

Sharing the social world via intersubject neural synchronisation

Lauri Nummenmaa^{1,2}, Juha M Lahnakoski³ and Enrico Glerean^{1,4}

Sociability and capability of shared mental states are hallmarks of the human species, and pursuing shared goals oftentimes requires coordinating both behaviour and mental states. Here we review recent work using indices of intersubject neural synchronisation for measuring similarity of mental states across individuals. We discuss the methodological advances and limitations in the analyses based on intersubject synchrony, and discuss how these kinds of model-free analysis techniques enable the investigation of the brain basis of complex social processes. We argue that similarity of brain activity across individuals can be used, under certain conditions, to index the similarity of their subjective states of consciousness, and thus be used for investigating brain basis of mutual understanding and cooperation.

Addresses

¹ Turku PET Centre, University of Turku, 20520 Turku, Finland

² Department of Psychology, University of Turku, Finland

³ Independent Max Planck Research Group for Social Neuroscience, Max Planck Institute of Psychiatry, 80804 Munich, Germany

⁴ Department of Neuroscience and Biomedical Engineering, Aalto University, Finland

Corresponding author: Nummenmaa, Lauri (lauri.nummenmaa@utu.fi)

Current Opinion in Psychology 2018, 24:7–14

This review comes from a themed issue on **Social neuroscience**

Edited by **David Amodio** and **Christian Keysers**

<https://doi.org/10.1016/j.copsyc.2018.02.021>

2352-250/© 2018 Elsevier Ltd. All rights reserved.

Introduction

Sociability and ability to pursue shared goals are defining features of our species [1]. This oftentimes requires coordinated behaviour among individuals. Spontaneous synchronisation is ubiquitous in humans, ranging from postural and facial mimicry to walking in pace and synchronised clapping after a performance. We also have a keen eye for spotting lack of synchrony: We notice immediately when the bass player is off beat, or when our conversation partner fails to ‘tune in’ with us at the verbal and nonverbal levels. Such interpersonal attunement occurs at multiple levels ranging from behaviour to central nervous system, and may serve various purposes ranging from simple preparation of others’ actions to in-depth understanding of their intentions.

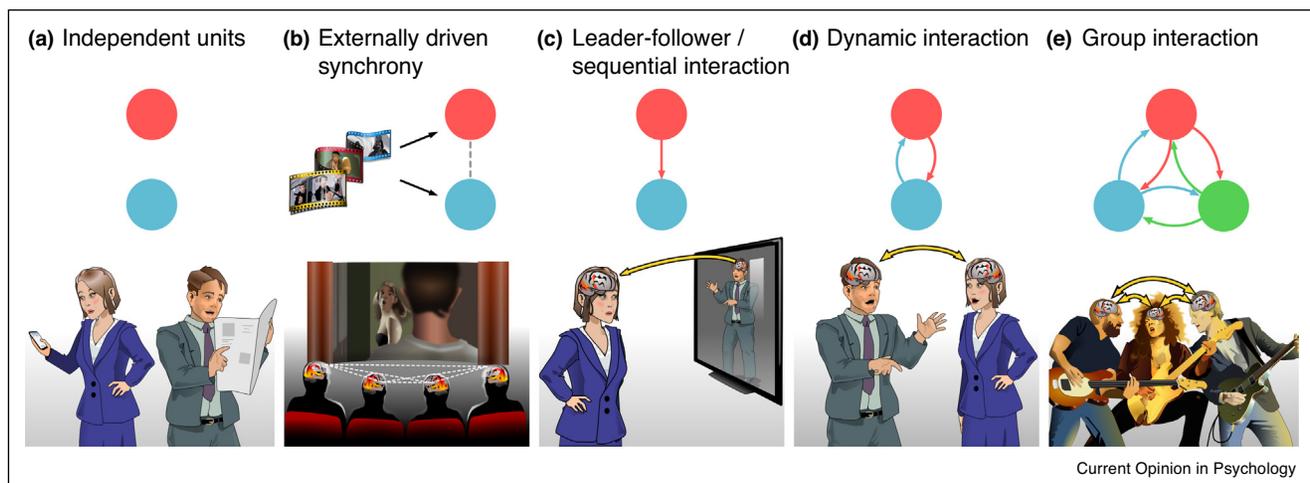
In physical terms, synchronisation is defined as time-locking of periodic, independent oscillators. In social interaction the ‘oscillators’ lack a direct physical coupling mechanisms, so the attunement of the psychological and neural processes across individuals is contingent on sensory and motor loops where sensory information regarding someone’s actions (or some other external source) is remapped to motor format in the observers’ brain, and used for generating motor responses that the interlocutor’s brain can then in turn use as output [2]. Five mechanisms for interindividual synchrony can be conceptualised (Figure 1). First, individuals may be fully independent and lack any means for attunement. Second, their actions and neural activations may be synchronised by an external source such as seeing similar events in the environment. Third, one ‘leader’ individual can provide unidirectional source of synchronisation, or fourth and fifth, two or more people can mutually influence each other in a dynamic fashion. Recently, methodological and theoretical developments have enabled researchers to tap into how the neural activity underlying such social interactions becomes synchronised across dyads and groups of individuals. Here we provide an overview of recent work of the neural, cognitive and social mechanisms supporting synchronisation of brain activation and behaviour across individuals, with special focus on methodological aspects in MR neuroimaging.

