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Physiological Synchrony Predicts Observational Threat Learning in Humans

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Abstract

Understanding how information about threats in the environment is shared and transmitted between individuals is crucial for explaining adaptive, survival-related behavior in humans and other animals, and for developing treatments for phobias and other anxiety disorders. Research across species has shown that observing a conspecific's, a "demonstrator's", threat responses causes strong and persistent threat memories in the "observer". Such observational threat learning is hypothesized to be supported by empathic processes. Here, we examined if physiological synchrony between demonstrator and observer can serve as a biomarker of the hypothesized empathic transfer. We find that synchronization of phasic skin conductance, which directly reflects autonomic nervous system activity and captures an organism's arousal when facing and responding to threats, between the demonstrator and observer during observational learning predicts the strength of the observer's later threat memories. Dynamic coupling between an observer's and a demonstrator's autonomic nervous system activity may reflect empathic experience sharing and determine the formation and later retrieval of observational threat associations.

In social species, like humans, knowledge about threats and dangers is often acquired through various forms of social transmission, for example through observation. Research across species has shown that observing a conspecific's - a "Demonstrator's" - threat responses to a previously neutral stimulus can cause strong and persistent threat memories in the "Observer" [1–12]. Such memories are expressed by heightened autonomic nervous system activity in the observer when later facing that stimulus alone. Observational threat learning is efficient, and minimizes risks to the individual

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arising from directly interacting with potential dangers [13]. Understanding how information about threats in the environment is observationally acquired is central to explaining adaptive, as well as maladaptive, survival related behavior in humans and other animals.

For observational learning to occur, the demonstrator's reactions to the threatening stimulus must function as unconditioned stimulus for the observer. It has been hypothesized that empathic processes, enabling the sharing or understanding of affective states between demonstrator and observer, facilitate observational learning [4, 10, 14–17]. Previous work has implicated trait measures of cognitive empathy in observational learning [10, 18], emphasizing the role individual differences in the observer's capacity to take the perspective of the demonstrator plays in learning. This overlooks another component of empathy known as experience sharing, which is characterized by an observer having similar emotional experiences as a target, even if the observer is not in the same situation as the target (e.g., when an audience member feels vicarious anxiety about their friend's performance on stage) [19–21]. It is possible that direct sharing of affective states between demonstrator and observer promotes learning and that momentary fluctuations in shared experience matter more than empathic traits. However, there is as of yet little direct evidence for the role of experience sharing in human threat learning. Here we attempted to provide evidence that experience sharing, as captured by synchronous patterns of arousal, influences observational threat learning.

Synchrony is a pervasive natural phenomenon and occurs when two systems become coupled so that their trajectories develop temporal interdependence [22, 23]. It is also a fundamental feature of interpersonal coordination and social cognition [21, 24–30]. For example, in humans, synchrony has been observed over multiple levels of analysis including intrapersonal limb coordination[23], interpersonal eye-movements during communication [31], shared attention [32], and postural sway in dyadic coordination tasks [33]. Importantly, synchrony has been related to interpersonal cohesion and cooperative outcomes [26, 34, 35]. Related individuals will show greater synchrony in their heart rates compared to non-related individuals during hazardous social rituals [34] and dyads who show higher degrees of synchrony will show greater team cohesion [35]. Recent advances in the cognitive neurosciences have led to the discovery of coupling in BOLD fMRI signals in several contexts [21, 36–38]. For example, neural coupling between individuals has been found to predict successful verbal communication, such that the more a listener's brain activity correlated with the speaker's, the better comprehension the listener would report [37]. Despite considerable evidence for the role of synchrony in diverse intra- and interpersonal processes, its role, if any, in social learning is not understood.

