



Sync to link: Endorphin-mediated synchrony effects on cooperation

Martin Lang^{a,b,*}, Vladimír Bahna^{b,c}, John H. Shaver^d, Paul Reddish^e, Dimitris Xygalatas^{f,g}

^a Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, 02138, USA

^b LEVYNA, Masaryk University, Brno, 60200, Czech Republic

^c Institute of Ethnology, Slovak Academy of Sciences, Bratislava, 81364, Slovakia

^d Religion Programme, University of Otago, Dunedin, 9012, New Zealand

^e Department of Psychology, National University of Singapore, 117572, Singapore

^f Department of Anthropology, University of Connecticut, Storrs, CT, 06269, USA

^g Interacting Minds Centre, Aarhus University, Aarhus, 8000, Denmark

ARTICLE INFO

Keywords:

Synchrony
Prosociality
Pain threshold
Endorphins
Cooperation
Self-other overlap

ABSTRACT

Behavioural synchronization has been shown to facilitate social bonding and cooperation but the mechanisms through which such effects are attained are poorly understood. In the current study, participants interacted with a pre-recorded confederate who exhibited different rates of synchrony, and we investigated three mechanisms for the effects of synchrony on likeability and trusting behaviour: self-other overlap, perceived cooperation, and opioid system activation measured via pain threshold. We show that engaging in highly synchronous behaviour activates all three mechanisms, and that these mechanisms mediate the effects of synchrony on liking and investment in a Trust Game. Specifically, self-other overlap and perceived cooperation mediated the effects of synchrony on interpersonal liking, while behavioural trust was mediated only by change in pain threshold. These results suggest that there are multiple compatible pathways through which synchrony influences social attitudes, but endogenous opioid system activation, such as β -endorphin release, might be important in facilitating economic cooperation.

1. Introduction

Across cultures, people engage in collective activities that involve the matching of behaviour in time, such as music production and singing, dancing, and collective rituals (Hagen and Bryant, 2003; Hagen & Bryant, 2003; Merker et al., 2009). It has long been speculated that such synchronous activities function to increase group cohesion (Durkheim, 1964; Marsh, Richardson, & Schmidt, 2009; McNeill, 1995), and experimental research has supported this conjecture: synchronous behaviour has been shown to facilitate rapport and interpersonal liking (Hove & Risen, 2009; Lang et al., 2016; Miles et al., 2009); entitativity (Lakens & Stel, 2011; Reddish et al., 2013); cooperation in economic games (Launay, Dean, & Bailes, 2013; Reddish, Bulbulia, & Fischer, 2014; Wiltermuth & Heath, 2009); and helping behaviour (Kokal, Engel, Kirschner, & Keysers, 2011; Valdesolo & Desteno, 2011). Despite this convergent evidence, the mechanisms mediating these effects are still poorly understood. Recently, two potential mechanisms were proposed by Tarr and colleagues: one related to self-other overlap and one related to the endogenous opioid system (Tarr, Launay, & Dunbar, 2014; see also Mogan, Fischer, & Bulbulia, 2017).

The self-other overlap mechanism builds on the literature describing the tight integration of perception and action systems (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011). Common neural encoding can be amplified by behavioural synchrony, which may, at some level of cognitive processing, lead to the blending of other-generated and self-generated behaviour (Paladino, Mazurega, Pavani, & Schubert, 2010). Perceiving interaction partners as part of oneself may lead to feeling closer to them (Overy & Molnar-Szakacs, 2009), as shown by studies on synchronous movement and singing (Reddish et al., 2013; Weinstein et al., 2015). However, the evidence for overlap-mediated synchrony is mixed, with some studies failing to find a direct relationship (Cohen, Mundry, & Kirschner, 2013; Fischer, Callander, Reddish, & Bulbulia, 2013; Reddish et al., 2013; Wiltermuth & Heath, 2009).

The β -endorphin release hypothesis, on the other hand, places emphasis on the biochemical basis of human sociality, suggesting that synchrony leads to increased affiliative and socially rewarding behaviour because it activates the endogenous opioid system (Loseth, Ellingsen, & Leknes, 2014; Machin & Dunbar, 2011). β -endorphin neurotransmitters and related μ -opioid receptors (MOR) have been previously implicated to play an important role in mother-infant

* Corresponding author at: Department of Human Evolutionary Biology, Harvard University, 11 Divinity Ave, Cambridge, MA 02138, USA.
E-mail address: martinlang@fas.harvard.edu (M. Lang).

attachment, distress vocalization, and social grooming in rodents and non-human primates (Graves, Wallen, & Maestripieri, 2002; Kalin, Shelton, & Lynn, 1995; Moles, Kieffer, & D'Amato, 2004; Panksepp, Nelson, & Siviý, 1994). In human studies, however, a direct assessment of brain opioid levels from cerebrospinal fluid is unfeasible. For this reason, researchers have instead employed pain threshold as a proxy measure for endorphin release (Dunbar, Baron et al., 2012; Johnson & Dunbar, 2016), utilizing the opioid analgesic effect (Akil et al., 1984; Petrovic et al., 2002; Zubieta et al., 2001; for alternative measurements see Inagaki, Irwin, & Eisenberger, 2015; Nummenmaa et al., 2015). Several studies investigating synchronous behaviour have found increased pain threshold following a group rowing exercise (Cohen, Ejsmond-Frey, Knight, & Dunbar, 2010; Sullivan, Rickers, & Gammage, 2014); synchronized singing (Weinstein et al., 2015); drumming (Dunbar, Kaskatis et al., 2012; Dunbar, Kaskatis, MacDonald, & Barra, 2012); and dancing (Tarr et al., 2016; Tarr, Launay, & Dunbar, 2016). However, the relationship between pain threshold, social reward, and cooperation has rarely been examined, despite a substantial number of studies using these variables as dependent measures.

A third mechanism pertains to a more social-cognitive account, according to which synchrony is not simply the matching of behaviours but an outcome of joint action with social motivations (Keller, Novembre, & Hove, 2014; Lumsden, Miles, Richardson, Smith, & Macrae, 2012; Obhi & Sebanz, 2011). Reddish et al. (2013) suggested that the effects of synchrony are driven by the perception of successful cooperation, which improves confidence and trust, and then transfers to future cooperative tasks. Path analysis empirically supported this model (Reddish et al., 2013), and further evidence (Kurzman, 2001; Launay et al., 2013) suggests that the perceived success of a synchrony task is a critical predictor of cooperative behaviour in economic games – more so than the precise matching of movements.