Stimulus-driven synchronisation of brain activity

The human brain processes vast amounts of complex social information all the time, posing major challenges for investigating neural processing of isolated sensory features by reducing them to stimulus models. Pioneering functional magnetic resonance imaging (fMRI) work developed the technique known as *intersubject correlation* (ISC) analysis, where voxelwise temporal correlation of BOLD-fMRI time series is computed across every pair of subjects and then averaged [3,4]. Each subjects’ response contains an intrinsic component, related to internal processes not time locked with the stimulus, and an extrinsic component that depends on the external source. With ISC, the intrinsic components are usually disregarded as essentially noise that cancel out in the averaging, leaving the extrinsic, stimulus-driven component to estimate the degree of similarity and robustness in voxelwise time courses across subjects (Figure 2a).

This type of analyses have revealed that human observers’ brain activity becomes time-locked in time scale of a few seconds in regionally specific manner during natural vision and hearing as measured by fMRI [3–5],

Figure 1



Different types of conceptual synchronies. **(a)** Independent units acting in parallel with no coupling. **(b)** Two units with no connection becoming synchronised due to a shared external signal **(c)** Unidirectional synchronisation from a leader to a follower. **(d)** Dynamic interaction where leader and follower have mutual influence on each other. **(e)** Group interaction with multiple mutually interconnected and co-dependent individuals.

and ECoG [6], and also with faster time scales in M/EEG [7,8]. Even though direct voxelwise correlations between fMRI and MEG signals during movie viewing are discordant, spatially filtered MEG data and particularly time course envelopes below 11 Hz show good correspondence with BOLD-fMRI signal. This reveals that slow evoked responses during natural stimulation can be measured concordantly with MEG and fMRI [9].

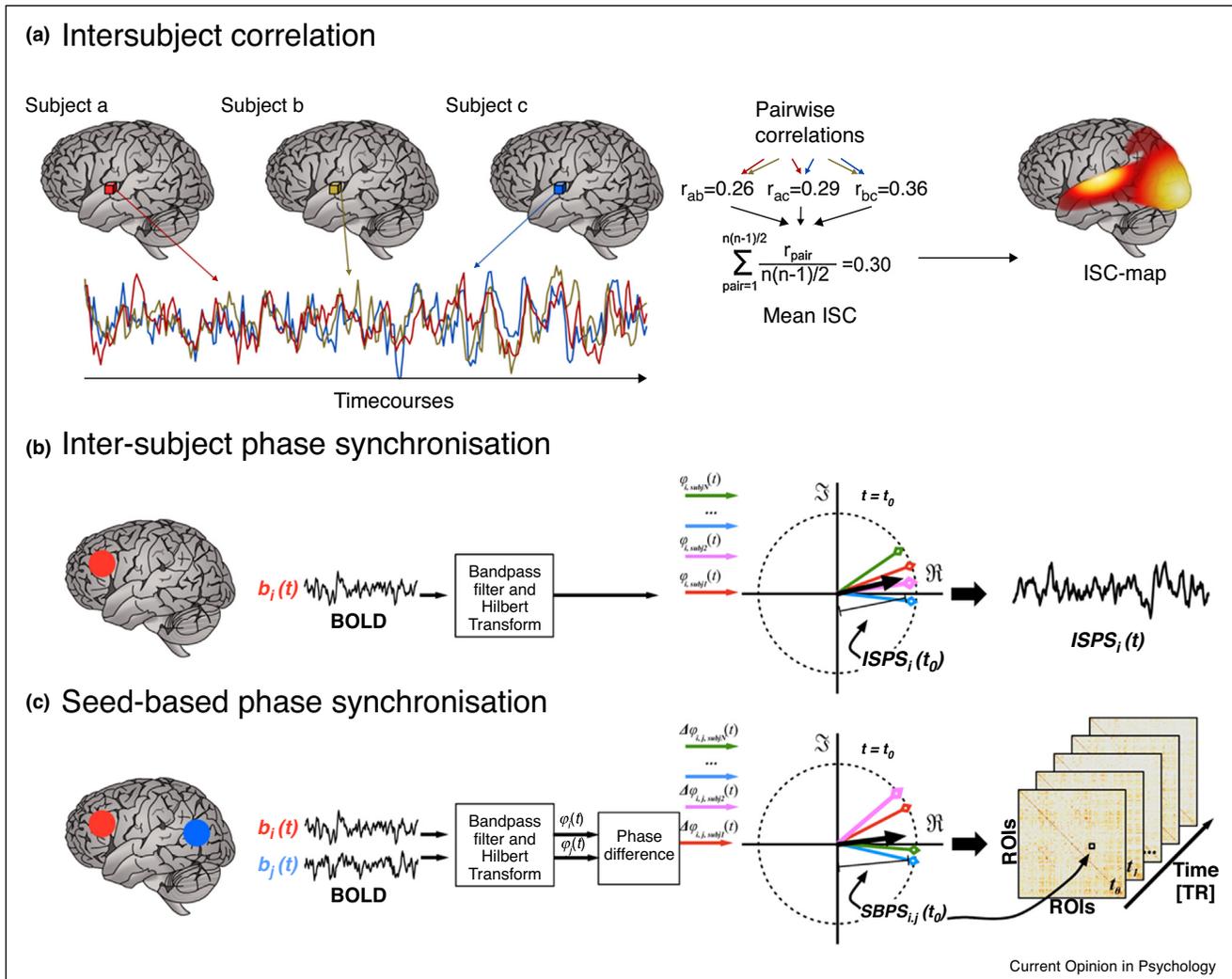
The ISC approach provides a model-free way for quantifying brain responses during dynamic, natural scene perception, and thus requires no a priori stimulation model to be defined. Such *data-driven analyses* are efficient for tackling research questions such as social perception where the stimulus space is too high-dimensional for generating complete set of a priori hypotheses for the appropriate feature model [10]. Yet, ISC analysis can also retrieve the activation patterns triggered by underlying stimulus model such as sensory responses in a conventional boxcar design [11]; for example, reverse correlating the activity timecourses in high-ISC areas of the lateral fusiform ‘face’ and parahippocampal ‘place’ cortices revealed peaks whenever faces and natural scenes were shown in a movie, respectively [3].

