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A metastable attractor model of self–other integration (MEAMSO) in rhythmic synchronization

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Human interaction is often accompanied by synchronized bodily rhythms. Such synchronization may emerge spontaneously as when a crowd’s applause turns into a steady beat, be encouraged as in nursery rhymes, or be intentional as in the case of playing music together. The latter has been extensively studied using joint finger-tapping paradigms as a simplified version of rhythmic interpersonal synchronization. A key finding is that synchronization in such cases is multifaceted, with synchronized behaviour resting upon different synchronization strategies such as mutual adaptation, leading–following and leading–leading. However, there are multiple open questions regarding the mechanism behind these strategies and how they develop dynamically over time. Here, we propose a metastable attractor model of self–other integration (MEAMSO). This model conceptualizes dyadic rhythmic interpersonal synchronization as a process of integrating and segregating signals of self and other. Perceived sounds are continuously evaluated as either being attributed to *self*-produced or *other*-produced actions. The model entails a metastable system with two particular attractor states: one where an individual maintains two separate predictive models for *self*- and *other*-produced actions, and the other where these two predictive models integrate into one. The MEAMSO explains the three known synchronization strategies and makes testable predictions about the dynamics of interpersonal synchronization both in behaviour and the brain.

This article is part of the theme issue ‘Synchrony and rhythm interaction: from the brain to behavioural ecology’.

1. Introduction

The ability to coordinate one’s movements with those of others is a critical aspect of daily life. An everyday action such as shaking hands in greeting is a complex feat of reciprocally anticipating and adjusting movements, yet we perform it with ease and without apparent conscious effort [1]. One of the most fascinating aspects of such adaptation is interpersonal synchronization, wherein periodic movements exhibit phase and frequency locking between persons [2]. Such synchronization often emerges spontaneously, as in the tendency towards synchronized walking, or in a crowd’s applause converging on a steady rhythm [3,4]. However, in many cases, interpersonal synchronization is necessary and intentional, for instance in human bucket brigades [5]. The most salient example is perhaps found in musical performance.

When musicians sing and play music together, each individual musician coordinates their actions towards producing sounds which in concert with other musicians creates the cohesive auditory patterns we identify as music [6]. A critical observation here is that a reactive approach is insufficient. To produce a

synchronized rhythm with other musicians, any action producing a sound needs to be initiated well before the actual sound is produced [7]. Hence, intentional rhythmic synchronization must rely on processes of anticipation and prediction [8,9].

An often-overlooked aspect of such predictive processes is the selection of *which* perceptual signal one should adapt to. Any decent musician in an ensemble is capable of recognizing whether another ensemble member is deviating from the ensemble's shared musical goal, and then swiftly perform an on-the-fly judgement whether the deviating member should be ignored, or adapted to. To do so, musicians continuously monitor how the actions of others relate to self-produced actions, as well as the combined action outcomes [10,11]. In laboratory settings, this type of interpersonal synchronization has predominantly been studied using joint finger-tapping paradigms [10,12–14].

In joint finger tapping, two participants are asked to perform simple isochronous rhythms together, often initiated by a few beats of a metronome, with instructions to maintain tempo and synchronize. A key finding from the field is that rhythmic interpersonal synchronization may be more than just a linear transition from unsynchronized to synchronized actions. Rather, different interpersonal strategies underlie synchronization, such as mutual adaptation and leading–following [10,12–14]. Note that here we use the term strategy loosely, as the emergence and dynamics of dyad synchronization behaviour is still a topic under active research. Mutual adaptation occurs when bidirectionally or omnidirectionally coupled dyad members continuously and reciprocally adapt to each other tap-by-tap, and has been observed in both musicians and non-musicians [10,12]. Leading–following can occur either due to experimental restraints or emerge from the interaction. For instance, in cases of unidirectional coupling wherein dyad member 1 hears themselves, and dyad member 2 hears dyad member 1, the dyad has to adapt a leader–follower strategy to maintain synchronization [12]. However, naturally emerging leader–follower behaviour has also been observed in bidirectionally coupled interactions between non-musicians [13] and is routinely found in musical interactions [15]. Common for all of these strategies is that they are not necessarily differentiable based on synchronization measures alone, but can instead be detected by looking at the interaction between the signals of the interacting members, i.e. using cross-correlation measures between participants' intertap intervals [12].

While these synchronization strategies are well documented and prevalent in the tapping literature, there are multiple open questions as to their emergence and nature. For instance, to what extent are synchronization strategies dynamic, in the sense that an interaction may conceivably continuously swing between different strategies? Or, which parameters of individual behaviour in an otherwise equally constrained interaction contribute to the prevalence of one synchronization strategy over another?