One reason for the lack of evidence for a role of experience sharing in human threat learning is that past experiments have all employed artifi-

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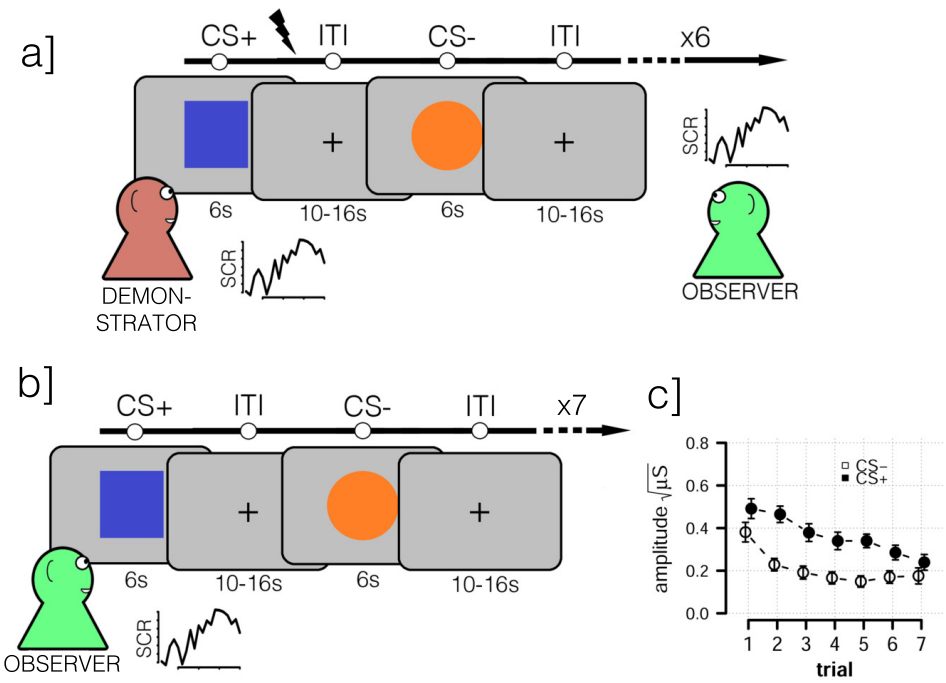

Figure 1: Overview of experiment. **a]** Learning phase. Demonstrator watched two images, one which terminated with an uncomfortable electrical shock during 4 of 6 presentations (CS+) and another that never terminated with a shock (CS-). Each CS presentation lasted 6s and inter-trial interval (ITI) varied between 10 and 16s. Valence (CS+/-) of the first image presented was randomly varied. While the Demonstrator watched the CS presentations and received shocks, the Observer watched both the Demonstrator and the CS's. The Observer was instructed to learn the shock contingency. The Observer received no shocks during the learning phase. Electrodermal activity was continuously recorded from both the Demonstrator and Observer. **b]** Testing phase. Immediately following the learning phase, the Observer was repeatedly shown both CS's again, instructed that they would receive shocks to the same image as the Demonstrator had received shocks to. Importantly, only the 7th, final presentation of the CS+ terminated with shock, to not interfere with the measurement of the vicariously acquired threat response. Greater SCR to the CS+ compared to the CS- in the Observer, in this phase, indicates successful threat learning. **c]** Average trial-by-trial data from testing phase showing average skin conductance responses to the CS+ (dark circles) and to the CS- (light circles) for the Observer. Error bars are 95% confidence intervals.

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cial situations involving confederate demonstrators, either in live settings [4–6, 16, 17], or more recently, displayed via video recording [8, 10, 12, 39]. Hence, to investigate synchrony we adapted an existing, standard video-based paradigm [39] to a more naturalistic situation. In our paradigm two naïve participants took turns being demonstrator and observer, the demonstrator undergoing a direct conditioning procedure and the observer learning from the demonstrator's reactions (see Fig. 1, Methods). The experiment consisted of two phases. First, a learning phase where the observer watched the demonstrator receive probabilistic shocks to one of two visual images serving as conditioned stimulus images (CS+), and never to the other (CS-). The learning phase was followed by a testing phase where both CSs were repeatedly presented again to the observer under threat of shock. To measure social learning no shocks were administered to the observer following CS+ presentations during this phase (except for the last presentation, see Materials and Methods). Both participants' electrodermal activity was continuously recorded throughout the experiment allowing for synchrony to be calculated during the learning phase. Threat learning was measured as CS differentiation - stronger skin conductance responses to CS+ compared to CS- images in the testing phase.