As a data driven method, ISC can show extensive areas of brain being synchronised across individuals with little specificity to particular cognitive functions. By introducing the temporal dimension, approaches using *sliding window ISC* (mean ISC for a temporal window of a few volumes) or instantaneous phase synchronisation [ISPS; 12] produce voxelwise indices of moment-to-moment synchrony [13]. These can subsequently be regressed

against stimulus models (e.g. emotional valence), providing an intermediate approach between stimulus-dependent and stimulus-free analyses with significantly relaxed constraints on the shape, local amplitudes, timescales and stationarity of the responses (Figure 2b). ISPS yields concordant results with ISC [12] yet it has a significant sensitivity advantage over ISC, and can reveal synchronisation effects going unnoticed in ISC analysis [14]: Because intersubject similarity is measured in phase rather than in statistical terms, ISPS has the maximal theoretical temporal resolution as no sliding-window averaging is needed. Critically, the ISPS approach also provides a time series phase-based connectivity measures between every voxel pair in the brain (Figure 2c). Thus, when participants are attending to a dynamic prolonged stimulus such as a movie or an audiobook, regressing ISPS time series with stimulus feature model provides a powerful approach for measuring stimulus-dependent dynamic connectivity changes [14,15].

ISC analysis can also be applied to model-free analysis of behavioural time series. As model-based analysis of eye tracking data during natural vision is oftentimes difficult [16], stimulus-free analysis of eye movements can be modelled as moment-to-moment ISC of fixation heat maps eye-ISC [14]. Human observers’ eye movements become tightly coupled during natural, task-free vision [14]. Furthermore, humans and macaque monkeys show correlated gaze patterns during natural stimulus viewing, with inter-species saliency caused by species-specific biologically relevant events [17], suggesting convergent and divergent visual sampling strategies across species. Indeed, eye-ISC is larger for humans focusing on social

Figure 2



Methods for quantifying intersubject synchronisation of brain activity. **(a)** Intersubject correlation (ISC). Voxelwise time courses are correlated across all subjects, and averaged voxelwise correlations are stored in an ISC map which is subjected to statistical thresholding. **(b)** Instantaneous inter-subject phase synchronisation. After bandpass filtering and Hilbert transform, mean voxelwise phase-based similarities are computed across subjects and stored into ISPS map. **(c)** Seed-based phase synchronisation can be computed between individual voxels or regions of interest (ROIs) by estimating mean moment-to-moment phase differences.

versus non-social features of exactly the same stimulus, highlighting the role of goal-related factors in eye movement control [18].

