Emotions promote social interaction by synchronizing brain activity across individuals

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Sharing others' emotional states may facilitate understanding their intentions and actions. Here we show that networks of brain areas "tick together" in participants who are viewing similar emotional events in a movie. Participants' brain activity was measured with functional MRI while they watched movies depicting unpleasant, neutral, and pleasant emotions. After scanning, participants watched the movies again and continuously rated their experience of pleasantness–unpleasantness (i.e., valence) and of arousal–calmness. Pearson's correlation coefficient was used to derive multisubject voxelwise similarity measures [intersubject correlations (ISCs)] of functional MRI data. Valence and arousal time series were used to predict the moment-to-moment ISCs computed using a 17-s moving average. During movie viewing, participants' brain activity was synchronized in lower- and higher-order sensory areas and in corticolimbic emotion circuits. Negative valence was associated with increased ISC in the emotion-processing network (thalamus, ventral striatum, insula) and in the default-mode network (precuneus, temporoparietal junction, medial prefrontal cortex, posterior superior temporal sulcus). High arousal was associated with increased ISC in the somatosensory cortices and visual and dorsal attention networks comprising the visual cortex, bilateral intraparietal sulci, and frontal eye fields. Seed-voxel–based correlation analysis confirmed that these sets of regions constitute dissociable, functional networks. We propose that negative valence synchronizes individuals' brain areas supporting emotional sensations and understanding of another's actions, whereas high arousal directs individuals' attention to similar features of the environment. By enhancing the synchrony of brain activity across individuals, emotions may promote social interaction and facilitate interpersonal understanding.

synchronization | feeling | empathy | somatosensation

Human emotions are highly contagious. Feelings of anger and hatred may spread rapidly throughout a peaceful protest demonstration and turn it into a violent riot, whereas intense feelings of excitement and joy can sweep promptly from players to spectators in an ever-so-important football final. It is well documented that observation of others in a particular emotional state rapidly and automatically triggers the corresponding behavioral and physiological representation of that emotional state in the observer (1–3). Neuroimaging studies also have revealed common neural activation for perception and experience of states such as pain (4–6), disgust (7), and pleasure (8). This automated mapping of others' emotional states in one's own body and brain has been proposed to support social interaction via contextual understanding: Sharing others' emotional states provides the observers with a somatosensory framework that facilitates understanding their intentions and actions and allows the observers to "tune in" or "sync" with other individuals (9–11).

Recent evidence suggests that during social situations, such synchronization of two individuals' brain activity actually may occur in the literal sense. Prolonged natural stimulation, such as viewing a movie or listening to a narrative, results in time-locked and functionally selective response time courses (i.e., intersubject correlation, ISC) in a multitude of brain areas. This synchronization of brain activity extends from the early projection cortices to areas involved in higher-order vision and attention and has been interpreted as reflecting similarity of cerebral information processing across individuals (12–16). In addition to reflecting sensory-driven neuronal responses, synchronized neural activity also could facilitate humans in assuming the mental and bodily perspectives of others and predicting their actions (17). Indeed, speaker–listener neural synchronization is associated with successful comprehension of a verbal message (18), and communication by hand gestures (19) and facial expressions (20) enhances neural synchronization between the communicating persons in a brain-region–selective manner. Because emotions make individuals to feel, act, and view the world in a similar fashion (9), emotion-dependent ISC in the limbic emotion systems, as well as in the networks supporting visual attention and simulating others' mental states, could form a crucial mechanism to facilitate interpersonal understanding during emotionally intense events.

In the present study, we used ISC analysis to test whether emotions triggered by affect-laden events in movies are associated with synchronization of viewers' brain activity. Rather than studying how emotions flow from one brain to another (e.g., ref 20), we focused on the tendency for emotional brain responses to become synchronized across the members of a group exposed to similar emotional events (21). Participants watched a set of unpleasant, neutral, and pleasant movies while their brain activity was measured with functional MRI (fMRI) (Fig. 1). After scanning, the participants viewed the movies again and evaluated online their subjective experiences of valence (pleasantness–unpleasantness) and arousal (calmness–activation). These valence and arousal time series then were used in the general linear model (GLM) to predict moment-to-moment ISC of brain activity during movie viewing. We demonstrate that emotions are associated with enhanced intersubject synchronization that extends beyond the sensory cortices to the limbic system and to visual attention and mental simulation networks. We propose that such synchronization of brain activation during emotional encounters supports enhanced contextual understanding across individuals.