Notwithstanding the ample empirical data linking synchrony with greater prosociality, as of yet, no study has systematically compared these mechanisms. Furthermore, previous research has focused on different aspects of prosociality such as liking, entitativity, and cooperation, or has conflated these aspects under terms like rapport (Cohen et al., 2013; Lakens & Stel, 2011; Tarr et al., 2015) or social bonding (Tarr et al., 2014; Wolf et al., 2016). To introduce an initial clarification, we identify two basic effects of synchrony that are representative of prosociality, one attitudinal and one behavioural (Tarr et al., 2014). Specifically, we break down prosociality into positive feelings about the other expressed in increased likeability, and trust-based behavioural cooperation as measured by an economic game. While liking and cooperation can fuel each other, liking is not a pre-requisite for economic exchange, and these two effects can be separated (Manson, Bryant, Gervais, & Kline, 2013; Tarr et al., 2016). Thus, our aim was to investigate the mechanisms that underlie the effects of synchronous movement on interpersonal liking and economic cooperation.

To this end, we manipulated synchrony and measured each of the three mediating variables via change in pain threshold measurements, self-other overlap, and perceived cooperation. We used a Trust Game to assess economic cooperation, and we also measured interpersonal liking towards the synchronizing partner. Furthermore, we employed a novel synchrony manipulation that involved individual participants interacting with another person (a pre-recorded confederate) through a video transmission with a high degree of synchrony (high-sync condition) or a low degree of synchrony (low-sync condition), and a control condition where participants did not view the video transmission. In line with previous studies, we predicted that high synchrony would lead to greater levels of cooperation and interpersonal liking in comparison to the low-sync and control conditions. Furthermore, we tested three possible pathways for these purported effects: a) a self-other overlap model, b) an endogenous opioid model, and c) a reinforcement of cooperation model. Below we assess the relative contribution of each mechanism to cooperative behaviour as measured by the Trust Game

and positive attitudes towards the confederate.

2. Method

2.1. Participants

We recruited 124 participants (80 females, M age = 22.71, SD = 3.43) from a student participant pool at Masaryk University, Czech Republic, in exchange for course credit and monetary earnings from the economic game. We used a between-subjects design with random assignment to one of three conditions: high-sync (n = 44, 31 females; M age = 23.31; SD = 4.44), low-sync (n = 44, 29 females; M age = 22.73; SD = 3.07), and control (n = 36, 20 females; M age = 21.97; SD = 2.14). Participants were debriefed after the experiment ended. The study was approved by the Ethics Committee of the Faculty of Arts, Masaryk University.

2.2. Procedure and stimuli

Upon individually entering the laboratory room, participants were informed about the procedure and then signed a consent form. The subsequent procedure comprised three 5-min-long exercises, each followed by a pain threshold measurement. Additionally, a baseline pain threshold measurement was obtained before the first exercise. After the last exercise, participants filled out a questionnaire, and finally played a Trust game (Table S1 outlines the experimental procedure).

Each exercise consisted of 75 repetitions of three symmetric arm movements. Participants in all conditions were instructed to start each movement repetition after hearing a start signal – a drum sound that occurred at irregular intervals. In the control conditions, participants performed these movements in front of a blank wall, while in the high-sync and low-sync conditions they were instructed to synchronize their movements with another participant in a live-streaming video. In reality, however, this was a pre-recorded confederate. In the high-sync condition videos, the confederate performed exercises at a steady speed with no errors. To inhibit synchronization in the low-sync condition, the confederate's movements were distorted in three ways: 1) the speed of movements in particular repetitions varied randomly among five different speeds; 2) the confederate's reaction time was set up to vary randomly between 0.1, 0.3, and 0.5 s; and 3) the confederate made 15 movement errors in each exercise (see Fig. 1A). During the recording, the confederate followed a designed guiding beat for each particular movement, which allowed us to control movement speed and delays that simulated reaction time and the placement of errors. To avoid bonding based on facial perception, the confederate's face in the video was covered with a grey rectangle (see Supplementary Video 1).

Our pain-threshold measurement was obtained by using a pressure algometer with a standardized, continuous, and automatic distribution of pain. Motor synchronization was captured by accelerometers positioned on participants' wrists, and successful synchrony was operationalized as the minimal time-difference between participants' and the confederate's maximum acceleration points (see Supplementary Methods for details on data collection and signal processing). Furthermore, we administered a questionnaire measuring five constructs: perceived synchrony; attention to the confederate; self-other overlap; perceived cooperation; and liking of the confederate (see Supplementary Methods for details on specific scale items, their factor loadings, and scale reliability). After completing the questionnaire, each participant played a version of the Trust Game (Berg et al., 1995; Berg, Dickhaut, & McCabe, 1995). Subjects in conditions with a video projection were told that they were playing the game with their interaction partner, while participants in the control condition were told that they were playing with another (anonymous) participant waiting in another room. All participants acted as player A (the trustor). Players started with 100 Czech crowns (CZK) (approximately 4 USD, enough to buy a meal locally), allocated in ten 10-CZK-coins, and chose