Measuring shared contents of consciousness

Despite living in a shared world and engaging in joint actions with others on a daily basis, the contents of our consciousness remain private and only accessible via inferences on others' actions and verbalisations. Could the ISC also index mutual information held in the subjective awareness? Strongest ISCs are generally observed in the sensory cortices as their activity is time-locked with the physical features of the stimulus. Yet, while viewing a film with coherent narrative, also parietal, temporal and frontal cortices show consistent response time courses

across individuals [19,20]. Intersubject response reliability in temporal, parietal and frontal (but not in sensory) cortices is, however, abolished when the temporal coherence of the narrative is broken by shuffling the order of the scenes in the movie thus disrupting the narrative. This suggests that there exist a hierarchy of temporal receptive windows in the brain that accumulate information across different time scales yet consistently across individuals [19]. Direct evidence for this synchrony-asimilarity of information processing comes from studies showing that ISC in higher-order association cortices is significantly dampened when the subjects cannot understand the language they listen to. On the other hand, when the linguistic form is altered by translation to a language the participants understand, ISC is minimally

to impaired social skills. All in all, the more aligned two individuals are at the psychological level, the more similar their brain activation time courses are, in task-specific manner. Due to this, model-free ISC analysis techniques have also provided a window to the minds of locked-in patients, showing that some of them could also maintain similar conscious experiences as healthy subjects [33**].

Face to face

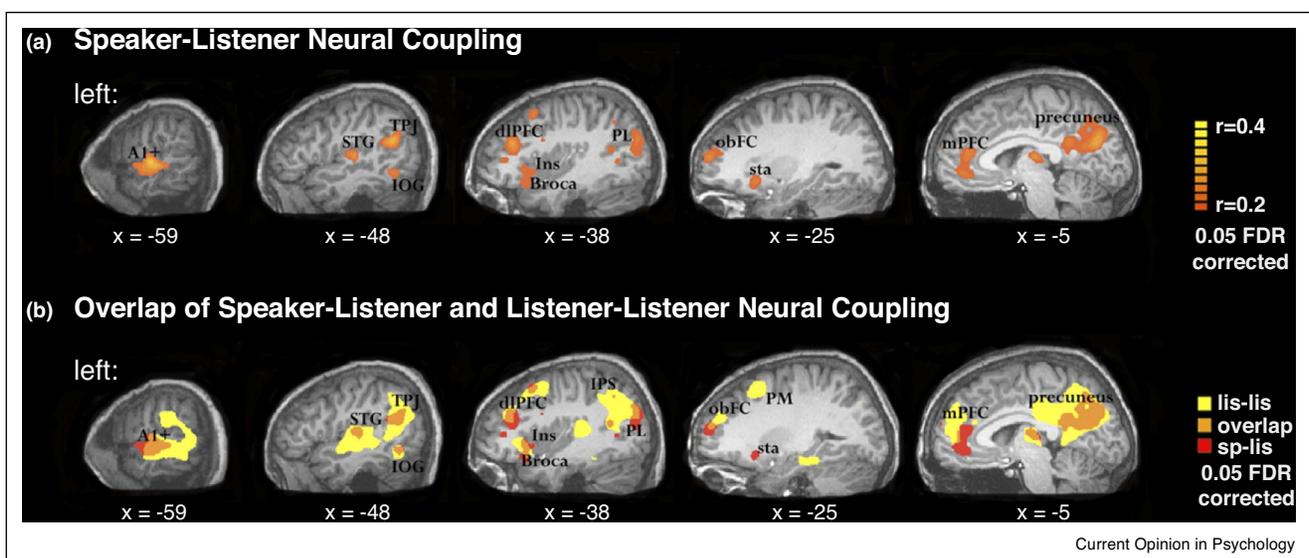
Other humans constitute of our most important environment, and brain activity in humans and nonhuman primates is markedly altered by the mere presence of conspecifics [34,35]. Nevertheless, the majority of social neuroscience is conducted with ‘spectator’ paradigms with artificial stimuli and limited subject influence over the social situation modelled in the experiment. Yet, most social processes occur in dyads, where information *flows* from one brain to another. Brain basis of social interaction thus consists of reciprocal interaction between two or more brains trying to understand and influence each other (Figure 1d,e). Individuals may thus not just operate in parallel, but their minds may get intertwined into a shared system facilitating reciprocation [36]. To account for this, experimental methods have been developed for scanning two people simultaneously, for example, in one MRI scanner [37] or connecting two scanners or MEG devices with a videolink for ‘hyperscanning’ two interacting people [38,39].