Results

Behavioral ratings (Fig. S1) confirmed that the movie stimuli elicited strong and time-variable emotional reactions, with mean valence ranging from 1.3 to 8.3 and mean arousal ranging from 2.6 to 8.0. Valence and arousal were negatively correlated ($r = -0.22$, $P < 0.001$). During movie viewing, the brain activity was highly time-locked across subjects in several brain regions (Fig. 2). Largest ISCs were observed in the occipito-parietal visual

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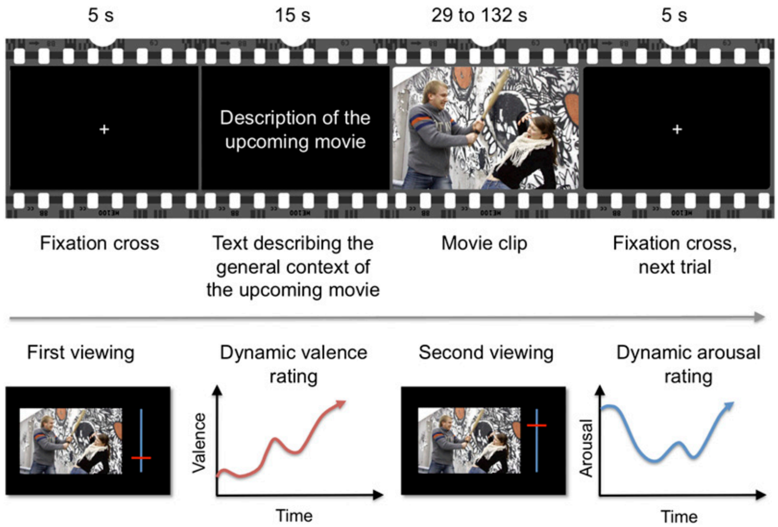

Fig. 1. Experimental design for fMRI (*Upper*) and subjective emotional ratings (*Lower*). Participants watched short movie clips depicting pleasant, unpleasant, and neutral events. The movies were preceded by a 5-s presentation of a fixation cross and were followed by a 15-s presentation of text that described the general context of the upcoming movie without revealing details of its actual events. After fMRI the participants watched the movies again and rated their moment-to-moment experiences of valence (pleasantness–unpleasantness) and arousal. Images reproduced from ref. 37.

cortices and in the inferior and superior temporal and frontal lobes. However, statistically significant ISCs also were observed in numerous limbic regions implicated in affective processing, such as the amygdala, anterior insula, and thalamus, as well as in somatosensory cortices.

Next, we tested whether the intersubject synchronization would be associated with the participants' emotional state. This analysis revealed a regionally selective association between emotional valence and ISC: As valence decreased from positive to negative, ISC increased in regions involved in emotional processing (thalamus, ventral striatum, and medial prefrontal and anterior cingulate cortex) as well as in default-mode function [temporoparietal junction (TPJ), precuneus, and ventromedial prefrontal cortex (VMPFC)] (Fig. 3). On the contrary, the level of emotional arousal was associated positively with ISC in visual and somatosensory cortices and in regions involved in top-down attention control [bilateral intraparietal sulcus (IPS) and frontal eye field]. Overlaying these images with the network images generated by seed-voxel correlation analysis (Fig. 4) confirmed that these effects were confined largely to well-known dissociable functional networks: whereas arousal-modulated ISC was mainly restricted to the visual and dorsal attention networks, valence-modulated ISC was observed in the default-mode network. Table S1 presents a summary of the observed ISC foci.

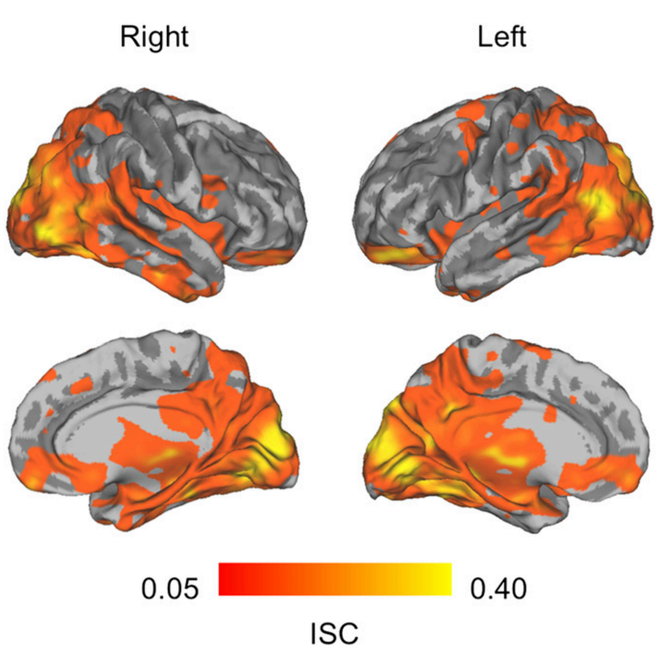

Fig. 2. Brain regions showing statistically significant ($P < 0.05$, FDR corrected) group-level ISCs during viewing of film clips.

