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Neural correlates of emotional synchrony

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Facial expressions can trigger emotions: when we smile we feel happy, when we frown we feel sad. However, the mimicry literature also shows that we feel happy when our interaction partner behaves the way we do. Thus what happens if we express our sadness and we perceive somebody who is imitating us? In the current study, participants were presented with either happy or sad faces, while expressing one of these emotions themselves. Functional magnetic resonance imaging was used to measure neural responses on trials where the observed emotion was either congruent or incongruent with the expressed emotion. Our results indicate that being in a congruent emotional state, irrespective of the emotion, activates the medial orbitofrontal cortex and ventromedial prefrontal cortex, brain areas that have been associated with positive feelings and reward processing. However, incongruent emotional states activated the dorsolateral prefrontal cortex as well as posterior superior temporal gyrus/sulcus, both playing a role in conflict processing.

Keywords: mimicry; imitation; social neuroscience; fMRI

INTRODUCTION

It is known in popular parlance that smiling is contagious; but what about a sorrowful frown? Already Theodor Lipps (1903) based his concept of empathy ('Einfühlung') on the idea of contagion and suggested that we have an unconscious 'natural instinct' that involves 'inner imitation' of the actions of others in order to feel with the other. Facial electromyographical studies provided empirical evidence in favour of this mimicry tendency. Viewing smiling and frowning faces implicitly activates the corresponding zygomaticus major and corrugator muscles in the viewer (Dimberg, 1982; Lang *et al.*, 1993; Doherty, 1998; Wild *et al.*, 2001; Dimberg *et al.*, 2002; Sato and Yoshikawa, 2007). This so called 'primitive contagion' has been conceptualized as a process in which the mimicry of facial expressions triggers afferent feedback from facial receptors involved in facial movements and thus evokes emotions (Hatfield *et al.*, 1992, 1994). Social psychology has described a related phenomenon, dubbed the 'chameleon effect', namely the unconscious tendency to mimic the postures, mannerisms and facial expressions of ones interaction partners. This has been shown to facilitate the smoothness of interaction and increase the liking between interaction partners (Chartrand and Bargh, 1999). But what makes those mimicry tendencies so pervasive?

In a recent neuroimaging study we explored the neural mechanisms that mediate the increased liking due to

mimicry. We have shown that observing a conversation in which a person that is filmed from a first-person perspective is mimicked by the conversational partner compared to not being mimicked elicits activation the medial orbitofrontal cortex and ventromedial prefrontal cortex (mOFC/vmPFC) (Kühn *et al.*, 2010). A correlation between activities in this reward-related brain area with the judgement of the participants how close they felt to the conversational partner suggests that mOFC/vmPFC mediates the positive consequences of being imitated. With the current study we wanted to address the question whether the content of the gesture that is mimicked matters; whether being imitated while being and looking sad would elicit the same brain activity as being imitated while being happy. We instructed participants to recollect a happy or sad situation and to display the corresponding facial expression. This combination of facial expression and felt emotion was used in order to make the situation more ecologically valid compared to previous studies employing facial expression only (Lee *et al.*, 2008). During the display of emotion participants saw a sequence of faces that were either looking happy or sad. After the presentation of each face participants had to judge how close they felt to the person. With this manipulation we created situations in which the self and the other were either displaying the same emotion (compatible) or were not displaying the same emotion (incompatible).

We assume that observing the imitation of gestures in the first study (Kühn *et al.*, 2010) was not very affect laden, whereas seeing a smiling face might come along with positive emotions. The interesting question is: What happens when someone is frowning? Based on the liking effects observed in

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mimicry situations (Chartrand and Bargh, 1999) one could assume that experiencing the same emotion should be a pleasant experience. Being in a different emotional state than the other person should on the other hand be unpleasant and a conflicting experience. In the cognitive control literature conflict processing has been associated with an enhanced involvement of brain areas such as anterior cingulate cortex (ACC) involved in detection of conflict, and dorsolateral prefrontal cortex (DLPFC) engaged to resolve conflict (Carter and van Veen, 2007; Lee *et al.*, 2006, 2008).

METHODS

Participants

Sixteen healthy students (four male; age: mean = 23.8, ranging from 19 to 30) participated on the basis of informed consent. The study was conducted according to the Declaration of Helsinki, with approval of the local ethical committee. All subjects had normal or corrected-to-normal vision. No subject had a history of neurological, major medical or psychiatric disorder. All participants were right-handed as assessed by the Edinburgh handedness questionnaire (Oldfield, 1971; mean score = 91).