In previous research, individual differences such as people's preferred tapping rate have been shown to influence synchronization, but their impact on the behaviour underlying synchronization remains unclear [16,17]. Similarly, the dynamics of responses to perturbations in synchronization tasks such as rate changes in the synchronization target may impact synchronization strategies and has been shown to depend on individual differences [18–21]. Interestingly, in a drumming task, toddlers (2- and 3-year olds) were able to

spontaneously coordinate rhythmic interaction with a peer, but only 4-year-old children exhibited continuous adaptability of their drumming [22]. This age distinction clearly links to the development of a cognitive self–other distinction as measured by the classic false-belief test that typical 3-year olds fail but typical 4-year olds pass [23]. These findings suggest that interpersonal synchronization is influenced both by development and individual differences, and crucially relies on the ability to distinguish between the self and the other.

Over the last four decades, multiple researchers have proposed models aiming to capture the underlying processes and dynamics of sensorimotor synchronization, and recently also for interpersonal synchronization [8,24–30]. Generally, these models can be classified as information processing event-based models or nonlinear coupled oscillator dynamic models. Both approaches have shown promise, with a dual-agent version of the adaptation and anticipation model (ADAM) capturing leading–following and mutual adaptation behaviour [31], and with our Kuramoto-oscillators model also managing to account for leading–leading behaviour [24]. A third alternative also exists in the strong anticipation hypothesis, wherein anticipatory behaviour in dynamical systems is shown to emerge from time delays [30,32,33]. Nonetheless, these models have not explicitly focused on the underlying neural basis for how and why dyadic synchronization strategies emerge. In this paper, we present a theoretical model that explains how simple predictive brain dynamics give rise to synchronization strategies. Furthermore, we show how to use the model for deriving testable hypotheses of dyadic synchronization behaviour.

2. The metastable attractor model of self–other integration

In previous work, we, and others, have argued that intentional interpersonal synchronization may be framed through mechanisms of self–other integration [2,24,34–40]. Specifically, we have proposed that mutual adaptation occurs when two dyad members both integrate the self and other, that leading–following occurs when one of the two dyad members (the follower) integrates the other while the other (the leader) segregates, and that leading–leading occurs when both dyad members are segregating between the self and other [24]. Here, *self* refers to actions performed by oneself and their related consequences, whereas *other* refers to information stemming from the person one is interacting with. This argument is based on observations of overlapping brain networks processing both perceived/observed and performed actions, wherein action-perception loops that blur the difference between self and other may emerge [34,41–44]. To explain how these processes account for not just synchronization, but also synchronization strategies, here we present a model where self–other integration is conceptualized as a continuous process wherein action and perception are constantly evaluated as either connected or unconnected.

The foundational assumption of the metastable attractor model of self–other integration (MEAMSO) is that the brain maintains predictive cognitive models for the *self*, i.e. the actions performed, and for the *other*, i.e. the perception of actions performed by the person one is interacting with [45]. In joint finger tapping, the self-model initiates finger taps, and then receives somatosensory and auditory feedback

when their finger hits the tapping device. The other-model relies on auditory feedback from the other dyad member's taps. If the dyad's goal is only to synchronize, then each dyad member needs to collectively minimize the difference between event predictions formed by their self- and other-model [2]. We propose that this process of integrating or segregating between the self- and other-model is the result of a continuous evaluation of percepts as either being attributed to the self or to the other; or, in other words, whether perceptions are causally linked to actions. We hypothesize that self–other integration and segregation act as attractors, or transiently stable states, in the configuration of brain network dynamics, underpinning synchronization strategies. By metastable, we mean a system exhibiting stable states other than the state of least energy, operationalized in the brain as neural oscillations existing in a dynamic system which switches between states due to both external perturbations or internal fluctuations [46–50]. The goal of the MEAMSO is therefore to formalize the qualities and dynamics of a dyadic interaction resulting in the dyad members either being in a state of self–other integration or segregation.

3. Mapping the dynamics of self–other integration

The first step in mapping the dynamics of self–other integration in joint action is to understand how we are aware that an action and its perceptual consequence are self-generated. In the last two decades, it has become increasingly evident that sensory predictions form a crucial part of determining the likelihood of an action and a concurrent perception being self-generated [35]. In a seminal study from the late 90s, Fourneret & Jeannerod [51] showed that participants are more aware of intended movements rather than actual deviated movements, but only up until a crucial threshold. In addition, people are prone to confuse self-produced hand movements with those performed by someone else given a high enough similarity [52,53]. Within the framework of predictive coding, these observations may be explained by predictions being formed about the sensory consequences of an action, where only prediction violations of a certain magnitude traverse high enough in the prediction error hierarchy to reach conscious appraisal [54]. It is also likely that top-down control modulates these decisions, through imposing a certain leniency on the conscious appraisal of a perceptual event deviating substantially from the predicted sensory consequences [55]. For instance, if only one isolated event is surprising in a series of predictable events, the surprising event may be considered just a lapse in attention [56].

An interesting avenue of exploring the latter component can be found in amplified musical performance settings. Here, musicians usually receive an amplified signal of their instrument as a monitor signal, in order to be able to self-monitor their performance and integrate with other musicians [57]. Due to the inherent delays in both digital and analogue audio equipment, and acoustic propagation delay, this signal may deviate by multiple milliseconds from the original output signal of the musical instrument. In these cases, performers are consciously aware that the auditory perceptions they hear are causally linked to their actions. Nonetheless, once the delay is sufficiently large, the situation becomes disruptive for the musicians and negatively impacts their performance [58].