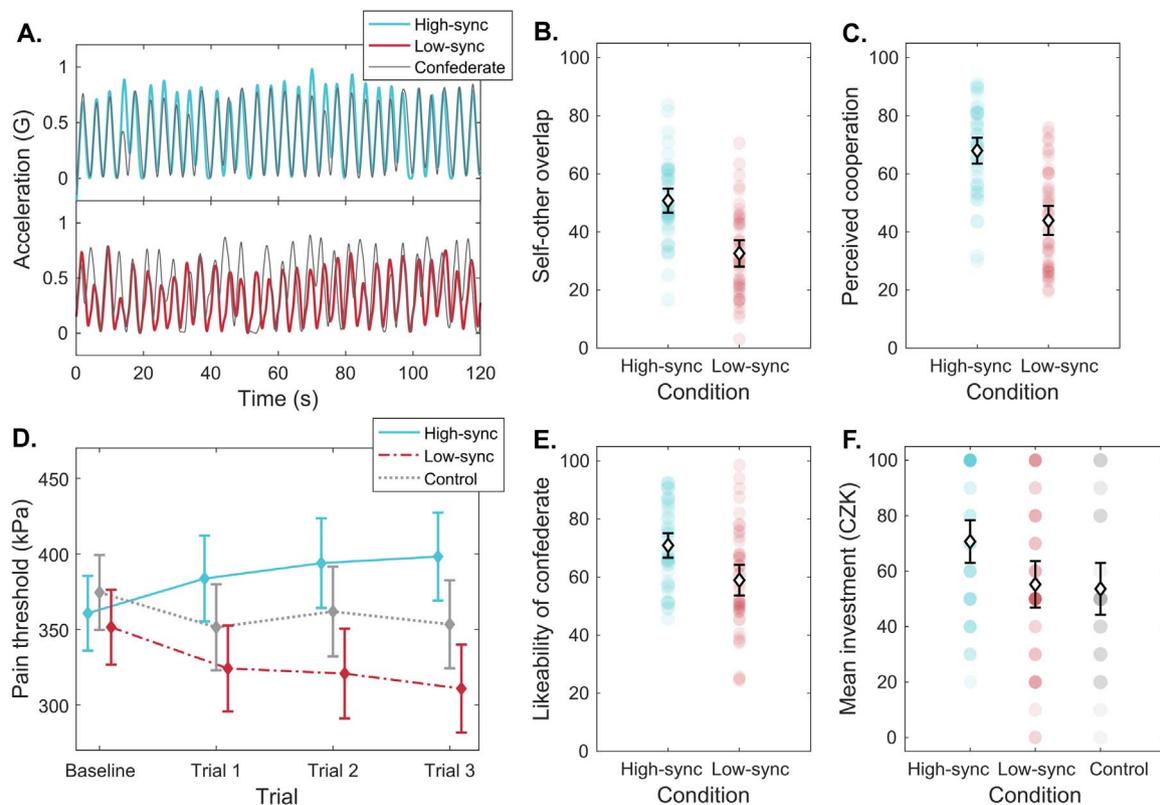


Fig. 1. Point Estimates with 95% CI for the Effects of Synchrony Manipulation. (A) Synchrony manipulation afforded different rates of motor coupling as captured by accelerometers. (B) Participants in the high-sync condition experienced more overlap with the confederate and (C) perceived his actions as more cooperative. (D) There was a significant linear increase in pain threshold in the high-sync condition, but no differences in the other two conditions. (E) Participants in the high-sync condition liked the confederate significantly more, and (F) invested significantly more money compared to the low-sync and control conditions.

how much of this money they wished to allocate to player B (the trustee). Participants were told that the amount allocated would be tripled and then sent to player B, who would then decide how much to return to player A. The amount player A invests is taken as a measure of trust towards player B and is considered as an indicator of cooperation. Player B's responses were determined by a standard algorithm (Launay et al., 2013).

2.3. Data analysis

All data were analysed in R (R Core Team, 2016). Confirmatory factor analysis of our latent variables was performed using the function *cfa* in the *lavaan* package (Rosseel, 2012). To model dependent variables with continuous predictors, we used multivariate linear regression and added predictors on the basis of their theoretical importance. To model the trial effect for pain threshold, we built a linear mixed model using the *lme* function in the *nlme* package (Pinheiro et al., 2014; Pinheiro, Bates, DebRoy, Sarkar, & Team, 2014) with participant ID as a nesting factor. To account for the possible correlations of intercepts and slopes of pain threshold, we modelled a random intercept and slope for each participant. All models assumed a normal distribution of residuals, despite the fact that the investment data were censored at 0 and 100. We built a model of the investment data to account for these bounds using the function *gamlss* in *gamlss* package (Stasinopoulos and Rigby, 2007; Stasinopoulos & Rigby, 2007); however, the final model's residual diagnostics revealed a better fit of the model with normally distributed errors, and the R^2 s were comparable (normal $R^2 = 0.075$ for $DF = 2$; Cox Snell pseudo $R^2 = 0.079$ for $DF = 4$). Therefore, we opted for keeping the simpler model. Pairwise comparisons were estimated using function *lsmeans* (Lenth, 2014). Path analysis was performed using the function *sem* in the *lavaan* package (Rosseel, 2012). We fitted a model for each of the proposed mechanisms and a full model combining these

mechanisms together. Subsequently, we removed non-significant pathways from the full model to arrive at a final model that combined different mechanisms.

3. Results

Looking at our manipulation of synchrony, an analysis of temporal-movement synchrony between participants and the confederate revealed a significant difference between the high-sync and low-sync conditions [$t(68.88) = 15.33, p < 0.001$], confirming that the mean time difference between movements was closer to zero in the former compared to the later condition (see Fig. 1A for illustration). This difference was also reflected in our measure of perceived synchrony [$t(80.90) = 6.97, p < 0.001$], with participants in the high-sync condition rating synchrony during the movement task higher than those in the low-sync condition (see Table 1 and Fig. S1 A-B). The measures of movement and perceived synchrony were also highly correlated ($r = 0.58, p < 0.001$). Perception of task difficulty was not significantly different [$t(84.63) = 1.74, p = 0.086$] between the high-sync and low-sync conditions. However, there was a significant difference in attention to the confederate, with participants in the high-sync condition reporting paying more attention than the participants in the low-sync condition [$t(83.14) = 4.28, p < 0.001$]. For descriptive statistics see Table 1 and Fig. S1 C-D.

3.1. Mediating variables

Next, we analysed the differences between conditions in the three mediating variables. First, our measure of perceived self-other overlap revealed that participants in the high-sync condition felt more overlap with the confederate [$t(85.18) = 5.81, p < 0.001$] compared to those in the low-sync condition. Second, perceived cooperation during the

Table 1
Descriptive Statistics of Synchrony Manipulation and Mediating and Dependent Variables.

Variable	High-sync (n = 44)			Low-sync (n = 44)			<i>d</i>	Control (n = 36)			<i>d</i>
	M	SD	CI	M	SD	CI		M	SD	CI	
Movement Sync	–234.51	47.32	[–248.49, –220.53]	–452.95	81.80	[–477.13, –428.78]	3.27	–	–	–	–
Perceived Sync ^a	67.29	14.59	[62.97, 71.60]	42.24	18.86	[36.67, 47.81]	1.49	–	–	–	–
Task Difficulty ^a	74.11	15.71	[69.74, 78.76]	79.59	13.83	[75.51, 83.68]	0.37	–	–	–	–
Attention ^a	78.01	14.35	[73.77, 82.25]	63.48	17.31	[58.37, 68.60]	0.91	–	–	–	–
Self-other Overlap ^a	50.77	13.93	[46.65, 54.89]	32.62	15.37	[28.07, 37.16]	1.24	–	–	–	–
PT Difference	37.48	56.93	[20.66, 54.30]	–40.64	56.89	[–57.45, –23.83]	1.37	–21.07	69.23	[–43.69, 1.55]	0.92
Cooperation ^a	67.98	15.14	[63.51, 72.46]	43.95	16.90	[38.96, 48.95]	1.50	–	–	–	–
Likeability ^a	70.92	14.33	[66.69, 75.15]	58.94	17.82	[53.68, 64.21]	0.74	–	–	–	–
Investment	70.68	26.09	[62.97, 78.39]	55.23	28.41	[46.83, 63.62]	0.57	53.61	28.61	[44.27, 62.95]	0.62

Note. CI = 95% Confidence intervals. Cohen's *d* is the effect size of comparisons between the high-sync condition and the other conditions. Movement synchrony refers to the difference in milliseconds between participants' and confederate's movements. PT = Pain Threshold difference between the baseline measurement and the final measurement after the third exercise in kPa. Investment is in CZK.

^a Factors constructed from the post-activity questionnaires (scores are between 0 and 100) were distributed only in the high-sync and low-sync conditions.

Table 2
Estimates with SE from a Linear Mixed Model for the Change in Pain Threshold over the Course of Three Trials.

