured alignment tasks suggest that individuals with ASD engage in atypical or reduced displays of conversational synchrony. For example, adolescents with ASD incorporated linguistic characteristics of a conversational partner's previous utterance into their own present utterance at similar levels as mental-age-matched peers. However, the adolescents with ASD were more likely to perform this incorporation in atypical ways by constructing an incoherent, though aligned, utterance, such as responding "most about myself is the teach" to the question "What do you like most about yourself?" [36,37]. Individuals with ASD may also be less sensitive to changes in the social context while aligning. When adults with ASD switch partners, they are less likely to realign their use of language to incorporate their new partner's contributions [38]. Recent reviews have highlighted the importance of continuing to explore the interpersonal coordination component of conversations in understanding ASD [39], which may lead to further understanding of conversational synchrony.

While these studies have identified atypical conversational synchrony in live face-to-face verbal exchanges, one novel design has allowed for the exploration of communicative synchrony independent from the demands of face-to-face conversation [8]. In this study, dyads composed of two adults with ASD, two adults with TD, or mixed ASD and TD took turns to communicate

messages about objects and their orientations in order to solve a series of progressively difficult puzzles [8]. Crucially, although the game was interactive, the partners could not see or speak to each other, and could only manipulate a digital puzzle board to exchange messages. While solving ambiguous problems, both the ASD-ASD dyads and the ASD-TD dyads were less likely than the TD-TD dyads to align to the communicative strategy used on the previous turn, and this reduced alignment correlated with poorer task performance [8]. Interestingly, the reduced alignment in dyads containing at least one participant with ASD was not due to the types of communication that were employed by individuals with ASD or flexibility in employing different signal types. Therefore, these reductions in alignment may reflect difficulties in predicting and updating mutual understanding to maintain alignment rather than reduced cognitive flexibility or atypical signal production. This work highlights the importance of controlled experimental paradigms that can reduce the demands of live social interaction to better assess the presence of synchrony outside of other demands that emerge in face-to-face interactions, complementing studies investigating synchrony in face-to-face interactions.

Physiological Synchrony

Physiological synchrony encompasses the alignment of sympathetic nervous system activity, parasympathetic nervous system activity, or adrenocortical activity between interacting partners, and it is associated with empathy and rapport in these social units [11]. While this domain of synchrony has been investigated broadly in the realm of parent-child interactions as the foundation of attachment relationships [9,40], including electrodermal synchrony, heart rate synchrony, and cortisol synchrony, only a few studies to our knowledge have investigated physiological synchrony in ASD. Across these studies, there is evidence of reduced physiological synchrony between children with ASD and their caregivers. Preschoolers with

ASD display reduced cortisol synchrony, defined as alignment of saliva cortisol levels measured at three time points during a two-hour home interaction, with their mothers compared to typically developing children [41]. Among children with ASD, the level of synchrony displayed may be dependent on symptom severity, as children with higher levels of ASD symptoms have reduced electrodermal synchrony with their caregivers compared to children with lower levels of symptoms [42].

To our knowledge only one pilot study has examined physiological synchrony in ASD outside of the parent-child relationship [43]. This preliminary study identified an absence of synchrony of inter-beat intervals between three adults with ASD and their TD conversational partners and highlights the feasibility of examining physiological synchrony outside of parent-child interactions for future exploration. Of course, physiological synchrony can both influence and be influenced by the degree of synchrony in behavior within dyads (parent and child or social partners) or similarities in their shared environment. Thus, to better understand typical and atypical aspects of synchrony in ASD, it will be useful to link both physiological and behavioral synchrony within the same dyads.

Neural Synchrony

Neural synchrony refers to the alignment of brain activity between interacting individuals. To the best of our knowledge, only two studies to date have investigated neural synchrony between individuals with ASD and interaction partners [44,45], and of those only one has incorporated a control group of individuals with TD [44]. Adults with ASD and TD played a joint attention game [44]. Both participants were simultaneously imaged in an MRI scanner while viewing their interaction partner's gaze in real time. ASD-TD dyads had reduced neural synchrony during the interaction compared to TD-TD dyads [44]. Another study investigated

neural synchrony between children with ASD and their mothers, who were simultaneously imaged in an MEG scanner while viewing either their partner's real-time facial expression or short video clips selected by the child [45]. The mother's degree of mu suppression, a putative index of mirror neuron system activity [46], was found to correlate with her child's degree of mu suppression during the interaction. This mu suppression was also correlated with autistic traits, such that mothers and children with higher degrees of mu suppression had fewer autistic traits [45]. Continuing to explore the presence of neural synchrony between individuals with ASD and their interaction partners will be important to develop an understanding of the neural basis of social interaction in ASD [47].