When the mean ISC time courses of all statistically significant voxels in each of the six intrinsic networks were correlated with valence and arousal time series, a similar pattern of results emerged: Arousal, but not valence, correlated positively with mean ISC in the visual and dorsal attention network, whereas valence, but not arousal, correlated negatively with ISC in the default-mode network. Similar results were observed when partial correlations were used to control for effects of valence on ISC by arousal or vice versa (Table S2). Correlations between ISC and valence versus ISC and arousal were statistically significantly different in all the aforementioned regions ($Z > 5.38$, $P < 0.001$, Fisher's test). ISCs in the sensorimotor, auditory, and executive control networks did not correlate significantly with valence or arousal ($P > 0.05$). As a control test, we also calculated correlations between whole-brain ISC, valence, and arousal. Neither valence nor arousal correlated significantly with the whole-volume average ISC ($P > 0.05$), suggesting that both valence and arousal had regionally specific rather than global effects on time-locking of brain activation across individuals.

Next we tested whether synchronization of subjective emotional states would be associated with enhanced synchronization of brain activity. Representational similarity analysis (RSA) revealed that pairwise similarity in valence ratings predicted similarity in brain activation time series, most notably in frontal components of the emotion circuit, namely, in the orbital and medial frontal cortex and anterior cingulum (Fig. S2 and Table S3). For arousal, the corresponding effect was much smaller and was restricted to temporal/hippocampal regions.

Finally, we assessed whether a self-reported tendency for empathy, that is, the disposition to catch others' emotional states, would be associated with intersubject synchronization of brain

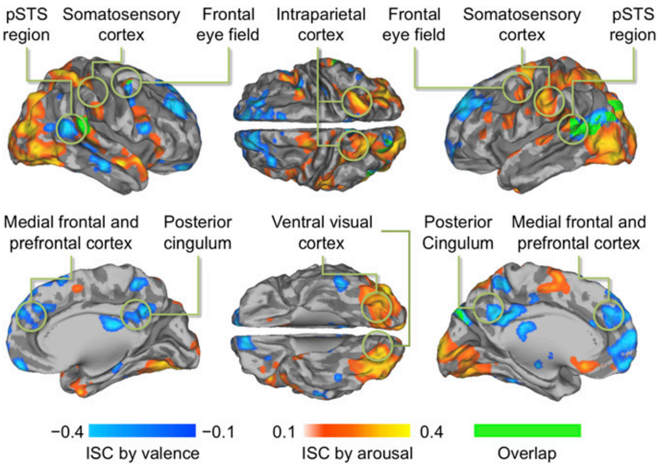

Fig. 3. Cerebral regions where ISC was statistically significantly correlated with self-reported valence (blue to turquoise) and arousal (orange to yellow) scores during viewing of film clips ($P < 0.05$, FDR corrected).

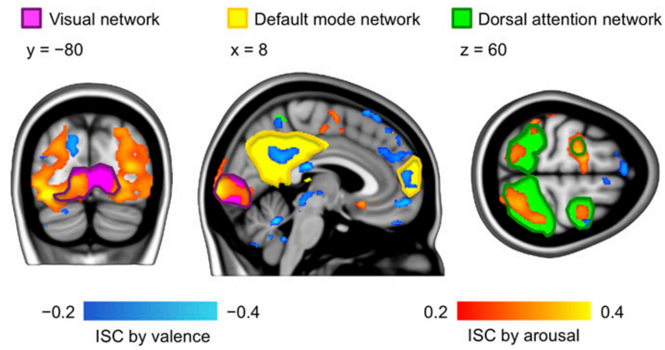

Fig. 4. Valence modulates ISC in the default-mode network (yellow) and arousal in the visual network (violet) and dorsal attention network (green). Brain regions where ISC was statistically significantly correlated with self-reported valence (blue to turquoise) and arousal (red to yellow) scores during viewing of film clips ($P < 0.05$, FDR corrected).

activity. We found that ISC in the posterior middle temporal gyrus region (MNI coordinates $x = 50$, $y = -48$, $z = -4$; $t = 5.10$) was positively associated with emotional empathy scores [$P < 0.05$, false discovery rate (FDR) corrected] (Fig. S3), suggesting that activity within this region was most similar in participants who considered themselves as highly empathetic.

Discussion

Catching emotions that other humans express—here in dynamic scenes resembling everyday life—is associated with intersubject synchronization of brain circuitries related to emotional, attentional, and mentalizing processes. This degree of the moment-to-moment synchronization of individuals' brain activity depended linearly on the intensity of the participants' emotional states as measured by valence and arousal dimensions. These data provide brain-level support for the notion that emotions help individuals "tick together," which subsequently may increase the similarity in the way the individuals perceive and experience their common world.

When viewing complex dynamic scenes, brain activity in sensory and attention-controlling systems becomes synchronized across individuals (12–16), and during movie viewing a nonselective ISC component (spanning to the insular cortex) is associated with emotional events in the movies (14). We extend these findings by demonstrating that the emotional brain circuits became synchronized in individuals viewing naturalistic affect-laden events: Throughout the whole set of movies, participants showed highly synchronized patterns of brain activity not only in the sensory cortices but also in the limbic brain circuitry (amygdala, insula, and thalamus) that is intimately involved in emotional processing (22, 23). Thus, higher-order evaluative processes, such as emotional assessment, also seem to occur at similar temporal scales across individuals.