Interestingly, the thresholds here appear to be both experience- and instrument-specific, yet at a latency of between 10 to 15 ms most musicians report performance issues [59]. This can be interpreted as the edge of a time-window wherein self-produced actions and perceptions are likely to be perceived as causally linked.

The second step in mapping the dynamics of self–other integration in joint action is understanding how perception, in this case sound, is related to another person's intentions and goals. A core tenet in social neuroscience is the ability to understand that others may hold mental states dissimilar to oneself, and that people's mental states form the basis of their behaviour [60,61]. In joint action, this entails understanding that the person we are interacting with may not hold the same idea of the task, or even the same goal. Nonetheless, experimental manipulation of underlying predictive models in a polyrhythmic interpersonal synchronization task shows that participants quickly harmonize their predictive models leading to synchronized behaviour [10]. Interestingly, if one considers two interacting brains wherein their respective sensory input is the output of their interacting partner's actions, this forms a reciprocally coupled system wherein mutual prediction, e.g. a harmonization of the predictive models, is achieved as an emergent property of the coupling [45]. In the MEAMSO we do not explicitly model a three-way separation of perception (i.e. perceiving something as linked to the self, to the other, or as unrelated to both), nor does the model explicitly model the combined joint action outcome, such as when two musicians are playing a duet together (wherein the music individually performed may differ in both melody and rhythm) and hence requiring monitoring of the shared goal [11,62]. Instead, we work on the premise that if perceptions stemming from the other (in this case the sound from their taps) cannot be causally attributed to one's own actions, they are instead sorted into the predictive model of the other. While this is a simplification, it is also a necessary step in order to reduce the number of comparisons and calculations performed by the MEAMSO.

4. The metastable attractor model of self–other integration modules

The MEAMSO (illustrated in figure 1) consists of three primary interconnected modules: (i) instantaneous comparisons, (ii) correlational comparisons and (iii) model selection. It takes two time series as input. In our example joint finger-tapping task, one of these time series represents the actions performed by the model's target person, and the other time series represents the perceptions stemming from the tapping partner. Throughout the description of the model, we refer to these as *actions* and *perceptions*, respectively. The main outcome from the model is a state indicating whether two time series are best described by one predictive model (self–other integration), or by two separate predictive models (self–other segregation). In the following paragraphs, we describe key parts of the model. A detailed overview including equations can be found in the electronic supplementary material, appendix S1.

(a) Instantaneous comparisons

This module handles the more-or-less instantaneous comparison between two events occurring simultaneously or in rapid