Variable	Estimate
Intercept	365.66 (23.65)***
Low-sync	–20.1 (33.45)
Control	2.48 (35.26)
Time	12.26 (3.10)***
Low-sync* ^a Trial	–24.79 (4.39)***
Control* ^a Trial	–17.54 (4.62)***

Note. The intercept is the high-sync condition at baseline pain threshold; low-sync and control are comparisons with the high-sync condition at baseline pain threshold; trial is the slope of the high-sync condition and the interaction terms are comparisons with this slope.

****p* < 0.001.

task differed between the two conditions [$t(84.98) = 7.02$, $p < 0.001$], revealing higher perceived cooperation in the high-sync condition compared to the low-sync condition (see Table 1 for descriptive statistics and effect sizes, and Fig. 1B,C). Finally, a linear mixed-model revealed no differences in baseline pain threshold between the high-sync and the other two conditions (low-sync: $p = 0.549$; control: $p = 0.944$). However, we observed a linear increase in pain threshold in the high-sync condition over the course of three trials ($p < 0.001$), and a significant Condition*^aTrial interaction, suggesting a higher increase in pain threshold over the course of three trials in the high-sync condition compared to the low-sync ($p < 0.001$) and control ($p < 0.001$) conditions (see Tables 1 and 2 and Fig. 1D). A one-way ANOVA with pain threshold after the third trial as a dependent variable, condition as an independent variable, and baseline pain threshold as a covariate revealed a significant main effect of condition [$F(2,120) = 22.890$, $p < 0.001$]. A subsequent post-hoc comparison with a Tukey correction showed a significant difference between the high-sync and each of the other two conditions ($ps < 0.001$), but not between the control and low-sync conditions ($p = 0.367$). The three mediating variables were highly correlated with one another (Overlap*^aPain-threshold change: $r = 0.33$, $p < 0.001$; Overlap*^aCooperation: $r = 0.84$, $p < 0.001$; Pain-threshold change*^aCooperation: $r = 0.43$, $p < 0.001$), suggesting that they were jointly influenced by the synchrony manipulation. Interestingly, the last pain threshold measurement and post-task self-reported mood were uncorrelated ($r = 0.12$, $p = 0.250$).

3.2. Liking and investment

We observed higher likeability ratings of the confederate in the high-sync condition relative to the low-sync condition [$t(85.52)$

$= 4.26$, $p < 0.001$, $d = 0.74$]. The mean amount of money sent by participants to the trustee differed between conditions [$F(2,120) = 4.89$, $p = 0.009$]. A post-hoc pairwise comparison with Tukey correction showed a statistical difference between the high-sync and low-sync condition ($p = 0.030$, $d = 0.57$), and between the high-sync and control condition ($p = 0.019$, $d = 0.62$). There was no difference between the low-sync and control condition ($p = 0.909$). Finally, self-reported liking and investment in the Trust Game were uncorrelated ($r = 0.14$, $p = 0.192$). See Table S3 and Fig. 1E,F for details.

3.3. Path analyses

To compare the proposed mediating models, we conducted three separate path analyses with the synchrony manipulation as the main predictor and likeability and investment as dependent variables. In the overlap model, the synchrony manipulation predicted differences in perceived self-other overlap ($p < 0.001$) that mediated the positive effects of synchrony on likeability ($p < 0.001$) but not on investment ($p = 0.437$). The endogenous opioid model, on the other hand, predicted elevated pain threshold in the high-sync condition ($p < 0.001$) that, in turn, mediated the effects of treatment on likeability ($p = 0.002$) and investment ($p = 0.032$). Finally, the cooperation model predicted the effects of the synchrony manipulation on perceived cooperation ($p < 0.001$), which further mediated the effects of treatment on likeability ($p < 0.001$) but not on investment ($p = 0.112$). While the self-other overlap and endogenous opioid models exhibited a mediocre fit, the cooperation model had the best fit to the data (see Table S3 for fit indices and Fig. 2A–C for the path models with standardized coefficients).

To test the combined effects of the three proposed paths, we constructed a full model containing all of the three pre-specified pathways to likeability and investment. However, this model was a poor fit to the data, so all non-significant pathways were removed to arrive at the best fitting model (CFI = 1.00, RMSEA = 0.00, SRMR = 0.062). The best fitting model was a combination of the endorphin and cooperation models (the standardized coefficients and *p*-values are plotted in Fig. 2D). However, since perceived cooperation and self-other overlap were highly correlated, substituting perceived cooperation with self-other overlap in the final path model yielded a comparably good fit (see Table S3 for all models' fit indices).

4. Discussion

Our study investigated and compared three proposed mediating mechanisms for synchrony's prosocial effects: self-other overlap, reinforced cooperation, and endogenous opioid system activation (indicated by increased pain threshold). Using a novel manipulation together with a digital assessment of synchrony, our findings revealed

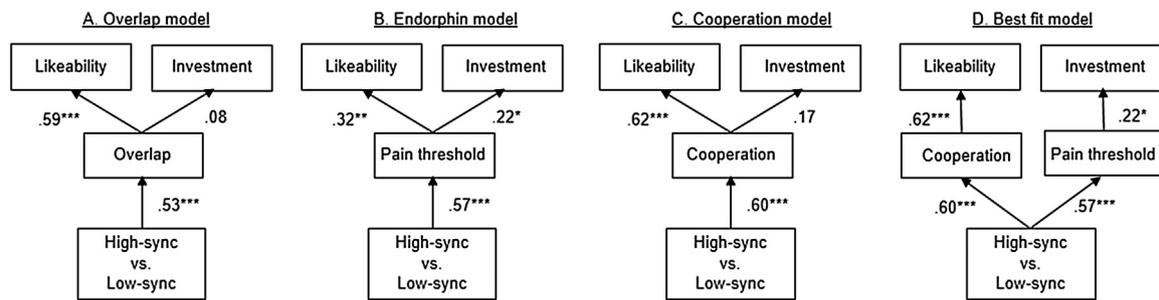


Fig. 2. Mechanisms Mediating Synchrony Effects on Prosociality. (A–C) Path models of three hypothesized mechanisms with standardized coefficients. (D) The best fitting path model revealed that pain threshold mediated the behavioural measure, while reinforced cooperation mediated the attitudinal measure. Perceived synchrony and increased attention in the high-sync condition further contributed to perceived cooperation.

Note. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

that synchronization between individuals positively activated all three of these mechanisms. We found that the confederate was rated as more likeable in the high-sync condition compared to the low-sync condition, and that participants in the high-sync condition entrusted the confederate with more money compared to the low-sync and control conditions. Because there was no significant difference between the low-sync and control conditions, it is unlikely that the failure to properly synchronize in the low-sync condition decreased trust towards the interaction partner. Interestingly, the likeability and investment measurements were uncorrelated, indicating that positive attitudes about others do not necessarily enter into economic decision-making (De Backer et al., 2016; De Backer, Larson, Fisher, McAndrew, & Rudnicki, 2016). These results support the notion that prosociality has multiple, and possibly independent, facets, thus an examination of each of the purported mechanisms in path analyses was warranted.