Humans have a tendency to synchronize with each others' actions as well as physiological and mental states during social encounters (1–3, 24, 25). Such intersubject synchronization of behavior facilitates social interaction. For example, nonconscious mimicry of others' postures and gestures (the "chameleon effect") creates affiliation, rapport, and liking (26, 27). Here we show that spatially selective time-locking of brain activation is associated with emotional responses across individuals: Observation of emotional events in the movies led to enhanced time-locking of brain activity of specific neural circuits across individuals, and this synchronization of neural time courses across brains may be the critical mechanism that enables mental simulation of other's emotional states and, ultimately, prediction of their intentions and actions.

Valence and arousal were associated with synchronization of independent, although partially overlapping, brain networks, and they also modulated ISC in opposite directions:† Whereas arousal was most prominently positively associated with ISC in the visual and dorsal attention networks (28), valence was negatively associated with ISC in regions involved in emotional processing, such as midbrain, thalamus, ventral striatum, insula, and anterior cingulate cortex (22, 23) and also in the default-mode network constituting of the TPJ, precuneus, superior temporal sulcus (STS), and VMPFC (29, 30). Our results thus demonstrate that valence and arousal have distinct roles in synchronizing brain activity—and possibly also behavior—across individuals. These opposite effects on ISC fit with the proposed distinction between valence and arousal representations in the brain (31, 32) and they also highlight the neurobehavioral functions that emotional arousal and valence may have in human social interaction.

The key mechanisms that may support similar emotional processing across individuals are automatic and spatially similar focusing of attention toward emotion-laden stimuli (23) and the subsequent mapping of others' emotional states in the body and brain (9). Our data suggest that the attention-related mechanism is arousal-contingent, whereas the mapping mechanism is valence-contingent. The contribution of enhanced arousal to synchronization of the attention networks is corroborated by studies showing that both pleasant and unpleasant highly arousing events engage the brain' attention circuitry, thus making individuals focus on similar locations occupied by emotional content (23, 33). Recruitment of the attention-controlling systems upon perception of emotional events allows rapid adaptation to potential dangers or beneficial events in the environment (23). Accordingly, during moments of high arousal, different individuals would focus their attention on similar emotional features in the environment, and this focus would be reflected in the enhanced time-locking of brain activity in the dorsal attention network. Because our study did not include behavioral measures of attentional orienting or eye-tracking recordings, we do not have any direct evidence that participants' eye gaze would have been more similar

†It must be noted that the directionality of the valence scale is arbitrary. The arousal scale is a genuine unipolar scale ranging from no activation to high arousal, but the bipolar valence scale ranges from unpleasant via neutral to pleasant, although it equally well could range from pleasant via neutral to unpleasant. The distinct directions of the valence and arousal effects thus should be interpreted in the conventional context of the valence–arousal model of emotions.

during the moments of high arousal. However, numerous independent studies have established that highly arousing events catch both the covert and overt attention (34, 35).

Emotional arousal also was associated with enhanced ISC in the somatosensory cortices which, in addition to their role in sensory and proprioceptive mapping of the body, are involved in the representation and encoding of the bodily states caused by emotions. Lesions of the somatosensory cortices dampen subjective emotional feelings (36), and the somatosensory cortices are activated when participants actively simulate others' emotional states (37). Recent models have proposed further that the somatosensory cortices might have a more general (i.e., non–emotion-specific) role in understanding actions (11). Our findings suggest that temporally synchronized somatosensory codes across individuals might be a critical mechanism supporting mutual understanding of actions and that highly arousing events would be particularly effective in triggering this kind of somatosensory resonance across individuals.

The activity of the default-mode network typically is suppressed during external stimulation (29), but here we found that its activity became synchronized across participants experiencing negative emotions caught from the movie clips. This finding corroborates recent suggestions that the default-mode network actually may be involved in the evaluation of potentially survival-relevant information from the body and the environment as well as in self-referential and social processing and perspective taking (29, 38). Such processes might be suppressed during free exploration of the environment but may be engaged rapidly in a similar manner across individuals when highly relevant social or emotional events are detected.

The negative association between valence and ISC in the default-mode and emotion networks also fits well with the functions that both human and animal studies have proposed for negative and positive emotions. Negative emotions are associated with narrowed mental focus and restricted processing styles, whereas positive emotions broaden the possible behavioral repertoire and promote exploration of the environment (39–41). Our data show that the restricted processing brought about by negative emotions is reflected in the intersubject similarity in time courses of brain activity: The more negative emotions individuals feel, the more similar is their brain activation in the emotion circuit as well as in the default-mode network, whereas when the subjects experience positive emotions promoting free exploration, their brains process the sensory input more individually, resulting in lower ISC.