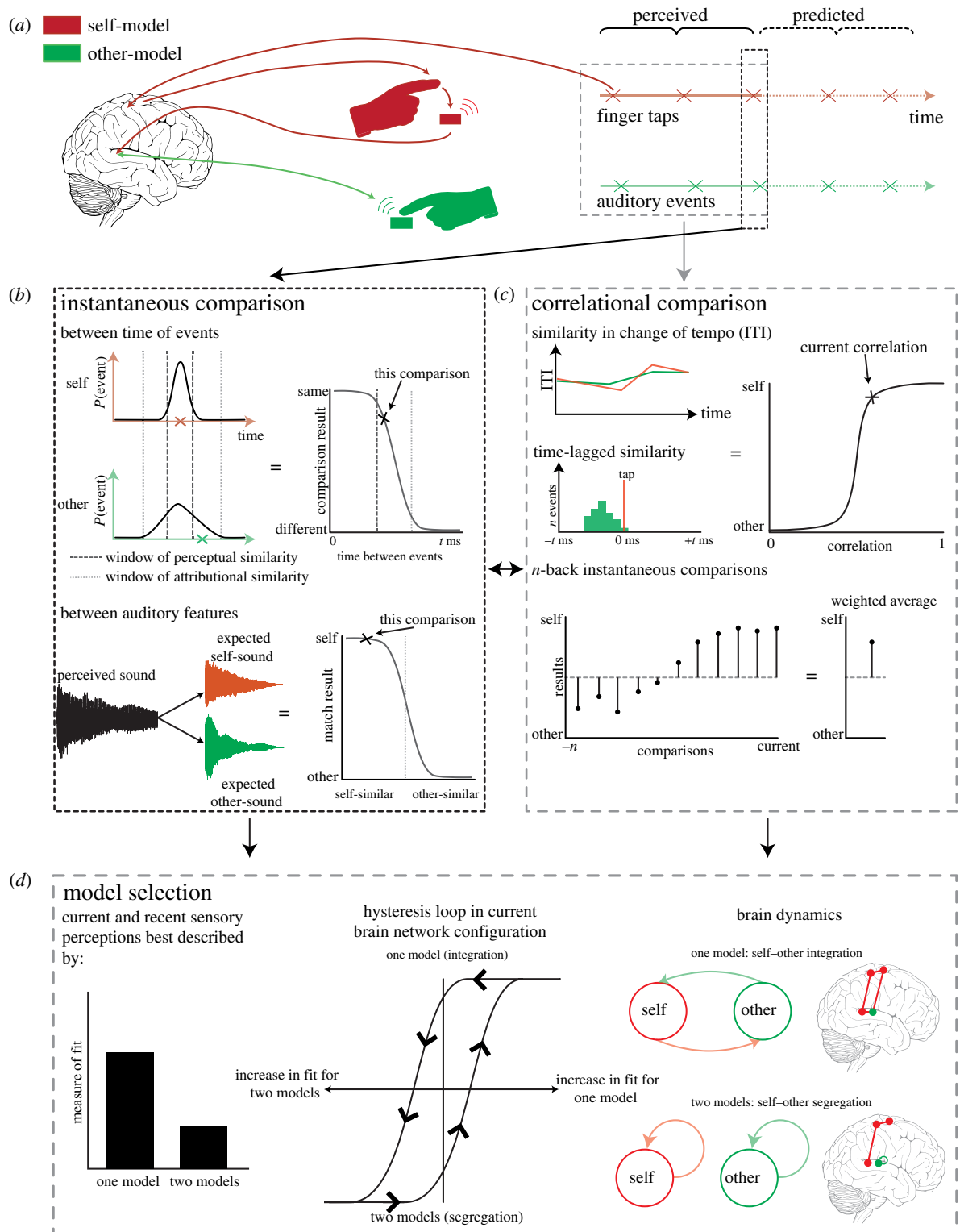


Figure 1. The MEAMSO. (a) An overview of the process that MEAMSO models, here illustrated for a joint finger-tapping task. MEAMSO assumes that a participant in the task maintains two predictive models, one self-model governing the actions performed and an other-model governing the perceptions from the actions of the other. Together these predictive models control the perception of sensations and predict upcoming sensations. We operationalize the MEAMSO in three modules: (b) Instantaneous comparisons performed between events occurring close in time. We highlight two main comparisons here, one between the relative time of events, and another between auditory features of the sounds of events. These comparisons both lead to a value indicating a likelihood of perceptions being linked to actions. (c) Correlational comparisons are performed over successive events, including a measure of similarity of tempo (measured by the intertap interval in the case of an isochronous rhythm), a time-lagged similarity to account for simple delays between a tap and a resulting sound, as well as an accumulation of previous instantaneous comparisons. (d) The two comparison modules are piped into a model selection wherein the corroboration for the current event best being described by one model (a collapse of the predictive self- and other-model), or by two separate predictive models, is collected. The most likely current state (integration or segregation) is fed through a hysteresis loop, which then determines the current state of brain dynamics best describing the stream of actions and perceptions. (Online version in colour.)

succession. The first component is a comparison between the time of events, leading to a decision or likelihood of whether the two events are causally linked. Under the assumption

that two predictive models are active, one for self-produced actions (the self-model) and one for other-produced actions (the other-model), this comparison is perceptually a measure

of the asynchrony between the self-performed finger tap, and the auditory perception of the other-performed finger tap. We propose that there are two time-windows at play here, one wherein there may exist a perceptual similarity, i.e. when the asynchrony is low, and another time-window for medium asynchronies where there may exist an attributional similarity, i.e. where top-down processes actively attribute the asynchronous event as being causally linked to the originating event. Computationally we can describe this by calculating the difference in time between events, and passing the value through a logistic function. As we can assume that a finger tap preceding an auditory signal is more likely to be causally related than the reverse chronology, we construct a transfer function taking this into account by using a reversed logistic function for asynchronies greater than 0, and a regular logistic function for asynchronies less than 0. By applying a min–max normalization to the input asynchrony, we can express this process with the following two equations:

$$\text{async}_s = \begin{cases} t_{\max} & \text{abs(async)} \geq t_{\max} \\ \frac{2(\text{abs(async)} - t_{\min})}{t_{\max} - t_{\min}} - 1 & t_{\min} < \text{abs(async)} < t_{\max} \\ t_{\min} & \text{abs(async)} \leq t_{\min} \end{cases} \quad (4.1)$$

$$\text{comp}_{\text{time}} = \begin{cases} \frac{2}{1 + e^{k_1(\text{async}_s)}} - 1 & \text{async} > 0 \\ 0 & \text{async} = 0 \\ \frac{2}{1 + e^{-k_2(\text{async}_s)}} - 1 & \text{async} < 0 \end{cases} \quad (4.2)$$

Here, async is the time between events from the point of view of the finger tap, which is scaled to a value between -1 and $+1$, where t_{\max} indicates a cut-off point in milliseconds representing the maximum length of the time-window wherein action and perception may be linked, and t_{\min} is equal to 0. Dependent on the sign of the async , this goes through a logistic function, where k_1 is the steepness of the curve for positive asynchronies, and k_2 for negative asynchronies. Their respective values are likely individual, and influenced by experience and expertise [63]. We can then construct a function where when $\text{comp}_{\text{time}}$ approaches 1, we assume that action and perception are causally linked, and when it approaches -1 , we assume they are not linked.