Behavioural task

Before the scanning sessions participants were requested to think of two situations: the most recent one in which they were really happy and the most recent one in which they were really sad. After having noted the situations down, we introduced them to the task. Participants were instructed to put themselves into the situation they had written down, whenever they saw the instruction screen 'HAPPY' or 'SAD'. We asked them to display these emotions on their face until the instruction screen asked them to 'RELAX'. Moreover, we documented the facial expression with an MR compatible camera in order to ensure task compliance and informed participants about that before the experiment. Each instruction screen was presented for 10 s. After each emotion instruction we presented eight photos taken from a subsample of 64 female and male photos of the Karolinska Directed Emotional Faces battery (Lundqvist *et al.*, 1998) displaying either a happy or sad face. Therewith we created situations in which the own emotion was 'compatible' or 'incompatible' to the emotion of the faces participants had to watch and evaluate. Each photo was preceded by a fixation cross presented for a variable jitter interval of 2, 2.5, 3 or 3.5 s. Then the photo was shown for 1.5 s followed by a blank of 0.5 s and an Aron rating scale on which participants had to indicate how close they felt towards the interaction partner by means of a 4-point scale version of the inclusion of other in the self (IOS) Scale (Aron *et al.*, 1992). On this pictorial measure of closeness participants select the picture that best describes their relationship from a set of four Venn-like diagrams each representing different degrees of overlap of two circles that represent the self and the other person. The scale was presented for 3 s during which the

participants responded with one of four buttons operated with their right and left index and middle fingers (Figure 1). Altogether the experiment consisted of four runs containing eight emotion instruction screens respectively. After each instruction screen eight faces were presented. Accordingly we acquired 64 trials for each of the four conditions (self happy–other happy, self happy–other sad, self sad–other happy, self sad–other sad).

Scanning procedure

Images were collected with a 3T Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany) using an eight-channel radiofrequency head coil. First, high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 2530 ms, TE = 2.58 ms, TI = 1100 ms, acquisition matrix = $256 \times 256 \times 176$, sagittal FOV = 220 mm, flip angle = 7° , voxel size = $0.86 \times 0.86 \times 0.9 \text{ mm}^3$). Whole brain functional images were collected using a T2*-weighted EPI sequence sensitive to BOLD contrast (TR = 2000 ms, TE = 35 ms, image matrix = 64×64 , FOV = 224 mm, flip angle = 80° , slice thickness = 3.0 mm, distance factor = 17%, voxel size $3.5 \times 3.5 \times 3 \text{ mm}^3$, 30 axial slices). Two hundred and sixty image volumes aligned to AC–PC were acquired per run.

fMRI data pre-processing and general linear model analysis

The fMRI data were analysed with statistical parametric mapping using SPM5 software (Wellcome Department of Cognitive Neurology, London, UK). The first four volumes of all EPI series were excluded from the analysis to allow the magnetisation to approach a dynamic equilibrium. Data processing started with slice time correction and realignment of the EPI data sets. A mean image for all EPI volumes was created, to which individual volumes were spatially realigned by rigid body transformations. The high resolution structural image was co-registered with the mean image of the EPI series. Then the structural image was normalized to the Montreal Neurological Institute (MNI) template, and the normalization parameters were applied to the EPI images to ensure an anatomically informed normalization. During normalization the anatomy image volumes were resampled to $1 \times 1 \times 1 \text{ mm}^3$. A filter of 8 mm FWHM (full-width at half maximum) was used. Low-frequency drifts in the time domain were removed by modelling the time series for each voxel by a set of discrete cosine functions to which a cut-off of 128 s was applied. The subject-level statistical analyses were performed using the general linear model. The model contained separate regressors for instruction screens indicating the happy or sad emotion as well as the relax instruction with a duration of 10 s. Furthermore, onsets of the photos were modelled as events (duration of 0 s) with separate regressors for all four combinations: self happy–other sad, self happy–other happy, self sad–other happy, self sad–other sad. Movement parameters were included to

account for variance associated with head motion. All resulting vectors were convolved with the canonical haemodynamic response function (HRF) and its temporal derivative to form the main regressors in the design matrix (the regression model). The statistical parameter estimates were computed separately for each voxel for all columns in the design matrix. Contrast images were constructed for each individual to compare the relevant parameter estimates for the regressors containing the canonical HRF. Next, a group-level random effects analysis was performed. One-sample *t*-test was performed for each voxel of the contrast images. The resulting statistical values were thresholded with a level of significance of $P < 0.001$ ($z > 3.09$, uncorrected) and a significant effect was reported when the volume of the cluster was greater than the Monte Carlo simulation determined minimum cluster size (>22 voxels) above which the probability of type I error was < 0.05 (AlphaSim, Ward, 2000). The resulting maps were overlaid onto a normalized T1 weighted MNI template (colin27) and the coordinates reported correspond to the MNI coordinate system.