First, the self-other overlap model displayed high predictive power in mediating the effects of synchrony on likeability but not on behaviour in the economic game. Similarly, perceived cooperation mediated synchrony effects on likeability but not on cooperative behaviour. Finally, the endogenous opioid model exhibited a significant positive relationship between pain threshold increase and both prosociality measures (likeability and investment). Combining all three suggested pathways in one model supported the distinction between the cognitive and physiological aspects of our measurements. The best-fitting model exhibited two main paths: one through pain-threshold increase to higher investments in the Trust Game; and another through perceived cooperation to likeability of the interaction partner. The purported opioid mechanism significantly predicted monetary investments, unlike the other two mediating variables, suggesting that physiological processes might play a crucial role in economic decision-making.

Together, these findings suggest that the matching of movement sequences between participants and the confederate in the high-sync condition produced motor resonance between the actors, as opposed to the low-sync condition where the attainment of such resonance was inhibited by prediction errors generated by the confederate's mistakes (Kilner, Friston, & Frith, 2007; Sebanz, Bekkering, & Knoblich, 2006; Sebanz & Knoblich, 2009). The joint motor resonance in the high-sync condition could further lead to the emergence of shared attention and action co-representation (indicated by higher attention to the confederate in the high-sync condition), which are crucial for a successful joint action (Knoblich & Sebanz, 2006; Pezzulo & Dindo, 2011). Cognizing in the we-mode (Gallotti & Frith, 2013; Hasson & Frith, 2016; Kirschner & Tomasello, 2010), participants acted simultaneously as a joint unit (Reddish et al., 2013), and that lead to an increase in perceived cooperation (Wolf et al., 2016). The resulting overlap and perceived cooperation then manifested in ratings of the confederate's likeability, supporting the assertion that humans preferably bond with similar and cooperative others (Cohen & Haun, 2013; Ip et al., 2006; Valdesolo & Desteno, 2011). Such bonds may be further buttressed by the activation of the brain's opioid system (as suggested by our pain-

threshold results), which produces a mild “high” (Dunbar, Kaskatis et al., 2012) that facilitates a state of ‘collective effervescence’ and promotes group bonding (Fischer et al., 2014; Konvalinka et al., 2011; Xygalatas et al., 2013).

Looking at the effects of synchrony on decision-making in the Trust Game, only pain threshold appeared as a significant mediator. This finding is in accordance with previous research showing that behaviour in trust games is affected by implicit attitudes and physiological processes (Kret, Fischer, & De Dreu, 2015; Stanley, Sokol-Hessner, Banaji, & Phelps, 2011). For example, Zak et al. (2005) suggested that oxytocin helps solve the investors' cooperation dilemma by inhibiting avoidance behaviour, thereby helping subjects approach other players (though see Nave, Camerer, & McCullough, 2015). We speculate that opioids such as β -endorphin can be an important component of the complex effects of the neuroendocrine system on trust decisions (Machin & Dunbar, 2011; Pearce et al., 2017). Similar to the oxytocin literature, previous studies with non-human animals have found that the opioid system plays a role in the regulation of social distress (Kalin et al., 1995; Moles et al., 2004), motivating individuals to seek out social contact or inhibiting sociality when opioids are abundant (such as through morphine administration). Extending these findings to the current results, synchronous activity may have helped overcome initial distress from the experimental situation and interaction with unknown people, and eventually lead to increased affiliation and behavioural trust. Importantly, these endorphin-mediated trust decisions seem to be partially independent of the conscious assessment of others.

The failure to observe any effect of self-other overlap on investments suggests that such overlap may be responsible for a host of prosocial attitudes, but is not sufficient for eliciting trustworthy economic exchange. Furthermore, past cooperation may help overcome avoidant behaviours in future economic interactions, yet a history of cooperation needs to be supported by physiological mechanisms to facilitate interpersonal bonds. These results are in accordance with a recent meta-analysis that examined the effects of synchrony on prosocial behaviours, social-bonding perception, social cognition, and positive affect, and found that the strongest effect of synchrony was on behavioural prosociality (Mogan et al., 2017). Interestingly, this effect was even stronger in larger groups, suggesting that the positive effects of synchrony are generated by an individual bias towards increased general prosociality, rather than through conscious evaluation of each group member (see also Reddish, Tong, Jong, Lanman, & Whitehouse, 2016). Individual biochemical mechanisms such as β -endorphin release may facilitate a bias towards prosociality, trust, and gregariousness.

However, a potential limitation to this interpretation is the fact that our measure of endogenous opioid system activation was only indirect, and while it has been validated as a reliable measure of β -endorphin release in non-human animals (for rodent studies see e.g. Gintzler, 1980), no such studies have been conducted with human subjects. Whereas pain perception has been associated with basal MOR availability and binding potential (Mueller et al., 2010; Zubieta et al., 2001),

other factors such as stress and the related blood-pressure response (Al'Absi and Petersen, 2003; Al'Absi & Petersen, 2003) or attentional control (Wiech et al., 2008; Wiech, Ploner, & Tracey, 2008) might have mediated inter-individual differences in nociception in our study. Furthermore, as our attitudinal measures were all highly correlated, future studies may help better distinguish the mediating variables by using different proxies such as eye-tracking for attention (Launay et al., 2014; Launay, Dean, & Bailes, 2014) or automatic imitation for self-other overlap (Shaw et al., 2013; Shaw, Czekóová, Chromec, Mareček, & Brázdil, 2013). For a closer investigation of causal connections between mediators and dependent variables, future research should also manipulate the mediating variables with and without the synchrony context, and assess their individual contribution to prosocial behaviours and attitudes (Tarr et al., 2015; Wolf et al., 2016).

In summary, our results identify cognitive and physiological pathways through which synchrony facilitates prosociality. A test of the mechanisms of self-other overlap, reinforcement of cooperation, and opioid system activation indicated by pain threshold revealed that self-reported liking of a confederate was predicted by all three mechanisms, while behaviour in the Trust Game was facilitated only by an increase in pain threshold. The purported role of the opioid system in economic decision-making might thus be related to facilitating interpersonal trust on a subconscious level, independent of how people explicitly report feeling about one another. Our study provides novel evidence for the importance of biochemical underpinnings in facilitating the effects of synchrony on interpersonal bonds and economic cooperation.

Conflict of interests

We declare no competing interests.

Authors' contributions

ML, VB, JS, PR, and DX designed the study; VB collected data; ML carried out statistical analyses; ML and VB drafted the paper; all authors provided comments and approved the final manuscript.