The second component is a comparison between auditory features. In a normal musical interaction, musicians are intimately familiar with the sounds of their own instrument. This relies on experience and learning where one builds a cognitive template of what perceptions match the actions performed on an instrument and consists of multiple acoustic features such as the frequency spectrum and envelope (known as timbre). There exist multiple perceptual models for how we identify and classify individual sounds from a combined sound source, which could be integrated into the MEAMSO [64–67]. Due to the complexity of this comparison, we set its value to zero for this iteration of our model, indicating that the comparison does not influence the later decisions made by the model.

(b) Correlational comparisons

We know from multiple joint finger-tapping studies that the intertap intervals (the time between successive taps) of the dyads rarely reach a high positive correlation value at lag 0 (regular correlation) [10,12–14]. Instead, positive correlation

values are found at both lag $+1$ and lag -1 for the mutual adaptation strategy, at either lag $+1$ or lag -1 for the leading–following strategy, or with weak positive values on all lags in the leading–leading strategy. Yet, and especially in mutual adaptation, even with alternating auditory feedback from their own tapping, participants still report a sense of agency over their perceptual feedback [68,69]. Hence, it is likely that a correlational similarity between perceptions and actions may, at a certain threshold, contribute evidence towards perceiving a causal relationship between the two. For instance, if considering the intertap intervals we presume that a constant event-lagged similarity may instil a likelihood of ascribing a causal relationship between actions and perceptions. As an example, we can consider a slow increase in tempo, an *accelerando*. Here, the intertap interval is decreased for each subsequent tap usually in a nonlinear manner. We assume that this behaviour may contribute to a sensation of causal links between action and perception, even if the changes are lagged one event behind the current action. To capture this, we calculate a cross-correlation at lag -1 and lag 0 between the intertap intervals of own actions versus others' actions, and select the highest correlation value. As this calculation necessitates a certain number of events before it becomes informative, we start the calculation only when there are four intertap intervals available (at event number five) and implement a sliding window wherein only the last eight events are included, hence building up the stability of the calculation as the length of the interaction increase.

As previously discussed, while the musicians will complain of the latency, they are capable of recognizing and performing with the perceptions of their actions being delayed by a certain time period. This is a time-lagged similarity, and we deem it likely that even a certain jitter in the time-lagged perception is acceptable in terms of causally relating the perception to the action. This calculation involves estimating the mean asynchrony between an action and a perception event, and its variability. If the variability is low, indicating a stationary latency, this calculation contributes towards linking action and perception.

The last correlational comparison included in the MEAMSO is an n -back instantaneous comparison. Here, we assume that a weighted average of previous comparisons is held, to decrease the influence of erroneous instantaneous comparisons. Here, we use a Bayesian average, which is updated by the four previous instantaneous comparisons, as shown in the following equation: $\bar{x} = Cm + \sum_{i=1}^n x_i/C + n$, with a prior m , and a constant C [70]. This is equal to padding the average with C datapoints of m . For every update of the calculation, we update the prior to be equal to its current output, thus creating a smoothed weighted average. Notably, the correlational comparisons described above assume that the rhythm performed is isochronous and would not function for complex rhythms, or rhythms with a high degree of syncopation. To do so one would need to implement an expectation template that accounts for multiple event types, due to the finding that perturbations to individual events within a complex rhythm differentially affects perception [71]. A promising approach to building such an expectation template can be found in the recently developed Phase Inference from Point Process Event Timing framework, which could serve as a filter prior to the correlational comparisons described above [72].