Results

We first evaluated the threat learning procedure and confirmed that observers readily acquired threat information from demonstrators. We tested 69 same-sex dyads and analyzed observers' skin conductance responses to the onset of the CS images. We found a robust learned threat response indicating CS differentiation (Bayesian multi-level regression; $b = 0.15$, $SE = 0.016$, CrI (95% Credible Interval) = [0.12, 0.19], BF_{10} (Bayes Factor) $> 10^6$, see Fig. 1), while controlling for Block (first or second) and the participants' initial Role (starting as observer or demonstrator). Importantly, we found no interaction between CS status and Block ($b = 0.03$, $SE = 0.019$, CrI = [-0.007, 0.069], $BF_{10} = 1.33$), or between CS status and Role ($b = 0.035$, $SE = 0.028$, CrI = [-0.019, 0.089], $BF_{10} = 1.33$). Together, this indicates that learning was equally effective during all stages of the experiment and we conclude from this that our procedure traslate standard video-based observational learning paradigms [8, 39] into the more realistic situation, involving two live participants, tested here.

Synchrony predicts observational threat responses

Next, we tested the main hypothesis: that demonstrator-observer synchrony of physiological arousal during the learning phase would predict the strength of the observer's threat responses in the test phase. To quantify synchrony we performed a cross-recurrence quantification analysis (CRQA; see Fig. 2,

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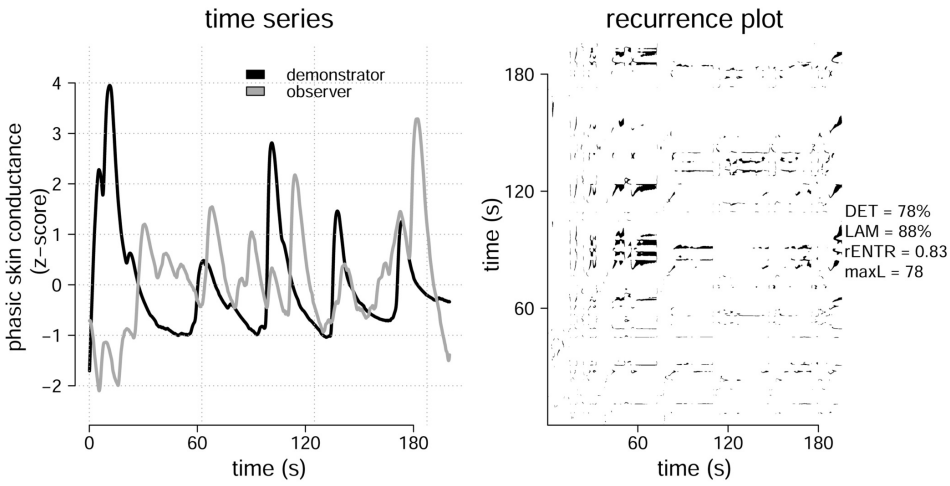

Figure 2: Left panel, example of an observer's and demonstrator's phasic skin conductance time series from a single learning phase, z-scored to facilitate comparison. Right panel, the resulting recurrence plot following cross-recurrence quantification analysis (CRQA) on the time series in the left panel. From each recurrence plot, four standard metrics capturing synchrony were computed; ratio of points in diagonal lines to all points (determinism, DET), maximal diagonal line length (maxL), entropy of diagonal line length distribution (rENTR), and the ratio of points in vertical lines to all points (laminarity, LAM). Resulting metrics computed from the left panel example series displayed.