Funding

This work was funded by the Laboratory for the Experimental Research of Religion [CZ.1.07/2.3.00/20.048], co-financed by the European Social Fund and the state budget of the Czech Republic, and the Faculty of Arts, Masaryk University, and the Cultural Evolution of Religion Research Consortium (CERC), funded by a partnership grant [895-2011-1009] from the Social Sciences and Humanities Research Council of Canada. VB was supported by VEGA grant [2/0062/17] 'Holidays and rituals – Their social context and functions'. JS acknowledges support from a Royal Society of New Zealand Marsden Fund Grant [ID: VUW 1321].

Acknowledgements

We are thankful to Joseph Bulbulia for providing comments on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biopsycho.2017.06.001>.

References

Akil, H., Watson, S. J., Young, E., Lewis, M. E., Khachaturian, H., & Walker, J. M. (1984). Endogenous opioids: Biology and function. *Annual Review of Neuroscience*, 7(1), 223–255. <http://dx.doi.org/10.1146/annurev.ne.07.030184.001255>.

Al'Absi, M., & Petersen, K. L. (2003). Blood pressure but not cortisol mediates stress

effects on subsequent pain perception in healthy men and women. *Pain*, 106(3), 285–295. [http://dx.doi.org/10.1016/S0304-3959\(03\)00300-2](http://dx.doi.org/10.1016/S0304-3959(03)00300-2).

Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, 10(1), 122–142.

Cohen, E., & Haun, D. (2013). The development of tag-based cooperation via a socially acquired trait. *Evolution and Human Behavior*, 34(3), 230–235. <http://dx.doi.org/10.1016/j.evolhumbehav.2013.02.001>.

Cohen, E., Ejsmond-Frey, R., Knight, N., & Dunbar, R. I. M. (2010). Rowers' high: Behavioural synchrony is correlated with elevated pain thresholds. *Biology Letters*, 6(1), 106–108. <http://dx.doi.org/10.1098/rsbl.2009.0670>.

Cohen, E., Mundry, R., & Kirschner, S. (2013). Religion, synchrony, and cooperation. *Religion, Brain & Behavior*, 4(1), 20–30. <http://dx.doi.org/10.1080/2153599X.2012.741075>.

De Backer, C. J., Larson, C., Fisher, M. L., McAndrew, F. T., & Rudnicki, K. (2016). When Strangers Start to Gossip: Investigating the Effect of Gossip on Cooperation in a Prisoner's Dilemma Game. *Evolutionary Psychological Science*, 2(4), 268–277.

Dunbar, R. I. M., Baron, R., Frangou, A., Pearce, E., van Leeuwen, E. J. C., Stow, J., & van Vugt, M. (2012). Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1731), 1161–1167. <http://dx.doi.org/10.1098/rspb.2011.1373>.

Dunbar, R. I. M., Kaskatis, K., MacDonald, I., & Barra, V. (2012). Performance of music elevates pain threshold and positive affect: Implications for the evolutionary function of music. *Evolutionary Psychology*, 10(4), 688–702. <http://dx.doi.org/10.1177/147470491201000403>.

Durkheim, E. (1964). *The elementary forms of the religious life*. London: George Allen & Unwin LTD [1912/1964].

Fischer, R., Callander, R., Reddish, P., & Bulbulia, J. (2013). How do rituals affect cooperation? An experimental field study comparing nine ritual types. *Human Nature*, 24(2), 115–125. <http://dx.doi.org/10.1007/s12110-013-9167-y>.

Fischer, R., Xygalatas, D., Mitkidis, P., Reddish, P., Tok, P., Konvalinka, I., & Bulbulia, J. (2014). The fire-walker's high: Affect and physiological responses in an extreme collective ritual. *PLoS ONE*, 9(2), e88355. <http://dx.doi.org/10.1371/journal.pone.0088355>.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119(2), 593–609. <http://dx.doi.org/10.1093/brain/119.2.593>.

Gallese, V., Gernsbacher, M. A., Heyes, C., Hickok, G., & Iacoboni, M. (2011). Mirror neuron forum. *Perspectives on Psychological Science*, 6(4), 369–407. <http://dx.doi.org/10.1177/1745691611413392>.

Gallotti, M., & Frith, C. D. (2013). Social cognition in the we-mode. *Trends in Cognitive Sciences*, 17(4), <http://dx.doi.org/10.1016/j.tics.2013.02.002>.

Gintzler, A. R. (1980). Endorphin-mediated increases in pain threshold during pregnancy. *Science*, 210(4466), 193–195. <http://dx.doi.org/10.1126/science.7414330>.

Graves, F. C., Wallen, K., & Maestripieri, D. (2002). Opioids and attachment in rhesus macaque (*Macaca mulatta*) abusive mothers. *Behavioral Neuroscience*, 116(3), 489–493. <http://dx.doi.org/10.1037/0735-7044.116.3.489>.

Hagen, E. H., & Bryant, G. A. (2003). Music and dance as a coalition signaling system. *Human Nature*, 14(1), 21–51. <http://dx.doi.org/10.1007/s12110-003-1015-z>.

Hasson, U., & Frith, C. D. (2016). Mirroring and beyond: Coupled dynamics as a generalized framework for modelling social interactions. *Philosophical Transactions of the Royal Society B*, 371, 20150366. <http://dx.doi.org/10.1098/rstb.2015.0366>.

Hove, M., & Risen, J. L. (2009). It's all in the timing: Interpersonal synchrony increases affiliation. *Social Cognition*, 27(6), 949–960. <http://dx.doi.org/10.1521/soco.2009.27.6.949>.

Inagaki, T. K., Irwin, M. R., & Eisenberger, N. I. (2015). Blocking opioids attenuates physical warmth-induced feelings of social connection. *Emotion*, 15(4), 494–500. <http://dx.doi.org/10.1037/emo0000088>.

Ip, G. W., Chiu, C., & Wan, C. (2006). Birds of a feather and birds flocking together: Physical versus behavioral cues may lead to trait- versus goal-based group perception. *Journal of Personality and Social Psychology*, 90(3), 368–381. <http://dx.doi.org/10.1037/0022-3514.90.3.368>.

Johnson, K. V.-A., & Dunbar, R. I. M. (2016). Pain tolerance predicts human social network size. *Scientific Reports*, 6, 25267. <http://dx.doi.org/10.1038/srep25267>.

Kalin, N. H., Shelton, S. E., & Lynn, D. E. (1995). Opiate systems in mother and infant primates coordinate intimate contact during reunion. *Psychoneuroendocrinology*, 20(7), 735–742. [http://dx.doi.org/10.1016/0306-4530\(95\)00023-2](http://dx.doi.org/10.1016/0306-4530(95)00023-2).

Keller, P. E., Novembre, G., & Hove, M. J. (2014). Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 369, 20130394. <http://dx.doi.org/10.1098/rstb.2013.0394>.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). The mirror-neuron system: A Bayesian perspective. *Neuroreport*, 18(6), 619–623. <http://dx.doi.org/10.1097/WNR.0b013e3281139ed0>.