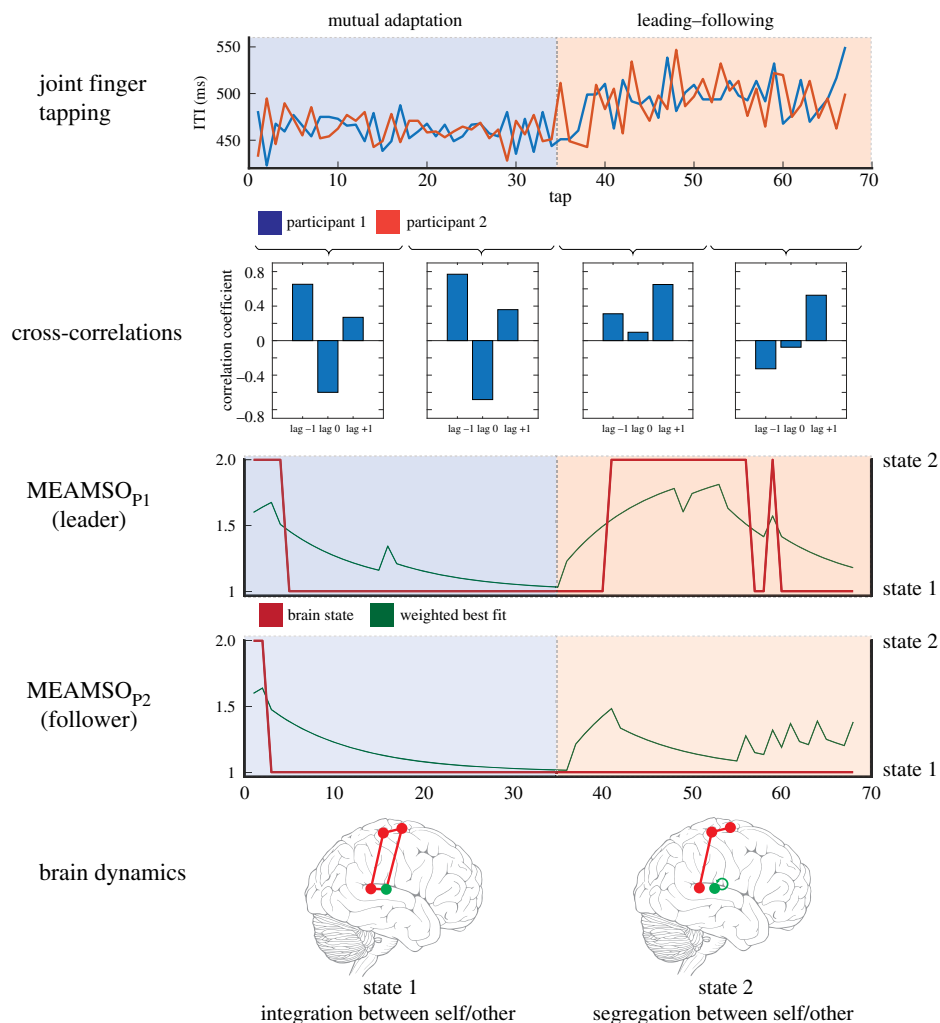


Figure 2. Application of the MEAMSO on tapping data. Here, we create an example interaction by combining joint finger-tapping data from a mutual adaptation and leading–following interaction. By looking at cross-correlation coefficients we can see how the interaction shifts. We run the MEAMSO from both participant’s perspective and plot the weighted best fit and the outcome brain state from the model. The model is initiated in state 2 (segregation of self/other). For dyad member 1 (P1), the leader, we can see the state switch shortly after the transition to leading–following, indicating a separation between self-performed actions and the sounds perceived from the other. For dyad member 2 (P2), the follower, we see that the state rapidly switches to state 1 (integration of self/other) and remains there throughout the interaction. In the last panel, we illustrate the brain dynamics associated with the two states. (Online version in colour.)

(c) Model selection

All the above-mentioned processes are constructed to produce a numeric output ranging from -1 to 1 , with values approaching -1 indicating that actions and perceptions are not causally linked, and values approaching 1 indicating a causal link between actions and perceptions. We can then sum all values greater than 0 as a measure of fit for self–other integration, and all values less than 0 for self–other segregation. By using a softmax normalization on the absolute measures of fit followed by an argmax to determine whether the fit is best for integration or segregation, we get an integer representing the best fitting state for the current event. This integer is then inserted into the same type of Bayesian averaging as described in the previous paragraph, and the rounded value of the averaged number is taken to indicate the current network configuration of the brain, with the value 1 representing integration and the value 2 representing segregation. Together, this causes a hysteresis loop wherein switching from one configuration necessitates both comparison modules to yield evidence for the other configuration over multiple events before a switch occurs, dependent on the parameter values chosen for the Bayesian averaging (for an example see electronic supplementary material, figure S1). In addition, depending on the parameters

chosen for the comparison, we can bias the model so that maintaining segregation becomes a metastable state reflecting the increased cognitive cost of holding two predictive models.

(d) Implementation

To exemplify how MEAMSO can be used on behavioural data, we implemented a minimal version of the model in MATLAB (code is available at github.com/OleAd/MEAMSO). Here we first created an example joint finger-tapping trial exhibiting a transition in synchronization strategy, by combining a section of mutual adaptation tapping with a section of leading–following tapping from a previous study as illustrated in figure 2 [12]. To show the change in synchronization strategy, we calculated cross-correlations in non-overlapping windows of 15 taps (figure 2). We then ran the behavioural data through the MEAMSO, both from the perspective of dyad member 1 and dyad member 2 (figure 2). For dyad member 1, we see that the brain state output from the model starts at state 2 (segregation of self and other), before quickly transitioning to state 1 (integration of self and other). It remains in state 1 until a few taps into the leading–following section, wherein dyad member 1 becomes the leading participant. It then

switches to brain state 2, indicating that the perceptions are no longer causally integrated with the actions. Towards the end of the trial, it rapidly switches, before settling back to state 1. For dyad member 2, the brain state output starts in state 2 and rapidly settles in state 1 throughout the trial, indicating integration of self and other. As dyad member 2 is the follower in this interaction, this is the expected behaviour of the model.