Materials and Methods). We first constructed cross-recurrence plots for each dyad's phasic skin conductance time series from the learning phase portion of each block (see Fig. 2 for example cross-recurrence plot). From these plots four standard metrics of CRQA were computed that capture predictability (% DETerminism), maximum strength of coupling (maxLine), complexity (rENTRopy) and stability (LAMinarity) of the relationship between the time series.

Since the four CRQA metrics were highly correlated in our sample (r = .33 to r = .74) we followed prior work and reduced these measures into a single value using principal components analysis [35]. The factor loadings resulting from the analysis and variance explained of each factor are displayed in Supplementary Table 1. The loadings suggested that the first component, which loaded roughly equally, and positively, on all metrics and captured 63% of the variance, should represent synchrony between participants best.

In line with our predictions, the first component we extracted (PC1), capturing synchrony, positively predicted CS differentiation (b = 0.040, SE = 0.009, CrI = [0.021, 0.058], BF_{10} = 487, see Fig. 3). The remaining

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principal components did not reliably predict CS differentiation (all b's $<$ 0.012, all $BF_{10} < 0.55$).

For completeness, we also analyzed each of the four cRQA metrics individually. All four metrics predicted CS differentiation with varying strength (see Supplementary Results). We additionally controlled that relationship between synchrony and CS differentiation was specific to synchrony computed between dyads from learning phase data by showing that synchrony computed from the testing phase (when observers and demonstrators were not both seeing the stimuli) did not predict CS differentiation (see Supplementary Results).

We next tested if the effect of synchrony (PC1) changed over the series of consecutive CS presentations as the participants' responses extinguished (cf. Fig. 1) . We included a Trial variable and its interactions to a model including CS status and the synchrony component. Unsurprisingly there was both a main effect of trial (b = -0.034, SE = 0.003, CrI = [-0.040, -0.029], $BF_{10} > 10^6$) and an interaction with CS status indicating faster extinction of responses to the CS+ (b = -0.013, SE = 0.005, CrI = [-0.023, -0.003], BF_{10} = 3.62). However, the relationship between synchrony and CS differentiation did not interact with trial, with strong evidence for null effect (b = 0.002, SE = 0.003, CrI = [-0.004, 0.008], BF_{10} = 0.074). The relationship between CS differentiation and synchrony was stable across all trials in the testing phase.

Specificity of synchrony as predictor of threat learning

To rule out non-synchrony based mechanisms explaining our findings we identified three measures based on the observer's arousal in the learning phase. Each measure could plausibly capture relevant aspects of the observer's learning process. The first measure was the average strength of the observer's skin conductance response to the social UCS (the demonstrator receiving shocks) during the learning phase. During direct conditioning it is well established that the strength of the UCS predicts the strength of later conditioned responses [40], and the social UCS is considered to play a similar role in observational learning [5, 6]. We therefore hypothesized that the observer's reactions to the social UCS might be indicative of its perceived strength. As such the UCS response might be capturing similar empathic processes as the synchrony component. The second measure was the average difference of the observer's responses to the CS+ over the CS- during the learning phase. While the observers were under no direct threat, it is possible that some observers began to develop responses to the CS+ anticipating the future shocks to the demonstrators. It is therefore possible that this early CS differentiation during the learning phase could be the source of the observed synchrony in that phase and account for the effect of synchrony we observed. Third, we included a time-lagged correlation between