Kirschner, S., & Tomasello, M. (2010). Joint music making promotes prosocial behavior in 4-year-old children. *Evolution and Human Behavior*, 31(5), 354–364. <http://dx.doi.org/10.1016/j.evolhumbehav.2010.04.004>.

Knoblich, G., & Sebanz, N. (2006). The social nature of perception and action. *Current Directions in Psychological Science*, 15(3), 99–104.

Kokal, I., Engel, A., Kirschner, S., & Keysers, C. (2011). Synchronized drumming enhances activity in the caudate and facilitates prosocial commitment-if the rhythm comes easily. *PLoS One*, 6(11), e27272. <http://dx.doi.org/10.1371/journal.pone.0027272>.

Konvalinka, I., Xygalatas, D., Bulbulia, J., Schjoedt, U., Jegindø, E.-M., Wallot, S., & Roepstorff, A. (2011). Synchronized arousal between performers and related spectators in a fire-walking ritual. *PNAS*, 108(20), 8514–8519. <http://dx.doi.org/10.1073/pnas.1016955108/-/DCSupplemental>. www.pnas.org/cgi/doi/10.1073/pnas.1016955108.

- Kret, M. E., Fischer, A. H., & De Dreu, C. K. W. (2015). Pupil mimicry correlates with trust in in-group partners with dilating pupils. *Psychological Science*, 26(9), 1401–1410. <http://dx.doi.org/10.1177/0956797615588306>.
- Kurzban, R. (2001). The social psychophysics of cooperation: Nonverbal communication in a public good game. *Journal of Nonverbal Behavior*, 25(4), 241–259. <http://dx.doi.org/10.1023/A:1012563421824>.
- Lakens, D., & Stel, M. (2011). If they move in sync, they must feel in sync: Movement synchrony leads to attributions of rapport and entitativity. *Social Cognition*, 29(1), 1–14. <http://dx.doi.org/10.1521/soco.2011.29.1.1>.
- Lang, M., Shaw, D. J., Reddish, P., Wallot, S., Mitkidis, P., & Xygalatas, D. (2016). Lost in the rhythm: Effects of rhythm on subsequent interpersonal coordination. *Cognitive Science*, 40(7), 1797–1815. <http://dx.doi.org/10.1111/cogs.12302>.
- Launay, J., Dean, R., & Bailes, F. (2013). Synchronization can influence trust following virtual interaction. *Experimental Psychology*, 60(1), 53–63. <http://dx.doi.org/10.1027/1618-3169/a000173>.
- Launay, J., Dean, R., & Bailes, F. (2014). Synchronising movements with the sounds of a virtual partner enhances partner likeability. *Cognitive Processing*, 15, 491–501. <http://dx.doi.org/10.1007/s10339-014-0618-0>.
- Lenth, R. (2014). *lsmmeans: Least-squares means*. *R Package Version*, 2, 12.
- Loseth, G. E., Ellingsen, D.-M., & Leknes, S. (2014). State-dependent mu-opioid modulation of social motivation. *Frontiers in Behavioral Neuroscience*, 8, 1–15. <http://dx.doi.org/10.3389/fnbeh.2014.00430>.
- Lumsden, J., Miles, L. K., Richardson, M. J., Smith, C. A., & Macrae, C. N. (2012). Who syncs? Social motives and interpersonal coordination. *Journal of Experimental Social Psychology*, 48(3), 746–751. <http://dx.doi.org/10.1016/j.jesp.2011.12.007>.
- Machin, A. J., & Dunbar, R. I. M. (2011). The brain opioid theory of social attachment: A review of the evidence. *Behaviour*, 148(9), 985–1025. <http://dx.doi.org/10.1163/000579511X596624>.
- Manson, J. H., Bryant, G. A., Gervais, M. M., & Kline, M. A. (2013). Convergence of speech rate in conversation predicts cooperation. *Evolution and Human Behavior*, 34(6), 419–426. <http://dx.doi.org/10.1016/j.evolhumbehav.2013.08.001>.
- Marsh, K. L., Richardson, M. J., & Schmidt, R. C. (2009). Social connection through joint action and interpersonal coordination. *Topics in Cognitive Science*, 1(2), 320–339. <http://dx.doi.org/10.1111/j.1756-8765.2009.01022.x>.
- McNeill, W. H. (1995). *Keeping together in time: dance and drill in human history*. Cambridge, MA: Harvard University Press.
- Merker, B. H., Madison, G. S., & Eckerdal, P. (2009). On the role and origin of isochrony in human rhythmic entrainment. *Cortex*, 45(1), 4–17. <http://dx.doi.org/10.1016/j.cortex.2008.06.011>.
- Miles, L. K., Nind, L. K., & Macrae, C. N. (2009). The rhythm of rapport: Interpersonal synchrony and social perception. *Journal of Experimental Social Psychology*, 45(3), 585–589. <http://dx.doi.org/10.1016/j.jesp.2009.02.002>.
- Mogan, R., Fischer, R., & Bulbulia, J. A. (2017). To be in synchrony or not? A meta-analysis of synchrony's effects on behavior, perception, cognition and affect. *Journal of Experimental Social Psychology*, 72, 13–20. <http://dx.doi.org/10.1016/j.jesp.2017.03.009>.
- Moles, A., Kieffer, B. L., & D'Amato, F. R. (2004). Deficit in attachment behavior in mice lacking the μ -opioid receptor gene. *Science*, 304(5679), 1983–1986. <http://dx.doi.org/10.1126/science.1095943>.
- Mueller, C., Klega, A., Buchholz, H. G., Rolke, R., Magerl, W., Schirmacher, R., & Schreckenberger, M. (2010). Basal opioid receptor binding is associated with differences in sensory perception in healthy human subjects: A [18F]diprenorphine PET study. *Neuroimage*, 49(1), 731–737. <http://dx.doi.org/10.1016/j.neuroimage.2009.08.033>.
- Nave, G., Camerer, C., & McCullough, M. (2015). Does oxytocin increase trust in humans? A critical review of research. *Perspectives on Psychological Science*, 10(6), 772–789. <http://dx.doi.org/10.1177/1745691615600138>.
- Nummenmaa, L., Manninen, S., Tuominen, L., Hirvonen, J., Kalliokoski, K. K., Nuutila, P., & Sams, M. (2015). Adult attachment style is associated with cerebral μ -opioid receptor availability in humans. *Human Brain Mapping*, 36(9), 3621–3628. <http://dx.doi.org/10.1002/hbm.22866>.
- Obhi, S. S., & Sebanz, N. (2011). Moving together: Toward understanding the mechanisms of joint action. *Experimental Brain Research*, 211(3–4), 329–336. <http://dx.doi.org/10.1007/s00221-011-2721-0>.
- Overy, K., & Molnar-Szakacs, I. (2009). Being together in time: Musical experience and the mirror neuron system. *Music Perception*, 26(5), 489–504. <http://dx.doi.org/10.1525/MP.2009.26.5.489>.