Prior studies have provided contradicting evidence on whether the activity in the frontal regions synchronizes across individuals during prolonged natural stimulation (14, 15). The present data contemplate these seemingly discrepant findings by showing that the degree of frontal ISC is contingent on whether negative or positive emotions are elicited. When positive emotions are triggered, frontal cortex may not synchronize across individuals, because the positive emotions trigger planning of novel, exploratory thoughts and actions that are bound to vary significantly across individuals. On the contrary, negative emotions may trigger specific biologically determined fight-or-flight responses for immediate survival, and this narrowing of behavioral repertoires would result in more similar frontal time courses across individuals. However, it is likely that frontocortical synchronization may be triggered both by external events (such as emotions) eliciting prototypical neural and behavioral patterns across individuals and by the similarity of endogenously maintained, shared cognitive task sets across individuals. For example, one recent study demonstrated that when two individuals are receiving and transmitting nonverbal information between one other (and thus require the sharing of mental states between the communicators), the activity in their frontal cortices becomes synchronized (19). Our representational similarity analysis also accords with the position that interindividual similarity of mental states is associated with similarity of frontocortical BOLD responses: The more similar the participants emotional feelings of pleasantness–unpleasantness were, the more similar were their brain activations in the orbital frontal cortices.

The overlap of the valence- and arousal-contingent ISC was maximal around the posterior middle temporal gyrus (MTG)/STS region that has been proposed to encode the intentions of an agent's actions (42, 43) and also to be associated more broadly with empathy, mentalizing, and theory of mind (44, 45). In line with these notions, we found that individual differences in the tendency to simulate others' emotions were positively associated with ISC in the posterior MTG: The higher the self-reported empathy scores were, the more similar were the MTG time courses in comparison with other individuals. However, although catching the emotions someone (here the movie character) expresses is thought to involve replication of observed emotions in one's own mind and body (9), empathy also might be related to mental simulation and prediction of others' feelings without actually sharing them in one's own mind and body (46). Accordingly, it is possible that the empathy-contingent ISC in the MTG/STS region might reflect this kind of simulation and prediction without feeling. The MTG/STS region thus may function as a hub that underlies the encoding of others' behavioral and emotional intentions. This information could be forwarded to the attention circuits to modulate sensory sampling of the environment as well as to emotion circuits to support transforming the observed agent's actions and intentions into a corresponding somatosensory and behavioral code in the observer.

Conclusions

Sharing other individuals' emotional states enables predictions of their behavior, and shared affective, sensory, and attentional representations may provide the key to understanding other minds. We argue that emotions enhance intersubject synchronization of brain activity and thus tune-in specific brain networks across individuals to support similar perception, experiencing, and prediction of the world. Our findings suggest that such synchronization of emotions across individuals provides an attentional and affective framework for interpreting others' actions. This hypothesis accords with the proposals that perceived emotional states in others are constantly mapped into corresponding somatic and sensory representations in the observers' brain (10, 11). Through this kind of mind-simulation, we may estimate others' goals and needs more accurately and tune our own behavior accordingly, thus supporting social interaction and coherence. We propose that high arousal serves to direct individuals' attention similarly to features of the environment, whereas negative valence synchronizes brain circuitries, supporting emotional sensations across individuals. Through these mechanisms emotions could promote social interaction by enhancing the synchrony between brain activity and behavior across different individuals.

Materials and Methods

Participants. The Ethics Committee of the Helsinki and Uusimaa Hospital District approved the study protocol, and the study was conducted in accordance with the Declaration of Helsinki. Sixteen healthy adults (age 25–49 y, mean age 32 y, 13 males) with normal or corrected-to-normal vision volunteered for the study. Individuals with a history of neurological or psychiatric disease or current medication affecting the central nervous system were excluded. All subjects were compensated for their time and travel costs, and they signed ethics committee-approved informed consent forms.

Experimental Design. Fig. 1 summarizes the stimuli and design. The video stimuli (*SI Text*) were 13 segments (on average, 92 ± 30 s in length) cut from Hollywood feature films such as *When Harry Met Sally* and *The Godfather*. The clips depicted humans experiencing strong positive or negative emotions or a neutral emotional state. Most stimuli were selected on the basis of a validation study for the emotional qualities of silent clips edited from several feature films (47). All participants were native Finnish speakers, and to reduce the potential confounds associated with the English speech in the movies, the movie clips were presented without sound.

The participants watched the films once in a fixed order while being scanned with fMRI. They were instructed to watch the movies as they would watch movies on television or at the cinema. Each movie was preceded (for 5 s) by a fixation cross and followed (for 15 s) by a short text that explained the general setting of the forthcoming film without revealing its actual content. The latter epoch both served as a washout period for the emotion elicited by the previous film and provided context for the forthcoming film segment. Total task duration was 24 min. An angled mirror above the participant's eyes reflected the stimuli, first projected onto a translucent screen in the bore of the magnet behind the participant's head. The stimulus presentation was controlled with Presentation computer program (Neurobehavioral Systems, Inc.).