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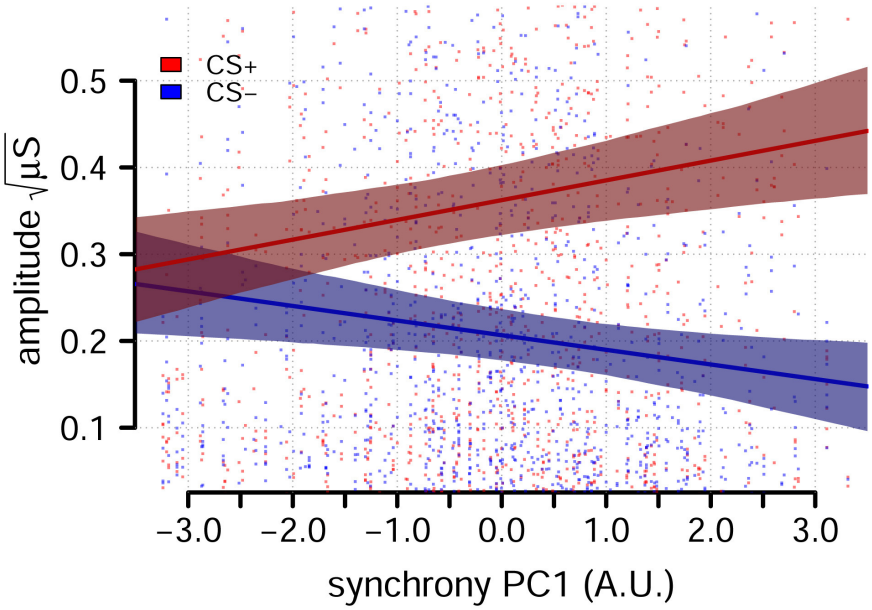

Figure 3: Posterior prediction of CS+ (red) and CS- (blue) responses as a function of synchrony captured by the first principal component of the CRQA measures. Points represent raw data. Shaded region indicates 95% posterior predictive interval.

the demonstrators' and observers' skin conductance time-series during the learning phase. Correlations capture a direct linear relationship between the signals and, unlike the previous two measures, take the whole time-series into account.

The three measures outlined above exhibited low correlations with each other (r = .14 to r = .20), so we jointly regressed each of them and the synchrony component identified earlier together with their interactions with CS status on observer's skin conductance responses from the testing phase. We found that while observers' average UCS responses were positively related to the strength of their average skin conductance responses (b = 0.045, SE = 0.012, CrI = [0.021, 0.069], BF_{10} = 237), they did not interact with CS status (b = 0.020, SE = 0.017, CrI = [-0.013, 0.052], BF_{10} = 0.64). Similarly, neither learning phase CS differentiation (b = -0.019, SE = 0.044, CrI = [-0.105, 0.066], BF_{10} = 0.93) nor lagged correlations (b = 0.006, SE = 0.013, CrI = [-0.018, 0.031], BF_{10} = 0.26) interacted with CS status. Importantly, the synchrony component continued to robustly predict CS differentiation in this model (b = 0.035, SE = 0.009, CrI = [0.017, 0.053], BF_{10} = 105), even when accounting for these additional measures capturing other aspects

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of the observer's skin conductance signals during the learning phase.

Together these analyses show that synchrony is a specific predictor of observational threat learning and that the findings are robust to several plausible alternative predictors.

Self-reported empathy does not account for threat learning

Next we considered if individual differences in self-reported trait empathy (see Supplementary Table 2 for descriptive statistics), as measured by the four sub-scales of the Interpersonal Reactivity Index [41], predicted observational threat learning and if this could explain the effects of synchrony. We regressed the four sub-scales together with CS status and the synchrony component. We found no interactions between any of the sub-scales and CS status nor with the synchrony component (all b's < 0.01, all $BF_{10} < 0.43$).

Similarly, all observers rated their perceptions of the demonstrator: how much pain the demonstrator appeared to be in, their quality as a learning model, how much compassion the observer felt for the demonstrator and how similar to the observer the demonstrator appeared to be. Again none of these measures interacted with CS status or with the synchrony component (all b's < 0.02, all $BF_{10} < 0.76$).

These results suggest the momentary physiological coupling between observers and demonstrators occurs beyond participants' introspective abilities and that synchrony might constitute a more fundamental feature of empathic learning than captured by trait scales.