To balance the technical complexity and potential conceptual difficulties in real-time two-person recording, so-called ‘pseudo-hyperscanning’ techniques have also been introduced as an intermediate solution for studying information

flow from brain to brain. Briefly, brain activity is first recorded from a ‘sender’ subject who generates the experimental stimuli by, for example, gesturing or speaking during the scan. The recorded speech and actions can then be used as stimuli for ‘observer’ subjects, enabling alignment of the neural time courses associated with sending and receiving social information. This kind of experiments have shown that speakers’ and listeners’ brain activation becomes synchronised in regionally selective manner with the activity in some parts of the listener’s brain even preceding that of the speaker’s by a few seconds (Figure 4). Moreover, the degree of this ‘predictive’ synchronisation predicted successful comprehension of a verbal message [40]. Similarly, communication by hand gestures [41] and facial expressions [42] enhances neural synchronisation between the communicating persons in a spatially selective manner. Such synchrony also codes specific shared information across the individuals transmitting and receiving the information, allowing pattern recognition based ‘mind reading’. A pattern classifier trained to recognise different hand actions made by one subject can successfully classify these actions from brain activity of another individual seeing the same actions. This is however possible only after the actors and observers brains have been functionally realigned based on their activation time courses [43] to account for discrepancies in mesoscopic functional organisation of the cortex across individuals [44].

The most advanced study of this kind to date demonstrated that, after matching the temporal order and duration of the events, brain activity recorded during recall of events in a TV show, matched that recorded while

Figure 4



Intersubject synchronisation (ISC) of brain activity as index of mutual brain states. (a) Brain regions whose activity becomes synchronised across speakers and listeners and (b) overlap between regions synchronised across speaker–listener and listener–listener pairs.

Source: Modified with permission from author and copyright holder from Ref. [40].

viewing the show or listening to someone else recalling the events [45**]. Specifically, activity patterns in small ‘searchlight’ spheres across the brain were more similar between people recalling the same events than between recall and perception (even though the latter was also significant), suggesting that event information is transformed in a similar way across individuals during memory encoding. Recently, intersubject synchrony of brain activity has also been extended to studying larger groups at the same time through portable EEG devices. While focus so far has been on externally driven synchrony (Figure 1b) in a group setting, these studies show promise for future investigation of group dynamics (Figure 1e) by showing that activity patterns demonstrated in the laboratory replicate ‘in the wild’ [46] and inter-subject similarity may predict social closeness of individuals [47*].

Conclusions: synchrony for imitation, bonding, and beyond

Synchronisation of brain activity across individuals reflects not only concordant time scales of sensory processes, but also index similarity of the contents of consciousness across individuals. At the most rudimentary level, constant remapping or ‘mirroring’ of seen or heard motor actions to a somatomotor format enables preparation of corresponding actions in the observer [2], thus serving an elementary function of social predictive coding and learning. However, such intersubject synchronisation might also promote shared understanding of the environment: Because mutual understanding requires that perception and action are sufficiently similar between participants, getting ‘in sync’ with others could generate a perceptual and somatomotor framework for promoting mutual understanding. Interestingly, neural responses to audiovisual movies are increasingly similar in individuals who are closer to each other in real-life social networks, highlighting that homophily in social relations is also reflected in neuronal activity: Humans are strikingly similar with their friends in the way they respond to their shared environment [48] - when it comes to friendship and similarity, more is more.

Interpersonal synchrony is also *causally* linked with social bonding. For example, non-conscious mimicry of others’ postures and gestures creates affiliation, rapport, and liking [49,50]. Behavioural, psychological, and neural synchronisation across individuals also promotes establishment of social bonds [51,52*], potentially due to concomitant analgesic and calming release of endogenous opioid peptides [53–55] serving as a safety signal. Such endogenous opioid release during synchronous group-based activities such as team sports [56], synchronised dancing [51,57], and social, contagious laughter [58**] might explain why we enjoy various team-based activities ranging from sports to playing in a band. We conclude that being in sync with others may be one of the most rudimentary signs of social affiliation and prosociality, explaining why we might be

so motivated to understand others’ minds and getting in tune with them in the first place.

Conflict of interest statement

Nothing declared.