5. What does the metastable attractor model of self-other integration explain, and what does it predict?

The main purpose of our conceptual model is to collate, develop, test and extend theory [73]. With MEAMSO, we show how synchronization strategies can be framed from a cognitive viewpoint, and in the following paragraphs, we describe how the MEAMSO explains the emergence of dyadic synchronization strategies and highlight some key predictions from the model.

(a) Dyadic synchronization strategies

The MEAMSO posits that there exist two metastable attractors in terms of brain dynamics during dyadic interpersonal synchronization, with one state indicative of self–other integration (maintaining the same predictive model for action and perception) and the other indicative of self–other segregation (maintaining two separate predictive models for action and perception). We can calculate the number of possible unique group combinations of these states by using the formula $\text{states} = (n + s - 1)! / n!(s - 1)!$, where n is the number of participants in a group, and s is the number of individual states. In our case, where $s = 2$, the formula reduces to $\text{states} = n + 1$, for $n > 1$. When considering a dyad, there then exist three possible combinations, which map onto the three known synchronization strategies in dyadic interaction: leading–leading, leading–following and mutual adaptation (illustrated in figure 3). Leading–leading may occur when both participants separate self from the other and hence do not use information from the other to influence their own actions. Leading–following necessitates that the leader separates the other's actions from their own actions, whereas the follower integrates (by adapting their tapping based on the preceding tap from the leader). In mutual adaptation, both participants integrate self and other, so that each other's actions reciprocally influence upcoming actions.

(b) Group synchronization dynamics

Following the equation for the number of states listed above, MEAMSO would predict that the number of possible synchronization strategies is always $n + 1$ where n is the number of interacting people. As our model is based on dyadic interaction, it will likely not capture all the intricacies present in group synchronization dynamics. In particular, as a group of interacting persons reach intermediate size, such as in the Human Firefly experiment, rich and diverse synchronization dynamics emerges [25,74]. In addition, the topology of feedback influences the group's synchronization behaviour [75,76]. Given our model's predictions for dyadic synchronization strategies, we would hypothesize that as the size of the group grows so does the instability of the strategies, meaning

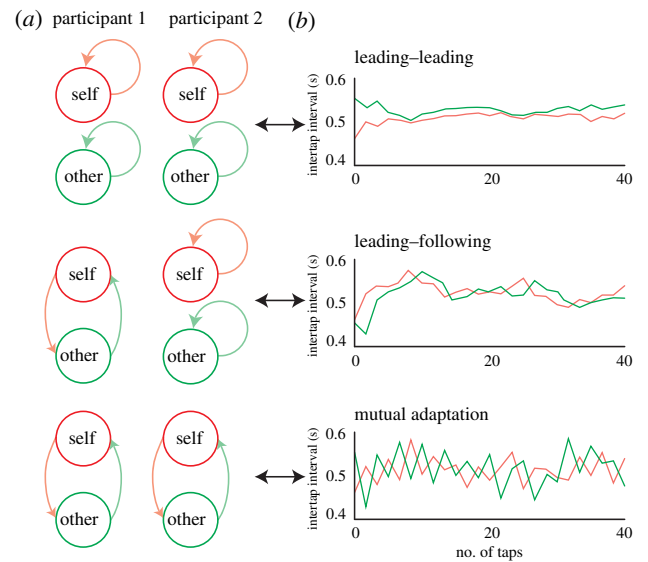


Figure 3. The emergence and selection of synchronization strategies. (a) The configuration of self–other integration/segregation for pairs of participants, and (b) the corresponding synchronization strategy. We propose that leading–leading occurs when both dyad members hold two separate predictive models through self–other segregation. In leading–following, one dyad member integrates and the other segregates. In mutual adaptation, both dyad members integrate, which when viewing the dyad as a whole collapses the dyad members' predictive models into one shared model. (Online version in colour.)

that there may be fewer viable and stable synchronization strategies for large groups. There are two main factors leading us to this conclusion. First, a leader may have many followers, but a follower can only follow one leader. This means that certain constellations (e.g. two leaders and one follower) are unlikely to produce a stable synchronized interaction. Second, there is likely a limit to the size of a group when individuals can no longer be individually monitored, and instead a measure of the group's performance as a whole, or sub-groups within the group, needs to be monitored [77]. This limit is likely dependent on the individuals' ability to perform auditory stream segregation, a complex ability that depends on multiple characteristics of the sounds being heard [78–80]. In addition, a recent study with 16 violinists performing a simple melody together, perturbed by the introduction of auditory delays between the violinists, showed that the musicians were able to rapidly ignore conflicting signals [76]. In our model, one way of incorporating this ability would be to add an attention weight to signals in groups of more than two, such that a signal that is kept segregated over a certain period of time is discarded from the computation until changes in the signal necessitate a re-evaluation. One way to explore this would be to design experiments wherein experienced groups of musicians perform joint finger tapping with designated roles (e.g. leader and follower) to evaluate the stability of interactions, and to investigate groups of musicians and non-musicians to evaluate how signals are weighted in a group interaction.