Discussion

We investigated if spontaneous synchrony between an observer's and a demonstrator's arousal states, as indexed by their electrodermal activity, during an observational threat learning procedure could predict the strength of the observer's later expressed learning. We found that the first principal component assessed from four common measures of synchrony, calculated using cross-recurrence quantification analysis, robustly predicted conditioned responses. Indeed, our findings indicated that at low levels of observer-demonstrator synchrony almost no differentiation in responses to threat-relevant versus threat-irrelevant stimuli was expected (Fig. 3). Together, this suggests a critical facilitating role of synchrony in observational threat learning. We discuss the interpretation and implications of our findings below.

Our findings are specific to shared patterns of arousal arising from the dynamics of the two participants' skin conductance signals.We demonstrated that competing predictors derived from the observers' electrodermal activity during learning showed no relation to the strength of the observers' conditioned responses and that controlling for these, did not remove the relationship between synchrony and conditioned responses. Importantly, this allows

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us to rule out that synchrony can be explained away as merely relating to co-occurrence of skin conductance responses caused by the observer responding particularly strongly to the CS+ or to the demonstrator receiving shocks.

In this study, synchrony likely reflects the observer mirroring the demonstrator's autonomic nervous system trajectories and shows that this experience sharing facilitates their learning of the CS contingencies. Some psychophysiologists have hypothesized that sharing another person's autonomic nervous system state is the physiological substrate of empathy [1, 42, 43]. Individual arousal levels from viewing another person in pain, as indexed by electrodermal activity, have been shown to correlate with later costly helping, which provides indirect evidence for a link between empathy and matches in arousal states [44]. The sharing hypothesis has also been supported by classic findings that empathic accuracy are greatest during periods of synchronized physiology can be interpreted in support of this view [43]. Both behavioral and neural synchrony has been linked to mirror neurons responsible for representing the actions and intentions of social partners [19, 21, 24, 25], and several accounts have attempted to extend these mechanisms to cover empathic responses [19, 25, 45]. However, to the best of our knowledge, the results reported here represent the first direct experimental evidence that coupling of autonomic nervous system trajectories serves as a marker of empathic sharing in a learning context.

The current work advances previous indirect evidence for the experience sharing hypothesis in social learning. For example, past research has found that individuals high in psychopathic traits exhibited impaired conditioned responses to a demonstrator getting shocks compared to normal controls [17] and that facial mimicry in response to watching a demonstrator getting shocks reflected empathic experience sharing [16]. In rodents, brain regions homologous to those supporting empathy and emotion sharing in humans, such as areas of the anterior cingulate cortex [46] have been shown to be necessary for successful observational threat learning [14, 15, 47]. However, these past findings concerned single individuals and not shared neural patterns between observers and demonstrators, while in the current study we have a direct measure of autonomic nervous system activity. A central question for future work is how this synchronization arises in the brain and how it interacts with neural systems known to be involved in threat learning. It might be possible to use hyperscanning techniques in humans using EEG or fMRI to address this question using the experimental paradigm established here. However, another promising method would be to begin with investigating if similar synchrony can be found in rodent models, where neural recordings of sub-cortical structures implicated in arousal are more readily available.

Apart from experience sharing, other forms of empathy have also been suggested to facilitate observational threat learning [10, 18]. For example, one study found that instructing observers to take the perspective of the

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demonstrator increased conditioned responses for observers who were also high in trait empathy [10]. This appraisal instruction engages mentalizing aspects of empathy that involve making explicit inferences about a partner's internal states [20, 48]. In the results reported here we found no relation between trait empathy, as captured by the interpersonal reactivity index, or empathic ratings of demonstrators and conditioned responses. Importantly, these measures could not explain the effect of synchrony on conditioned responses, which therefore suggest that we should interpret previous links between mentalizing empathy and observational threat learning with some caution, especially given the large sample size of the present study. Nevertheless, there are several differences in method between the current study and studies mentioned above, most notably the absence of appraisal instructions and the use of live versus video-filmed demonstrators. Further work is necessary to fully understand the contributions of multiple empathic systems on processing social stimuli during threat learning.