Acknowledgments

This research was supported by the Academy of Finland (grant #294897 to LN), ERC Starting grant #313000 to LN and Finnish Cultural Foundation (grant #150496 to JML). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Dunbar RIM: **Bridging the bonding gap: the transition from primates to humans.** *Philos Trans R Soc B-Biol Sci* 2012, **367**:1837-1846.
 2. Hari R, Kujala MV: **Brain basis of human social interaction: from concepts to brain imaging.** *Physiol Rev* 2009, **89**:453-479.
 3. Hasson U, Nir Y, Levy I, Fuhrmann G, Malach R: **Intersubject synchronization of cortical activity during natural vision.** *Science* 2004, **303**:1634-1640.
 4. Bartels A, Zeki S: **The chronoarchitecture of the human brain – natural viewing conditions reveal a time-based anatomy of the brain.** *NeuroImage* 2004, **22**:419-433.
 5. Wilson SM, Molnar-Szakacs I, Iacoboni M: **Beyond superior temporal cortex: intersubject correlations in narrative speech comprehension.** *Cerebral Cortex* 2008, **18**:230-242.
 6. Honey Christopher J, Thesen T, Donner Tobias H, Silbert Lauren J, Carlson Chad E, Devinsky O, Doyle Werner K, Rubin N, Heeger David J, Hasson U: **Slow cortical dynamics and the accumulation of information over long timescales.** *Neuron* 2012, **76**:423-434.
 7. Lankinen K, Saari J, Hari R, Koskinen M: **Intersubject consistency of cortical MEG signals during movie viewing.** *NeuroImage* 2014, **92**:217-224.
 8. Chang W-T, Jääskeläinen IP, Belliveau JW, Huang S, Hung A-Y, Rossi S, Ahveninen J: **Combined MEG and EEG show reliable patterns of electromagnetic brain activity during natural viewing.** *NeuroImage* 2015, **114**:49-56.
 9. Lankinen K, Saari J, Hlushchuk Y, Tikka P, Parkkonen L, Hari R, Koskinen M: **Consistency and similarity of MEG- and fMRI-signal time courses during movie viewing.** *NeuroImage* 2018, **173**:361-369.
 10. Adolphs R, Nummenmaa L, Todorov A, Haxby JV: **Data-driven approaches in the investigation of social perception.** *Philos Trans R Soc B: Biol Sci* 2016:371.
 11. Kauppi J-P, Pajula J, Niemi J, Hari R, Tohka J: **Functional brain segmentation using inter-subject correlation in fMRI.** *Human Brain Mapp* 2017, **38**:2643-2665.
 12. Glerean E, Salmi J, Lahnakoski JM, Jaaskelainen IP, Sams M: **Functional magnetic resonance imaging phase synchronization as a measure of dynamic functional connectivity.** *Brain Connect* 2012, **2**:91-101.
 13. Nummenmaa L, Glerean E, Viinikainen M, Jaaskelainen IP, Hari R, Sams M: **Emotions promote social interaction by synchronizing brain activity across individuals.** *Proc Natl Acad Sci U S A* 2012, **109**:9599-9604.
 14. Nummenmaa L, Smirnov D, Lahnakoski JM, Glerean E, Jaaskelainen IP, Sams M, Hari R: **Mental action simulation**