Cognitive and Neural Mechanisms of Atypical Synchrony in ASD

A variety of mechanisms have been proposed for atypical synchrony in ASD. Here, we distinguish between intra-individual mechanisms that may promote atypical synchrony in ASD, such as atypical social attention, and inter-individual processes that arise from interactions between individuals with ASD and their social partners. These mechanisms are not mutually exclusive; furthermore, intra-individual mechanisms, such as atypical motor control or atypical predictive coding, can give rise to atypical inter-individual processes such as motor resonance [48] or social prediction [49,50], which would influence the achievement and maintenance of synchronization in the dyad. As a result, the mechanisms underlying synchrony are best considered in a dyadic context that takes into account the unique contributions of each individual and allows for examination of both intra- and inter-individual mechanisms (Figure 1).

Intra-individual Mechanisms

Motor performance. ASD is associated with deficits in fine and gross motor skills and postural control [51], increased variability in motor output, and slower motor planning [18,52]. As motor synchrony relies on the alignment of behaviors in both time and form, atypical motor processing could account for the diminished motor synchrony observed between individuals with ASD and individuals with TD. In support of this hypothesis, atypical intrapersonal motor performance often correlates with atypical interpersonal motor synchrony [19,22]. However, differences between individuals with ASD and individuals with TD in maintaining interpersonal synchrony remained after controlling for performance on a motor skills battery and maximum velocity obtained in a non-social repetitive movement task [22], suggesting that additional factors beyond motor coordination may play a role in atypical motor synchrony.

Temporal processing. Atypical temporal processing in ASD may manifest in atypical use of sensory information to guide motor actions and atypical integration of sensory events. These could both play a role in reduced interpersonal synchrony, as temporal coordination of one's own perceptions and behavior is an important component of coordinating with others [12]. One recent study in ASD directly examined temporal processing of audiovisual events, finding that individuals with ASD report audiovisual events as simultaneous at longer intervals apart—i.e., at a wider binding window—than individuals with TD [20]. Wider binding windows negatively correlate with interpersonal motor synchrony achieved with a clinician for children with TD but not children with ASD [20]. Together, these findings highlight temporal processing differences in ASD and suggest future research to determine the ways in which these differences may give rise to diminished synchrony between individuals with TD and ASD.

Social attention. ASD is characterized by reduced attention to social information [53,54], which would correspond to reduced attention to visual and auditory cues from a social partner with which to synchronize [55]. Related research in imitation has found that attention to social stimuli predicts accuracy of imitation in toddlers with ASD [56]. However, further research is necessary to quantify the extent to which visual attention to a social partner accounts for reduced synchrony in ASD.

Motivation and reward. Atypical social motivation may contribute to reduced synchrony. The social motivation hypothesis predicts a diminished response in the brain's motivation and reward circuitry in ASD that manifests as reduced interest in social engagement and reduced feelings of reward from social stimuli [57,58]. Viewed through this lens, the reduced synchronous behavior seen in ASD could be the result of reduced motivation to align with a social partner or reduced enjoyment in alignment. Adults with ASD were less likely to report wanting to continue to play a synchronous movement game than adults with TD, and this preference correlated with the amount of time they spent in synchrony with their partner [22]. In contrast, adults with ASD enjoyed a motor synchrony game to the same degree as peers with TD [22] and made similar time trade-offs in communicating game-relevant information to a partner, suggesting a motivation to communicate social information [8]. Future research examining links between social motivation and synchrony will be necessary to clarify the extent to which the motivation for and reward felt from achieving synchrony with a social partner is affected in ASD.