We found that the observers' responses to the social UCS predicts their general level of arousal during the testing phase, but not the strength of their conditioned response. This was surprising since responses to the social UCS have typically been taken to index the strength of observer's empathic responses to the demonstrator and should translate into stronger threat memories available for later recall, analogous to how a stronger UCS works during direct conditioning. In our data, observers who react strongly to seeing the demonstrator being shocked have higher response amplitudes to both the CS- and the CS+, perhaps reflecting an anxious or fear-like state during the testing phase. This suggests that the direct response to the social UCS might be less important for the observer's learning than previously theorized, especially when compared to mirroring and directly sharing the dynamics of the demonstrator's electrodermal activity and might represent an uncharted difference to direct learning.

Outstanding questions arising from this study concern the factors that can affect the degree of demonstrator-observer coupling, and how these can be manipulated. Past work has demonstrated that people tend to synchronize more with people they are more positively disposed towards [49, 50] or closer to [34]. Similarly, observers learn about threats better from demonstrators who are similar to them [51]. Hence, an important avenue for future work is to manipulate the relationships between participants, for example by minimal group induction or by using natural covariates such as friendship [38], to investigate if and how this affects synchrony's role in learning.

A better understanding of the conditions during which synchrony emerges is important for establishing whether synchrony affects phenomena related to observational learning, like social buffering and social safety learning [52, 53]. There observational learning protects the individual from experiencing strong threat responses and provides a safe route towards extinction of previously learned threat associations. If synchrony attunes the observer to the demon-

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strators experiences, as we have interpreted our findings here, then it is possible that similarly synchrony will serve to aid vicarious extinction, which in turn has clinical relevance as a model for understanding phobias and other anxiety disorders.

Methods

Participants

We recruited a total of 138 participants who formed 69 unique demonstrator-observer dyads. Dyads were matched by gender (24 male, 45 female). Average age was 25 years ($SD = 4.1$). Participants were recruited from the student population at Karolinska Institutet and the surrounding local community. We ensured that participants did not already know each other prior to participating in the experiment. Participants were screened from having previously partaken in conditioning experiments. Participants were given two cinema ticket vouchers as thanks for their participation. The experimental procedure was approved by the local ethics committee (2015/2115-32).

Equipment

Electrodermal activity was recorded using a BIOPAC MP150 system and AcqKnowledge software as a skin conductance signal measured in microsiemens (μS). Recording was at 1000Hz from the distal phalanges of the middle and index fingers from the hand belonging to the arm not receiving shocks. Ag-AgCl electrodes were used together with a conducting gel, following standard recommendations [54]. Electric shocks, consisting of a single 100ms DC pulse, were administered using a Biopac STM200 module (Biopac Systems Inc.) applied to the lower forearm. The strength of the electric shocks was individually calibrated so that participants experienced the shocks as being "unpleasant but not painful". Stimulus presentation and shock administration was controlled by scripts programmed in PsychoPy [55].

Procedure

The experiment was divided into four blocks of alternating learning and testing phases and followed established protocols for video-based observational learning paradigms [39]. During each learning phase there were six alternating presentations of each CS+ and CS- image. Each CS was shown for six seconds. Four of the six CS+ presentations, randomly determined, terminated with a shock to the demonstrator. There was a variable length 10-16 second inter-trial interval between each CS presentation. After this learning phase on-screen instructions informed the observer that now they would view the same images and receive shocks to the same image that they

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had observed the demonstrator receive shocks to. The demonstrator was instructed to close their eyes and a screen was placed between demonstrator and observer. These steps were taken to ensure that the observer would not be able to pick up any cues during the testing phase about the valence of the CS images. During the testing phase each CS image was shown seven times. Only the final CS+ presentation terminated with a shock - this to ensure that observers didn't learn that no shocks would be given which would interfere with the next testing phase. The whole procedure was repeated the following block. Demonstrators and observers switched roles after the second block. Full experimental procedures are described in the Supplementary Methods.