Behavioral Measurements. After the fMRI experiment, the participants viewed the film clips again and rated their emotional experiences online (Fig. 1, *Lower*). Ratings were conducted separately rather than during scanning, because a reporting task influences neural responses to visual emotional stimulation (48, 49), but repeated viewing of emotional stimuli has only a negligible effect on self-reported emotional feelings. Ratings for valence and arousal were acquired on separate runs. While viewing each movie, participants used a mouse to move a small cursor at the edge of the screen up and down to indicate their current experience of valence or arousal; data were collected at 5 Hz. The actual valence–arousal scale was arbitrary for participants; for the analyses the responses were rescaled to range from 1 (negative valence/low arousal) to 9 (positive valence/high arousal). A participant's disposition for catching emotions from others was assessed by the Measure of Emotional Empathy questionnaire (50).

fMRI Acquisition and Analysis. MRI was performed with General Electric Signa 3 Tesla MRI scanner with Excite upgrade at the Advanced Magnetic Imaging Centre of the Aalto University School of Science. Whole-brain data were acquired with T2*-weighted echo-planar imaging (EPI) sensitive to BOLD signal contrast (27 axial slices, voxel size $3 \times 3 \times 3$ mm^3, 2-mm slice gap; TR = 1,737 ms; TE = 32 ms; FOV = 192 mm). A total of 850 volumes were acquired, and the first five volumes were discarded to allow for equilibration effects. T1-weighted structural images were acquired at a resolution of $1 \times 1 \times 1$ mm^3. Data were preprocessed using SPM8 software (www.fil.ion.ucl.ac.uk/spm/). The EPI images were sinc-interpolated in time to correct for differences in slice time and were realigned to the first scan by rigid body transformations to correct for head movements. EPI and structural images were coregistered and normalized to the T1 standard template in MNI space using linear and nonlinear transformations and were smoothed with a Gaussian kernel of FWHM 8-mm.

Intersubject Synchronization. The data were analyzed using an ISC toolbox developed by Kauppi et al. (13). Pearson's correlation coefficient was used to derive the multisubject similarity measures (ISCs). The ISCs were computed in two ways. First, voxelwise temporal correlation between every pair of subjects was calculated for the whole time series (845 volumes), and an average ISC map was generated from the pairwise ISC maps over whole time series. In this map, the voxel intensities reflect the degree of ISC across all participants throughout the experiment. As an intermediate stage, this process also resulted in subjectwise ISC maps in which each voxel reflects the average degree of temporal synchronization of that particular individual with all of the other individuals in the sample. To test whether the tendency to catch others' feelings would be associated with enhanced intersubject synchronization of brain activity, we used GLM to predict ISC in these maps with subjectwise scores on the Measure of Emotional Empathy.

In the second approach, we computed dynamic ISC of brain activity by computing the average ISC for each acquired EPI using a 10-sample moving average. This approach resulted in 836 ISC maps, each reflecting the moment-to-moment degree of intersubject synchronization across participants. Time series of mean valence and arousal ratings during movie viewing were downsampled to one TR and aligned with the ISC time series assuming a delay of three TRs (5.1 s). A Gaussian filter rather than an ideal hemodynamic response function (HRF) was used for alignment, because the ISC time series have a complex nonlinear relationship with the BOLD signal, rendering the canonical HRF inappropriate. Gaussian filtering, on the contrary, accounts for both the HRF delay and autocorrelation of the ISC time series without making any assumptions about the shape of the filter. Finally, the aligned and orthogonalized valence and arousal time series were used to predict voxelwise ISC time courses in the GLM. Data acquired during the prestimulus introductory text and fixation screens were not included in the analysis. Resulting β-values were stored in separate valence-by-ISC and arousal-by-ISC maps in which voxel intensities reflect the degree to which ISC depended on emotional valence and arousal.

To test the statistical significance of the ISC maps, we performed a fully nonparametric voxelwise permutation test for the *r* statistic (13). The test was performed against the null hypothesis that the *r* statistic is the same as for unstructured data, which would be expected in the absence of any ISC. To generate the permutation distribution, we circularly shifted each subject's time series by a random lag so that they were no longer aligned in time across the subjects and then calculated the *r* statistic. This way we could account for temporal autocorrelations present in the BOLD data. We approximated the full permutation distribution with A = 100,000,000 realizations. Sampling was randomized over every brain voxel and shifting point without restrictions. We corrected the resulting *P* values using FDR-based multiple comparisons correction with the assumption of independence (or positive dependence).