Oxytocin. Oxytocin is a neuropeptide associated with synchronous behaviors [59] and related to social symptoms in ASD[60]. In neurotypical samples, exogenous administration of oxytocin modulates processing of social and synchronous actions [61,62], promotes interbrain

synchrony between social partners [63], and leads to better cooperative performance on tasks [64]. Endogenous oxytocin is enhanced by synchronous social interactions, suggesting reciprocal effects between oxytocin and synchrony in social interaction [65]. Thus, reduced levels of oxytocin in relevant brain circuits in ASD may relate to reduced synchronous behaviors.

Mirror neuron system. The mirror neuron system (MNS), or observation-execution system, describes a system of brain regions encompassing inferior frontal, premotor, and inferior parietal regions that demonstrate similar responses during both observation and execution of actions [66]. This “mirroring” between actor and observer is proposed to play a role in social abilities such that disruption to this system could result in reduced understanding of others through difficulties simulating others’ goals and perspectives [67,68]. While there is limited empirical support for widespread dysfunction of the mirror neuron system in ASD [69], some have suggested that spontaneous mimicry may be mediated by distinct pathways in the MNS and these specific pathways, as well as the modulation of these pathways by top-down systems sensitive to social context, are atypical in autism [70–72]. In the context of social interaction, this reduced spontaneous mimicry and modulation by social context could lead to reduced alignment or mimicry that is not contextually appropriate. This type of contextually inappropriate mimicry could also have negative effects on social interaction; for example, indiscriminate mimicking is associated with reduced perceptions of the mimicker’s social competence [73].

Predictive coding. Using principles from Bayesian approaches, the predictive coding framework argues that the brain develops predictions of the environment based on past experience and knowledge (priors). Mismatches between these predictions and sensory input lead to a prediction error that propagates through the brain hierarchically [74,75]. There is evidence for atypical predictive coding in autism [76] including weaker use of priors [49,77].

These differences could lead to intra-individual differences, such as atypical sensorimotor control and less weighting of the social context or history of the interaction in generating a prediction or interpreting sensory input [50], all of which could lead to reduced alignment with an interaction partner.

An alignment system. Another proposal that invokes predictive coding as a mechanism of synchrony is the Extended Integration Model of Alignment, which argues for interplay between multiple systems to promote and maintain alignment between social partners [15]. Individuals build up a prediction that they will be in alignment, and information generated from the self and other provides input as to whether this prediction is met. If a gap in alignment is detected, the observation-execution system (or MNS) works to repair the alignment, and if no gap is detected, then the reward system is engaged for receipt of a hedonic response (or reward). This reward experience drives further predictions for alignment and generation of alignment behaviors. This model is argued to support not just motor alignment but also emotion contagion and social conformity. A strength of this proposal is that it integrates across multiple systems that contribute to a complex phenomenon of alignment. However, it is not presently clear that the same mechanisms would underlie these diverse forms of synchrony. Further, the specific features of this model await further testing to determine the model's applicability for disruptions of synchrony in ASD; for example, as discussed above, evidence supporting atypical mirror neuron or reward systems in ASD is mixed.

Inter-individual Mechanisms

While intra-individual mechanisms focus on the individual's ability to promote and maintain synchronous behaviors, inter-individual mechanisms focus on the ways in which interactions between individuals affect the dyad's ability to promote and maintain synchrony.

For example, due to the coupling of observation-execution systems between social partners [78], feedback loops can be created at the inter-individual level [15], such that each person's motor output feeds into their partner's perceptual input. Discrepancies between individuals in the processes that constitute this feedback loop will therefore influence the dyadic synchrony. For example, differences in predictive coding between individuals may lead to interpersonal mismatches within interactions [49,50], such that synchrony is a reflection of the similarity or dissimilarity of the dyad beyond each member's individual predictive coding system. Similarly, individual differences in motor control could give rise to mismatches in the degree to which individuals would perceive others' movements as similar to their own, which may disrupt the achievement of synchrony [48]. Thus, it is not only one individual's processes that lead to atypical synchrony but the ways in which one's own intra-individual traits and abilities align with and affect the interaction partner. Further investigation of these inter-individual mechanisms will require increased focus on the dyadic context of synchrony (Figure 1).