- Paladino, M. P., Mazzurega, M., Pavani, F., & Schubert, T. W. (2010). Synchronous multisensory stimulation blurs self-other boundaries. *Psychological Science*, 21(9), 1202–1207. <http://dx.doi.org/10.1177/0956797610379234>.
- Panksepp, J., Nelson, E., & Siviy, S. (1994). Brain opioids and mother-infant social motivation. *Acta Paediatrica*, 83(4), 40–46. <http://dx.doi.org/10.1111/j.1651-2227.1994.tb13264.x>.
- Pearce, E., Wlodarski, R., Machin, A., & Dunbar, R. I. M. (2017). Variation in the β -endorphin, oxytocin, and dopamine receptor genes is associated with different dimensions of human sociality. *Proceedings of the National Academy of Sciences*, 114(20), 201700712. <http://dx.doi.org/10.1073/pnas.1700712114>.
- Petrovic, P., Kalso, E., Petersson, K., & Ingvar, M. (2002). Placebo and opioid analgesia—imaging a shared neuronal network. *Science*, 295(5560), 1737–1740. <http://dx.doi.org/10.1126/science.1067176>.
- Pezzulo, G., & Dindo, H. (2011). What should I do next? Using shared representations to solve interaction problems. *Experimental Brain Research*, 211(3–4), 613–630. <http://dx.doi.org/10.1007/s00221-011-2712-1>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2014). nlme: linear and nonlinear mixed effects models. *R Package Version*, 3, 1–117.
- R Core Team (2016). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Reddish, P., Fischer, R., & Bulbulia, J. (2013). Let's dance together: Synchrony, shared intentionality and cooperation. *PLoS One*, 8(8), e71182. <http://dx.doi.org/10.1371/journal.pone.0071182>.
- Reddish, P., Bulbulia, J., & Fischer, R. (2014). Does synchrony promote generalized prosociality? *Religion, Brain & Behavior*, 4(1), 3–19. <http://dx.doi.org/10.1080/2153599X.2013.764545>.
- Reddish, P., Tong, E. M. W., Jong, J., Lanman, J. A., & Whitehouse, H. (2016). Collective synchrony increases prosociality towards non-performers and outgroup members. *British Journal of Social Psychology*, 55(4), 722–738. <http://dx.doi.org/10.1111/bjso.12165>.
- Rosseel, Y. (2012). lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software*, 48(2), 1–36.
- Sebanz, N., & Knoblich, G. (2009). Prediction in joint action: what, when, and where. *Topics in Cognitive Science*, 1(2), 353–367. <http://dx.doi.org/10.1111/j.1756-8765.2009.01024.x>.
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: bodies and minds moving together. *Trends in Cognitive Sciences*, 10(2), 70–76. <http://dx.doi.org/10.1016/j.tics.2005.12.009>.
- Shaw, D. J., Czékóvá, K., Chromec, J., Mareček, R., & Brázdil, M. (2013). Copying you copying me: Interpersonal motor co-ordination influences automatic imitation. *PLoS One*, 8(12), e84820. <http://dx.doi.org/10.1371/journal.pone.0084820>.
- Stanley, D. A., Sokol-Hessner, P., Banaji, M. R., & Phelps, E. A. (2011). Implicit race attitudes predict trustworthiness judgments and economic trust decisions. *Proceedings of the National Academy of Sciences of the United States of America*, 108(19), 7710–7715. <http://dx.doi.org/10.1073/pnas.1014345108>.
- Stasinopoulos, D., & Rigby, R. (2007). Generalized additive models for location scale and shape (GAMLSS) in R. *Journal of Statistical Software*, 23(7), 1–46.
- Sullivan, P., Rickers, K., & Gammage, K. (2014). The effect of different phases of synchrony on pain threshold. *Group Dynamics: Theory, Research, and Practice*, 18(2), 122–128. <http://dx.doi.org/10.1037/gdn0000001>.
- Tarr, B., Launay, J., & Dunbar, R. I. M. (2014). Music and social bonding: Self-other merging and neurohormonal mechanisms. *Frontiers in Psychology*, 5, 1–10. <http://dx.doi.org/10.3389/fpsyg.2014.01096>.
- Tarr, B., Launay, J., Cohen, E., & Dunbar, R. I. M. (2015). Synchrony and exertion during dance independently raise pain threshold and encourage social bonding. *Biology Letters*, 11, 20150767. <http://dx.doi.org/10.1098/rsbl.2015.0767>.
- Tarr, B., Launay, J., & Dunbar, R. I. M. (2016). Silent disco: Dancing in synchrony leads to elevated pain thresholds and social closeness. *Evolution and Human Behavior*. <http://dx.doi.org/10.1016/j.evolhumbehav.2016.02.004>.
- Valdesolo, P., & Desteno, D. (2011). Synchrony and the social tuning of compassion. *Emotion*, 11(2), 262–266. <http://dx.doi.org/10.1037/a0021302>.
- Weinstein, D., Launay, J., Pearce, E., Dunbar, R. I. M., & Stewart, L. (2015). Singing and social bonding: Changes in connectivity and pain threshold as a function of group size. *Evolution and Human Behavior*, 37(2), 152–158. <http://dx.doi.org/10.1016/j.evolhumbehav.2015.10.002>.
- Wiech, K., Ploner, M., & Tracey, I. (2008). Neurocognitive aspects of pain perception. *Trends in Cognitive Sciences*, 12(8), 306–313. <http://dx.doi.org/10.1016/j.tics.2008.05.005>.
- Wiltermuth, S. S., & Heath, C. (2009). Synchrony and cooperation. *Psychological Science*, 20(1), 1–5. <http://dx.doi.org/10.1111/j.1467-9280.2008.02253.x>.
- Wolf, B., Launay, J., & Dunbar, R. I. M. (2016). Joint attention, shared goals, and social bonding. *British Journal of Psychology*, 197, 322–337. <http://dx.doi.org/10.1111/bjop.12144>.
- Xygalatas, D., Mitkidis, P., Fischer, R., Reddish, P., Skewes, J., Geertz, A. W., & Bulbulia, J. (2013). Extreme rituals promote prosociality. *Psychological Science*, 24(8), 1602–1605. <http://dx.doi.org/10.1177/0956797612472910>.
- Zak, P. J., Kurzban, R., & Matzner, W. T. (2005). Oxytocin is associated with human trustworthiness. *Hormones and Behavior*, 48(5), 522–527. <http://dx.doi.org/10.1016/j.jybeh.2005.07.009>.
- Zubieta, J.-K., Smith, Y., Bueller, J., Xu, Y., Kilbourn, M., Jewett, D., & Stohler, C. (2001). Regional mu opioid receptor regulation of sensory and affective dimensions of pain. *Science*, 293(5528), 311–315. <http://dx.doi.org/10.1126/science.1060952>.