- synchronizes action-observation circuits across individuals.** *J Neurosci* 2014, **34**:748-757.
15. Nummenmaa L, Saarimäki H, Glerean E, Gotsopoulos A, Jääskeläinen IP, Hari R, Sams M: **Emotional speech synchronizes brains across listeners and engages large-scale dynamic brain networks.** *NeuroImage* 2014, **102(Part 2)**:498-509.
 16. Hayhoe M, Ballard D: **Eye movements in natural behavior.** *Trends Cogn Sci* 2005, **9**:188-194.
 17. Shepherd SV, Steckenfinger SA, Hasson U, Ghazanfar AA: **Human-monkey gaze correlations reveal convergent and divergent patterns of movie viewing.** *Curr Biol* 2010, **20**:649-656.
 18. Lahnakoski JM, Glerean E, Jääskeläinen IP, Hyönä J, Hari R, Sams M, Nummenmaa L: **Synchronous brain activity across individuals underlies shared psychological perspectives.** *NeuroImage* 2014, **100**:316-324.
 19. Jääskeläinen IP, Koskentalo K, Balk MH, Autti T, Kauramäki J, Pomren C, Sams M: **Inter-subject synchronization of prefrontal cortex hemodynamic activity during natural viewing.** *Open Neuroimag J* 2008, **2**:14-19.
 20. Hasson U, Yang E, Vallines I, Heeger DJ, Rubin N: **A hierarchy of temporal receptive windows in human cortex.** *J Neurosci* 2008, **28**:2539-2550.
 21. Honey CJ, Thompson CR, Lerner Y, Hasson U: **Not lost in translation: neural responses shared across languages.** *J Neurosci* 2012, **32**:15277-15283.
 22. Ames DL, Honey CJ, Chow MA, Todorov A, Hasson U: **Contextual alignment of cognitive and neural dynamics.** *J Cogn Neurosci* 2015, **27**:655-664.
 23. Smirnov D, Glerean E, Lahnakoski JM, Salmi J, Jaaskelainen IP, Sams M, Nummenmaa L: **Fronto-parietal network supports context-dependent speech comprehension.** *Neuropsychologia* 2014, **63**:293-303.
 24. Lahnakoski JM, Jaaskelainen IP, Sams M, Nummenmaa L: **Neural mechanisms for integrating consecutive and interleaved natural events.** *Human Brain Mapp* 2017, **38**:3360-3376.
 25. Bransford JD, Johnson MK: **Contextual prerequisites for understanding — some investigations of comprehension and recall.** *J Verbal Learn Verbal Behav* 1972, **11**:717-726.
 26. Nummenmaa L, Saarimäki H, Glerean E, Gotsopoulos A, Jaaskelainen IP, Hari R, Sams M: **Emotional speech synchronizes brains across listeners and engages large-scale dynamic brain networks.** *NeuroImage* 2014, **102**:498-509.
 27. Saarimäki H, Gotsopoulos A, Jääskeläinen IP, Lampinen J, Vuilleumier P, Hari R, Sams M, Nummenmaa L: **Discrete neural signatures of basic emotions.** *Cereb Cortex* 2016, **6**:2563-2573.
 28. Schmalzle R, Hacker FEK, Honey CJ, Hasson U: **Engaged listeners: shared neural processing of powerful political speeches.** *Soc Cogn Affect Neurosci* 2015, **10**:1137-1143.
 29. Hasson U, Avidan G, Gelbard H, Vallines I, Harel M, Minshew N, Behrmann M: **Shared and idiosyncratic cortical activation patterns in autism revealed under continuous real-life viewing conditions.** *Autism Res* 2009, **2**:220-231.
 30. Salmi J, Roine U, Glerean E, Lahnakoski J, Nieminen-von Wendt T, Tani P, Leppämäki S, Nummenmaa L, Jääskeläinen IP, Carlson S *et al.*: **The brains of high functioning autistic individuals do not synchronize with those of others.** *NeuroImage Clin* 2013, **3**:489-497.
 31. Hahamy A, Behrmann M, Malach R: **The idiosyncratic brain: distortion of spontaneous connectivity patterns in autism spectrum disorder.** *Nat Neurosci* 2015, **18**:302.
 32. Glerean E, Pan RK, Salmi J, Kujala R, Lahnakoski JM, Roine U, Nummenmaa L, Leppämäki S, Nieminen-von Wendt T, Tani P *et al.*: **Reorganization of functionally connected brain subnetworks in high-functioning autism.** *Hum Brain Mapp* 2016, **37**:1066-1079.
 33. Naci L, Cusack R, Anello M, Owen AM: **A common neural code for similar conscious experiences in different individuals.** *Proc Natl Acad Sci* 2014, **111**:14277-14282.
- An fMRI study using model-free analysis (intersubject correlation) of brain activation during natural audiovisual perception shows that certain locked-in patients likely have similar conscious states as healthy individuals.
34. Monfardini E, Redoute J, Hadj-Bouziane F, Hynaux C, Fradin J, Huguet P, Costes N, Meunier M: **Others' sheer presence boosts brain activity in the attention (but not the motivation) network.** *Cereb Cortex* 2016, **26**:2427-2439.
 35. Pönkänen LM, Alhoniemi A, Leppänen JM, Hietanen JK: **Does it make a difference if I have an eye contact with you or with your picture? An ERP study.** *Soc Cogn Affect Neurosci* 2011, **6**:486-494.
 36. Hasson U, Ghazanfar AA, Galantucci B, Garrod S, Keysers C: **Brain-to-brain coupling: a mechanism for creating and sharing a social world.** *Trends Cogn Sci* 2012, **16**:114-121.
 37. Lee RF, Dai W, Jones J: **Decoupled circular-polarized dual-head volume coil pair for studying two interacting human brains with dyadic fMRI.** *Magn Reson Med* 2012, **68**:1087-1096.
 38. Montague PR, Berns GS, Cohen JD, McClure SM, Pagnoni G, Dhamala M, Wiest MC, Karpov I, King RD, Apple N *et al.*: **Hyperscanning: simultaneous fMRI during linked social interactions.** *NeuroImage* 2002, **16**:1159-1164.
 39. Baess P, Zhdanov A, Mandel A, Parkkonen L, Hirvenkari L, Makela JP, Jousmaki V, Hari R: **MEG dual scanning: a procedure to study real-time auditory interaction between two persons.** *Frontiers Hum Neurosci* 2012, **6**:7.
 40. Stephens GJ, Silbert LJ, Hasson U: **Speaker-listener neural coupling underlies successful communication.** *Proc Natl Acad Sci U S A* 2010, **107**:14425-14430.
 41. Schippers MB, Roebroek A, Renken R, Nanetti L, Keysers C: **Mapping the information flow from one brain to another during gestural communication.** *Proc Natl Acad Sci U S A* 2010, **107**:9388-9393.
 42. Anders S, Heinzle J, Weiskopf N, Ethofer T, Haynes J-D: **Flow of affective information between communicating brains.** *NeuroImage* 2011, **54**:439-446.
 43. Haxby JV, Guntupalli JS, Connolly AC, Halchenko YO, Conroy BR, Gobbini MI, Hanke M, Ramadge PJ: **A common, high-dimensional model of the representational space in human ventral temporal cortex.** *Neuron* 2011, **72**:404-416.
 44. Smirnov D, Lachat F, Peltola T, Lahnakoski JM, Koistinen O-P, Glerean E, Vehtari A, Hari R, Sams M, Nummenmaa L: **Brain-to-brain hyperclassification reveals action-specific motor mapping of observed actions in humans.** *PLoS One* 2017, **12**: e0189508.
 45. Chen J, Leong YC, Honey CJ, Yong CH, Norman KA, Hasson U: **Shared memories reveal shared structure in neural activity across individuals.** *Nat Neurosci* 2017, **20**:115-125.
- Using advanced searchlight-based analyses on two-person 'pseudo-hyperscanning' data, the authors show the shared neural substrates for encoding and recall of memory traces.
46. Poulsen AT, Kamronn S, Dmochowski J, Parra LC, Hansen LK: **EEG in the classroom: synchronised neural recordings during video presentation.** *Sci Rep* 2017, **7**:9.
 47. Dikker S, Wan L, Davidesco I, Kaggen L, Oostrik M, McClintock J, Rowland J, Michalareas G, Van Bavel JJ, Ding MZ *et al.*: **Brain-to-brain synchrony tracks real-world dynamic group interactions in the classroom.** *Curr Biol* 2017, **27**:1375-1380.
- A 'wild type' EEG study measuring multi-subject synchronization of brain activity in classroom setting.
48. Parkinson C, Kleinbaum AM, Wheatley T: **Similar neural responses predict friendship.** *Nat Commun* 2018, **9**:332.
 49. Lakin JL, Jefferis VE, Cheng CM, Chartrand TL: **The chameleon effect as social glue: evidence for the evolutionary significance of nonconscious mimicry.** *J Nonverbal Behav* 2003, **27**:145-162.
 50. Lakin JL, Chartrand TL: **Using nonconscious behavioral mimicry to create affiliation and rapport.** *Psychol Sci* 2003, **14**:334-339.