(c) Synchronization strategies are dynamic

MEAMSO predicts that synchronization strategies are dynamic, yet that they are transiently stable. By this, we mean that the strategy may change during an interaction, for instance switching between a leading–following strategy to a

mutual adaptation strategy. This would occur if there is a sudden change in comparison calculations indicating that the current state is no longer supported by perceptual evidence. Yet, due to the hysteresis inherent in the MEAMSO calculations, such change would need to surpass a critical threshold before a re-evaluation of the best fitting state is performed. In addition, if the brain tends towards computational efficiency, one would predict mutual adaptation to be more frequent and stable than the other synchronization strategies. This is due to both interacting brains only needing to maintain one predictive model of the task, which has been proposed to be more computationally efficient [2].

To empirically test this prediction, one could design a paradigm wherein an adaptive virtual tapping partner gradually introduces perturbations in the interaction. Here, we would predict that small, isolated, perturbations would not disrupt a mutual adaptation interaction, but larger and sustained perturbations would switch the interaction to a leading–following synchronization strategy. The inherent metastability in the MEAMSO would also point towards it being easier to go from leading–following to mutual adaptation, than the other way around. Here, there is also an opportunity for incorporating the MEAMSO with our Kuramoto-based coupled oscillators model [24]. In the Kuramoto-based model, the coupling strengths that govern the behaviour of the model were fixed throughout the interaction. By using the MEAMSO to dynamically update the coupling strengths throughout a simulated tapping trial, we can formalize predictions on the stability of synchronization strategies.

(d) Similar sounds are more likely to lead to self–other integration

The instantaneous comparison between auditory features is a technical and cognitively complex component of the MEAMSO, whose inner workings we have not explored in detail in this paper. Nonetheless, the ability to match an action with a predicted auditory perception is an interesting aspect of the model. Here, the model predicts that a precise predictive model of action-related auditory feedback will increase the likelihood of self–other segregation. This may entail that dyads of musicians, who through training develop fine-tuned predictive models due to their instrument-specific expertise [81–83], are more likely than the general public to exhibit leading–following and leading–leading behaviour. Another prediction would be that self–other integration should be increased in interactions where participants are unsure about the auditory feedback from their actions. A possible example of this can be found in multiple musical settings, such as ritual music and group singing, which promote group cohesion and facilitate prosocial behaviour [84,85]. Here, the auditory output produced by individuals is often highly similar or embedded in the group’s auditory output. We would predict this contributes to self–other integration, and perhaps to the sense of belonging and meaningfulness sometimes attributed to group singing [86].

6. The metastable attractor model of self–other integration in the brain

The output from MEAMSO is a state indicating whether self–other integration or segregation is currently taking place and

should be identifiable on a neural level. One of the proposed neural mechanisms involved in self–other integration is the alignment of neural self/other representations [2]. This view finds support in recent research on interacting mice wherein populations of neurons in the dorsomedial prefrontal cortex selectively encode self-related and other-related behaviour [87]. Notably, this activity may underlie the inter-brain synchronization reported between interacting people. Nonetheless, human social interaction inherently relies on many complex cognitive tasks, as evident by the diverse brain regions involved in social tasks [44,60]. In a controlled experimental setting, such as with a joint finger-tapping task, some of this variability is constrained by placing limits on the actions performed and on the perceptual feedback (often just simple transient sounds are used) [10,12,14]. Hence, tightly controlled joint action paradigms offer a promising avenue towards identifying the neural correlates of self–other integration and segregation.

In previous work, we used a data-driven approach to identify a functional brain network selectively associated with mutual adaptation and leading–leading synchronization strategies [88]. Mutually adapting participants exhibited a higher occurrence of synchronized activity within this network, perhaps representing the proposed synchronization between self- and other representations in the brain. Information flow within this network, measured with directed phase transfer entropy, indicated a key role of the right precuneus and its connections to the supramarginal gyrus, auditory cortex and temporoparietal junction. As such, coherent activity within this network and between its key regions may be a candidate for a neural correlate of the MEAMSO’s output, an avenue we intend to pursue in future work.

7. Summary

In this paper, we have introduced the MEAMSO. This event-based model proposes an interconnected set of mechanisms describing how self–other integration occurs in dyadic interaction, and how this process gives rise to metastable synchronization strategies. We use a minimal implementation of the MEAMSO to illustrate how the model could capture the dyadic imbalance in a transition between mutual adaptation and leading–following. The MEAMSO is therefore a model which can encompass dynamic shifts in synchronization strategies over time. Furthermore, MEAMSO can be used to formulate key predictions on the dynamics of rhythmic interpersonal synchronization and to point to neural mechanisms underlying interpersonal synchronization. It is our hope that the MEAMSO will prove useful in approximating the complexity of rhythmic interpersonal synchronization.

Data accessibility. A minimum implementation of MEAMSO and example data used in figure 2 can be found at: <https://github.com/OleAd/MEAMSO>.

Authors’ contributions. All authors contributed to the development of the model. O.A.H. implemented the model and wrote the first draft of the manuscript. All authors revised the manuscript, and all authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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