Synchrony as a Potential Mechanism of Intervention to Improve Social Abilities

Multiple meta-analyses have demonstrated the effects of synchrony on prosocial behavior, empathy, and social enjoyment in adults with TD [4–6]. As in TD, correlational evidence in ASD suggests that for some types of synchrony, increased synchrony is associated with positive outcomes. For example, parental synchronous behavior around age 4 predicts joint attention skills in children with ASD one year later and language skills up to 16 years later [79]. Additionally, synchronous behavior in an interpersonal motor game predicts reported affect during the game for adults with ASD [22]. However, in studies that experimentally manipulate synchrony, synchrony does not seem to be associated with the same outcomes in adults with

ASD as TD. For example, in a finger tapping task with a virtual avatar, adults with ASD did not report more empathy towards a synchronous partner compared to an asynchronous partner, while adults with TD did [26]. These results highlight the importance of continuing to investigate the outcomes of inducing synchrony in ASD and the ways in which they differ from the outcomes of synchrony in TD.

In light of these potential prosocial outcomes of synchrony, multiple studies have begun to examine the effectiveness of synchrony interventions [80–82]. Although interventions designed to increase interpersonal synchrony have generally been successful in improving interpersonal motor performance, there have been mixed results in generalizing these improvements to other social domains such as empathy, emotion recognition, or joint attention [80–82]. School-age children who received an intervention with rhythmic movement components improved in the performance of synchronous movements over the course of the intervention [82]. A synchrony intervention in adults with ASD that focused on interpersonal motor activities improved interpersonal synchrony, automatic imitation, and emotion inference, but not feelings of empathy [80]. Toddlers who received an intervention with a supplemental curriculum designed to encourage social synchrony performed significantly better on an imitation task at a follow-up time point, but did not show significant increases in joint attention or shared affect compared to toddlers who received a control intervention [81]. Together, these studies provide preliminary evidence that interpersonal synchrony intervention can improve synchronous behavior. However, the extent to which increasing the presence of synchrony affects other social abilities (e.g., joint attention or empathy) remains unclear. Future work to clarify whether factors such as age of participants, duration of intervention, and type of synchrony determine the outcomes and correlates of synchronous interaction in ASD will be

crucial to better understand the role of synchrony in intervention and in daily experience for individuals with ASD.

Conclusions

Interpersonal synchrony between individuals with ASD and individuals with TD is diminished across a variety of domains, including motor, conversational, physiological, and neural synchrony. Given these persistent differences, atypical synchrony has been proposed as a potential biomarker for diagnosis, stratification, and/or intervention response in ASD [13,24]. Recent technological developments demonstrate the feasibility of examining synchronous behaviors in ASD. For example, wearable technology allows for capture of large amounts of movement and physiological data [24], while other developments allow for the assessment of synchrony from video recordings in a non-invasive yet time-effective way [20,21,25]. However, questions remain as to the mechanisms that contribute to atypical synchrony and the extent to which synchrony itself can be a mechanism of intervention. Specifically, reduced or atypical synchrony may reflect the influence of both intra-individual and inter-individual mechanisms, and additional research will be important to clarify the relative importance of these mechanisms to the different domains of synchrony. Further, while synchrony interventions have demonstrated some early results in improving synchronous behavior, additional research is needed to determine the extent to which these outcomes generalize to other forms of social behavior for individuals with ASD. Additionally, because appropriate displays of synchrony may be sensitive to the context of the interaction [73] future research is needed to understand the contextual dynamics that determine appropriate synchrony.

Synchrony is an inherently dyadic construct (Figure 1). As such, the emergence of synchrony during an interaction depends not on a single individual, but the ways in which each individual promotes synchrony or compensates for their partner's behavior. Similarity to the interaction partner may be an important determinant of synchrony, such that individuals who are concordant on diagnosis (two individuals with ASD or two individuals with TD) may achieve better alignment than individuals who are discordant on diagnosis [49]. Given that the majority of the literature characterizes interactions between individuals with ASD and individuals with TD, additional research can enhance our understanding of the unique nature of interactions between individuals with ASD [83].

At present, investigating interpersonal synchrony in ASD is a promising avenue to characterizing social interactions and determining their outcomes. Further understanding of the mechanisms and outcomes of synchrony as well as how dyadic characteristics affect synchrony may lead to the development of new biomarkers and interventions to understand and support social functioning in ASD.