Signal processing

Electrodermal activity was continuously measured from both participants throughout the experiment. The raw signal from each participant was filtered offline with a low-pass filter (1Hz) and a high-pass filter (0.05Hz). Using CS onset and shock delivery as event markers and following established protocols [39], skin conductance responses (SCRs) were measured as the largest peak-to-peak amplitude difference in the phasic skin conductance signal in the 0.5 to 4.5 second window following stimulus onset. Responses below $0.02\mu S$ were scored as zero. SCRs were square-root transformed prior to analysis. The full phasic skin conductance signal from both participants was also exported for use in the cross-recurrence quantification analysis (see below).

Cross-Recurrence Quantification Analysis

Cross-Recurrence Quantification Analysis (CRQA) is the bivariate extension of Recurrence Quantification Analysis (RQA) a method to analyze the structure and revisitation (recurrence) patterns in non-linear time-series [56]. RQA is based on the analysis of recurrence plots [57]. In a recurrence plot (see 1), each dot marks a point of recurrence in a reconstructed phase space of the signal. The phase space is constructed using time-delay embedding. Points are considered to be recurrent if they are within some radius of one another in the resulting high dimensional phase space. Hence, three parameters need to be set to compute a recurrence plot from a time-series: time delay, number of embedding dimensions and radius (see [57] for a rigorous treatment). CRQA works analogously but where the patterns of revisitation are compared between two signals [27, 58]. CRQA yields cross-recurrence plots, analogous to regular recurrence plots.

We used the *crqa* package [59] implemented in the R statistical language to construct the cross-recurrence plots. Each cross-recurrence plot was based on the phasic skin conductance signal from the demonstrator and observer from each learning phase. The signals were down-sampled to 8Hz and then

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z-scored. Optimal parameters for the CRQA analysis (delay, embedding dimensions and radius) were determined individually for each pair of signals so that they would yield an average recurrence rate between 2% and 4% [34, 57]. From each resulting cross-recurrence plot various metrics can be computed that capture the dynamics of the system being analyzed [27, 57, 59]. Here we computed four metrics: DETerminism, LAMinarity, maximum line (maxL) and relative Entropy (rENTR). DET represents the relative amount of recurrent points forming diagonal segments, as such DET measures the predictability of the time-series as they evolve over time. LAM is analogous to DET but instead represents recurrent points forming vertical line segments, which can be thought of capturing relative stability in the system. maxL is length of the longest diagonal sequence of recurrent points, capturing the maximal strength of coupling between the two time series. rENTR calculates the Shannon entropy of the histogram of the deterministic (diagonal) sequences and indexes the complexity of the relationship between the time series.

Analysis

All analyses were performed in the R statistical language using the *brms* package [60]. We analyzed the data using Bayesian multi-level regression including varying intercepts and slopes by participant and between intercept and slope correlations. All categorical regressors were deviation coded (0.5/-0.5) and all continuous regressors were standardized. Weakly informative priors were used for all analyses to regularize estimates. These were Normal(0,0.5) for the intercept, Normal(0,0.2) for the slope of CS, and Normal(0,0.05) for all other slopes which usually contained the parameters of interest. LKJ(2) priors were placed on the correlation matrix and Normal(0,1) priors on the group standard deviations and the model residual standard deviation. For all estimates 95% credible intervals were computed as well as Bayes Factors based on the Savage-Dickey ratio for the parameter at the value 0.

Data availability

All processed data are available from the Open Science Framework (`https://osf.io/mkv8c/?view_only=5789aa6170984416b9c9fb6ae4626fbe`), and raw data are available from the authors upon request.

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