51. Tarr B, Launay J, Dunbar RIM: **Silent disco: dancing in synchrony leads to elevated pain thresholds and social closeness.** *Evol Hum Behav* 2016, **37**:343-349.
52. Tarr B, Launay J, Cohen E, Dunbar R: **Synchrony and exertion during dance independently raise pain threshold and encourage social bonding.** *Biol Lett* 2015:11.
Behavioural study demonstrating that synchronous bonding behaviour (dancing) leads to increased pain threshold, linking synchrony and concomitant opioid release to human bonding.
53. Nummenmaa L, Tuominen LJ: **Opioid system and human emotions.** *Br J Pharmacol* 2017.
54. Machin AJ, Dunbar RIM: **The brain opioid theory of social attachment: a review of the evidence.** *Behaviour* 2011, **148**:985-1025.
55. Saanijoki T, Tuominen L, Tuulari JJ, Nummenmaa L, Arponen E, Kallioikoski K, Hirvonen J: **Opioid release after high-intensity interval training in healthy human subjects.** *Neuropsychopharmacology* 2018, **43**:246-254.
56. Cohen EEA, Ejsmond-Frey R, Knight N, Dunbar RIM: **Rowers' high: behavioural synchrony is correlated with elevated pain thresholds.** *Biol Lett* 2010, **6**:106-108.
57. Tarr B, Launay J, Benson C, Dunbar RIM: **Naltrexone blocks endorphins released when dancing in synchrony.** *Adapt Hum Behav Physiol* 2017, **3**:241-254.
58. Manninen S, Tuominen L, Dunbar RIM, Karjalainen T, Hirvonen J, Arponen E, Jääskeläinen IP, Hari R, Sams M, Nummenmaa L: **Social laughter triggers endogenous opioid release in humans.** *J Neurosci* 2017, **37**:6125-6131.
Using positron emission tomography with mu-opioid receptor specific ligand [¹¹C]carfentanil, the authors show that social laughter triggers endogenous opioid release in the brain, highlighting the role of the opioid system in human bonding.