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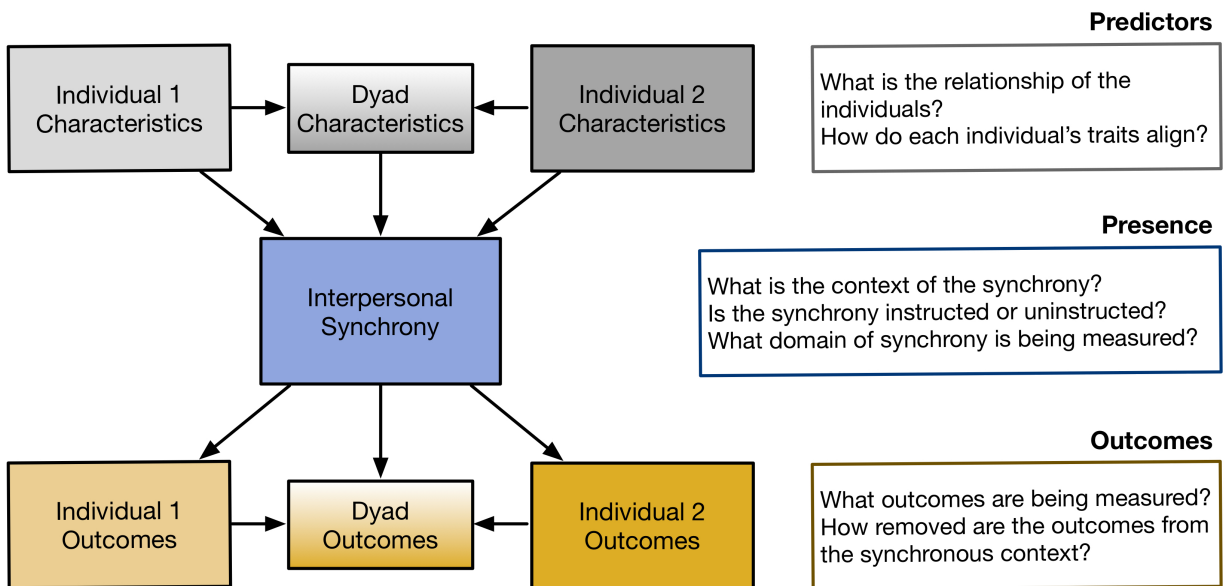


Figure 1. The synchrony that emerges in an interaction between two individuals reflects not only their individual traits (e.g. diagnosis), but also the alignment of their intra-personal attributes. The synchrony also depends on the task demands and the context in which the synchrony is elicited, whether the synchrony is intentional or spontaneous, and in what domain the synchrony is occurring. Finally, the experience of synchrony may give rise to individual outcomes (e.g. increased empathy) as well as dyad outcomes (e.g. increased interaction success). The outcomes of synchrony may also differ based on the context in which these outcomes are evaluated, for example whether an individual shows enhanced empathy towards the partner s/he synchronized with or enhanced empathy more generally.

Table 1.

Recent papers investigating the presence of motor, conversational, physiological, and neural synchrony in ASD.

Author	<i>n</i>	Synchronous Behavior	Findings
Motor Synchrony			
Brezis et al., 2017 [22]	34 ASD, 35 TD	Percent highly synchronized movement in a game with an experimenter	ASD < TD
		Duration of highly synchronized movement	ASD < TD
Delaherche et al., 2013 [21]	7 ASD, 14 TD	Strength of coherence with adult during instruction task	ASD < TD
		Variability in amount of coherence with adult during instruction task	ASD > TD
Fitzpatrick et al., 2016 [17]	9 ASD, 9 TD	Entrainment of pendulum swings to parent's when instructed to synchronize	ASD < TD
		Entrainment of pendulum swings to parent's when not instructed to synchronize	ASD < TD
Fitzpatrick et al., 2017 [19]	45 ASD, 53 TD	Coherence of hand motion with an experimenter during an instructed social-motor battery	ASD < TD
		Coherence of hand motion with an experimenter during hand clapping game	ASD < TD
Kaur et al., 2018 [18]	24 ASD, 12 TD	Percent of time moving in synchrony with an experimenter during instructed clapping, marching, and drumming tasks	ASD < TD
Kawasaki et al., 2017 [84]	24 ASD, 24 TD	Rate of synchronous tapping (within 50 ms) to a human partner	ASD < TD
		Rate of synchronous tapping to a variable computer partner	ASD < TD
		Rate of synchronous tapping to a non-variable computer partner	ASD = TD