Seed-Voxel Correlation Analysis. To assess whether valence and arousal were associated with enhanced intersubject synchronization of functional networks rather than distinct brain regions, we conducted seed-voxel–based correlation (SVC) analysis, which enables characterization of task-independent patterns of functional connectivity and mapping of the functional organization of large-scale brain networks (51, 52). Six intrinsic brain networks were delineated by first defining the maximally synchronized voxels in the ISC-by-arousal and ISC-by-valence GLMs within anatomical constraints of the regions typically used in SVC analysis. The seed regions for the networks were as follows: for the visual network, the calcarine sulcus ($x = -10$, $y = -96$, $z = 0$); for the sensorimotor network, the precentral gyrus ($x = 40$, $y = 0$, $z = 48$); for the auditory network, the superior temporal gyrus ($x = 56$, $y = -22$, $z = 0$); for the default-mode network, the posterior cingulate cortex ($x = 0$, $y = -50$, $z = 30$); for the dorsal attention network, the IPS ($x = 32$, $y = -46$, $z = 56$); for the executive control network, the superior frontal gyrus ($x = 0$, $y = 44$, $z = 28$). Spherical regions of interest (ROIs) with a 5-mm radius were generated around these coordinates, and mean time series were extracted for each ROI and participant. Mean ROI time series were subsequently used to identify individual correlation maps, which were then combined with the Fisher transformation. A fully nonparametric voxelwise permutation test was applied to determine the final population-level statistical threshold ($P < 0.01$, FDR corrected) for the maps. Next, an average time series of ISC was extracted within each thresholded network. Finally, we correlated these average ISC time series within each network with the valence and arousal time series described above.

RSA of Emotional Feelings and ISC. Because participants gave individual valence and arousal ratings for the movies, we also could test if similarity in participants' subjective feelings would be associated with similarity in their brain-activation time courses. We took advantage of second-order isomorphism and compared the representations of the voxelwise ISC time series and valence and arousal time series with RSA (53), in which the similarity matrices are compared nonparametrically. First, we identified the pairwise similarity matrices of the BOLD time series across subjects for each voxel. Next, we computed a similar pairwise similarity matrix for the valence (or arousal) time series across subjects. We then used RSA to compare the agreement of valence (or arousal) time series with the voxelwise agreement of BOLD time series and generated RSA maps in which the voxel intensities reflect the degree to which the similarity in the subjective valence (or arousal) ratings predict the similarity in BOLD time series across subjects. Finally, we conducted permutation testing with circular sampling on the surrogate ratings to determine the statistical significance level at $P < 0.01$ (FDR corrected).

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1. Dimberg U, Thunberg M (1998) Rapid facial reactions to emotional facial expressions. *Scand J Psychol* 39:39–45.
2. Hietanen JK, Surakka V, Linnankoski I (1998) Facial electromyographic responses to vocal affect expressions. *Psychophysiology* 35:530–536.
3. Wild B, Erb M, Bartels M (2001) Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: Quality, quantity, time course and gender differences. *Psychiatry Res* 102:109–124.
4. Jackson PL, Meltzoff AN, Decety J (2005) How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage* 24:771–779.
5. Saarela MV, et al. (2007) The compassionate brain: Humans detect intensity of pain from another's face. *Cereb Cortex* 17:230–237.
6. Singer T, et al. (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303:1157–1162.