Koehne et al., 2016 [26]	20 ASD, 22 TD	Deviation from synchronous tapping with perceived human partner	ASD = TD
		Deviation from synchronous tapping with computer partner	ASD = TD
Marsh et al., 2013 [16]	8 ASD, 15 TD	Alignment of phase of rocking with parent	ASD < TD
Noel et al., 2018 [20]	12 ASD, 15 TD	Coherence of head movement with clinician	ASD < TD
		Coherence of hand movement with clinician	ASD < TD
		Coherence of torso movement with clinician	ASD = TD
Romero et al., 2016 [23]	43 ASD, 47 TD	Recurrent hand activity while drumming with an experimenter	ASD = TD
		Recurrent hand activity during hand clapping game with an experimenter	ASD = TD
		Alignment of phase of hand activity while drumming with an experimenter	ASD < TD
		Alignment of phase of hand activity during hand clapping game with an experimenter	ASD < TD
Romero et al., 2018 [25]	28 ASD	Coherence of whole-body motion with clinician during structured conversation	ASD: above chance synchronization
Stoit et al., 2011 [85]	28 ASD, 28 TD (paired 14 ASD-ASD, 14 TD-TD)	Proportion of highly synchronized (< 100ms difference) incidences of joint movement	ASD < TD
		Differences in reaction time to initiate joint movement	ASD = TD
Zapata-Fonseca et al., 2019 [27]	10 ASD matched with 10 TD	Complexity matching of movements in a 1-D space	ASD-TD: above chance complexity matching
Conversational Synchrony			
Allen et al., 2011 [32]	12 ASD, 24 TD	Alignment of syntax to experimenter's syntax	ASD = TD
Branigan et al., 2016 [34]	15 ASD, 30 TD	Alignment of object name to experimenter's chosen object name	ASD = TD

Hobson et al., 2012 [36]	12 ASD, 12 with intellectual disability (verbal-age-matched)	Proportion of utterances that were frame grabs (utterances incorporating 3 or more linguistic elements from previous utterance)	ASD = verbal-age-matched peers
		Proportion of frame grabs that were appropriate	ASD < verbal-age-matched peers
Hopkins et al., 2015 [33]	17 ASD, 17 TD	Alignment of syntax to experimenter's syntax	ASD = TD
		Alignment of syntax to peer's syntax	ASD = TD
Nadig et al., 2015 [38]	13 ASD, 13 TD	Maintenance of previously developed referential pact when new partner is introduced	ASD > TD
Slocombe et al., 2013 [35]	17 ASD, 17 TD	Alignment of syntax to confederate's syntax	ASD = TD
		Alignment of object names to confederate's choice of object names	ASD = TD
		Alignment of frame of reference to confederate's frame of reference	ASD = TD
Wadge et al., 2019 [8]	22 ASD, 30 TD (paired 7 ASD-ASD, 8 ASD-TD, 11 TD-TD)	Alignment of communication strategy in all games	ASD-ASD < ASD-TD = TD-TD
		Alignment of communication strategy in ambiguous games	ASD-ASD = ASD-TD < TD-TD
Physiological Synchrony			
Baker et al., 2015 [42]	28 ASD	Covariation of electrodermal activity with parent	Relationship between increased covariation and lower levels of ASD severity
Dunsmore et al., 2019 [43]	3 ASD paired with 3 TD	Physiological linkage of heart-rate inter-beat-intervals	ASD: linkage not above chance
Saxbe et al., 2017 [41]	39 ASD, 40 TD	Cortisol synchrony with mother	ASD < TD
		Cortisol synchrony with father	ASD = TD

Neural Synchrony			
Hasegawa et al., 2016 [45]	8 ASD	Correlation of mu suppression with mother	Significant correlation right (not left) precentral area
Tanabe et al., 2012 [44]	21 ASD, 59 TD (paired 21 ASD-TD, 19 TD-TD)	Correlation of neural activity in right IFG with scan partner	ASD-TD < TD-TD

Abbreviations: = no difference

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