NEUROSCIENCE

PSYCHOLOGICAL AND COGNITIVE SCIENCES

7. Wicker B, et al. (2003) Both of us disgusted in My insula: The common neural basis of seeing and feeling disgust. *Neuron* 40:655–664.
8. Jabbi M, Swart M, Keysers C (2007) Empathy for positive and negative emotions in the gustatory cortex. *Neuroimage* 34:1744–1753.
9. Hatfield E, Cacioppo J, Rapson RL (1994) *Emotional Contagion* (Cambridge Univ Press, New York).
10. Niedenthal PM (2007) Embodying emotion. *Science* 316:1002–1005.
11. Keysers C, Kaas JH, Gazzola V (2010) Somatosensation in social perception. *Nat Rev Neurosci* 11:417–428.
12. Malinen S, Hlushchuk Y, Hari R (2007) Towards natural stimulation in fMRI—issues of data analysis. *Neuroimage* 35:131–139.
13. Kauppi J-P, Jääskeläinen IP, Sams M, Tohka J (2010) Inter-subject correlation of brain hemodynamic responses during watching a movie: Localization in space and frequency. *Front Neuroinform* 4:5.
14. Hasson U, Nir Y, Levy I, Fuhrmann G, Malach R (2004) Intersubject synchronization of cortical activity during natural vision. *Science* 303:1634–1640.
15. Jääskeläinen IP, et al. (2008) Inter-subject synchronization of prefrontal cortex hemodynamic activity during natural viewing. *Open Neuroimaging J* 2:14–19.
16. Wilson SM, Molnar-Szakacs I, Iacoboni M (2008) Beyond superior temporal cortex: Intersubject correlations in narrative speech comprehension. *Cereb Cortex* 18: 230–242.
17. Hasson U, Ghazanfar AA, Galantucci B, Garrod S, Keysers C (2012) Brain-to-brain coupling: A mechanism for creating and sharing a social world. *Trends Cogn Sci* 16: 114–121.
18. Stephens GJ, Silbert LJ, Hasson U (2010) Speaker-listener neural coupling underlies successful communication. *Proc Natl Acad Sci USA* 107:14425–14430.
19. Schippers MB, Roebroeck A, Renken R, Nanetti L, Keysers C (2010) Mapping the information flow from one brain to another during gestural communication. *Proc Natl Acad Sci USA* 107:9388–9393.
20. Anders S, Heinzle J, Weiskopf N, Ethofer T, Haynes J-D (2011) Flow of affective information between communicating brains. *Neuroimage* 54:439–446.
21. Barsade SG (2002) The ripple effect: Emotional contagion and its influence on group behavior. *Adm Sci Q* 47:644–675.
22. Kober H, et al. (2008) Functional grouping and cortical-subcortical interactions in emotion: A meta-analysis of neuroimaging studies. *Neuroimage* 42:998–1031.
23. Vuilleumier P (2005) How brains beware: Neural mechanisms of emotional attention. *Trends Cogn Sci* 9:585–594.
24. Hari R, Kujala MV (2009) Brain basis of human social interaction: From concepts to brain imaging. *Physiol Rev* 89:453–479.
25. Konvalinka I, et al. (2011) Synchronized arousal between performers and related spectators in a fire-walking ritual. *Proc Natl Acad Sci USA* 108:8514–8519.
26. Lakin JL, Jefferis VE, Cheng CM, Chartrand TL (2003) The chameleon effect as social glue: Evidence for the evolutionary significance of nonconscious mimicry. *J Nonverbal Behav* 27:145–162.
27. Lakin JL, Chartrand TL (2003) Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychol Sci* 14:334–339.
28. Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215.
29. Raichle ME, et al. (2001) A default mode of brain function. *Proc Natl Acad Sci USA* 98: 676–682.
30. Fox MD, et al. (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc Natl Acad Sci USA* 102:9673–9678.
31. Anderson AK, et al. (2003) Dissociated neural representations of intensity and valence in human olfaction. *Nat Neurosci* 6:196–202.
32. Posner J, Russell JA, Peterson BS (2005) The circumplex model of affect: An integrative approach to affective neuroscience, cognitive development, and psychopathology. *Dev Psychopathol* 17:715–734.
33. Yiend J (2010) The effects of emotion on attention: A review of attentional processing of emotional information. *Cogn Emotion* 24:3–47.
34. Nummenmaa L, Hyönä J, Calvo MG (2006) Eye movement assessment of selective attentional capture by emotional pictures. *Emotion* 6:257–268.
35. Brosch T, Sander D, Scherer KR (2007) That baby caught my eye… attention capture by infant faces. *Emotion* 7:685–689.
36. Johnsen EL, Tranel D, Lutgendorf S, Adolphs R (2009) A neuroanatomical dissociation for emotion induced by music. *Int J Psychophysiol* 72:24–33.
37. Nummenmaa L, Hirvonen J, Parkkola R, Hietanen JK (2008) Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy. *Neuroimage* 43:571–580.
38. Schilbach L, Eickhoff SB, Rotarska-Jagiela A, Fink GR, Vogeley K (2008) Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the "default system" of the brain. *Conscious Cogn* 17:457–467.
39. Fredrickson BL (2001) The role of positive emotions in positive psychology. The broaden-and-build theory of positive emotions. *Am Psychol* 56:218–226.
40. Panksepp J (1998) *Affective Neuroscience: The Foundations of Human and Animal Emotions* (Oxford Univ Press, New York).
41. Bishop SJ (2007) Neurocognitive mechanisms of anxiety: An integrative account. *Trends Cogn Sci* 11:307–316.
42. Nummenmaa L, Calder AJ (2009) Neural mechanisms of social attention. *Trends Cogn Sci* 13:135–143.
43. Pelphrey KA, Viola RJ, McCarthy G (2004) When strangers pass: Processing of mutual and averted social gaze in the superior temporal sulcus. *Psychol Sci* 15:598–603.
44. Gallagher HL, Frith CD (2003) Functional imaging of 'theory of mind'. *Trends Cogn Sci* 7:77–83.
45. Frith U, Frith CD (2003) Development and neurophysiology of mentalizing. *Philos Trans R Soc Lond B Biol Sci* 358:459–473.
46. Preston SD, de Waal FBM (2002) Empathy: Its ultimate and proximate bases. *Behav Brain Sci*, 25:1–20, discussion 20–71.
47. Hewig J, et al. (2005) A revised film set for the induction of basic emotions. *Cogn Emotion* 19:1095–1109.
48. Hutcherson CA, et al. (2005) Attention and emotion: Does rating emotion alter neural responses to amusing and sad films? *Neuroimage* 27:656–668.
49. Lieberman MD, et al. (2007) Putting feelings into words: Affect labeling disrupts amygdala activity in response to affective stimuli. *Psychol Sci* 18:421–428.
50. Mehrabian A, Epstein N (1972) A measure of emotional empathy. *J Pers* 40:525–543.
51. Fox MD, Corbetta M, Snyder AZ, Vincent JL, Raichle ME (2006) Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proc Natl Acad Sci USA* 103:10046–10051.
52. Raichle ME (2010) Two views of brain function. *Trends Cogn Sci* 14:180–190.
53. Kriegeskorte N, Mur M, Bandettini PA (2008) Representational similarity analysis - connecting the branches of systems neuroscience. *Front Syst Neurosci 2*, 10.3389/neuro.06.004.2008.