Percent signal change analysis

For the signal change analysis we used a sphere with a radius of 6 mm around the peak coordinate of interest. For each subject, region and condition separately the mean percent signal change over a time window of 4–6 s after stimulus onset was computed (<http://marsbar.sourceforge.net/>, Brett *et al.*, 2002). The percent signal changes were entered into a repeated measures ANOVA with the factors own emotion (self happy vs self sad) and others emotion (other happy vs other sad).

RESULTS

Behavioral results

We computed a repeated measures ANOVA with the factors own emotion (self happy vs self sad) and others emotion (other happy vs other sad) on the ratings on the IOS scale measuring the closeness to the person depicted on the photo. Both factors revealed a significant main effect [own emotion: $F(1,15) = 28.97$, $P < 0.001$; others emotion: $F(1,15) = 10.47$, $P < 0.01$] with higher closeness ratings for both happy own and others emotion. Moreover the data revealed a significant interaction of own and others emotion [$F(1,15) = 450.31$, $P < 0.001$; Figure 2] resulting from higher closeness ratings whenever the instructed emotion was compatible to the emotion of the person depicted on the photo.

fMRI results

In order to test which brain areas are involved in experiencing the same emotion as another person compared to experiencing a different emotion we compared the fMRI signal in the compatible and incompatible condition. Due to the strong closeness effect, namely that compatible emotion lead to higher closeness ratings and therefore right hand responses compared to incompatible emotions that lead to

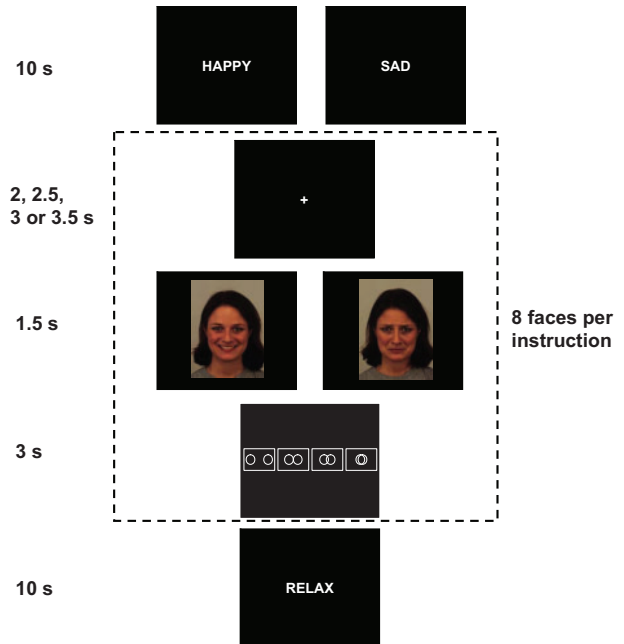


Fig. 1 Schema of the experimental design.

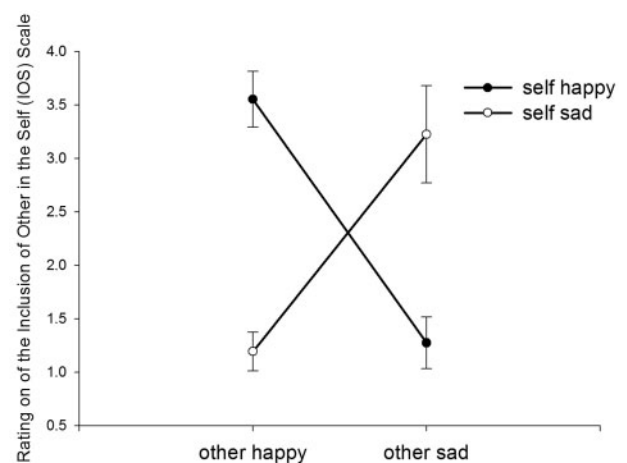


Fig. 2 Results of the Inclusion of Other in the Self (IOS) scale showing higher closeness ratings when the instructed emotion was compatible to the emotion displayed by the face on the photo.

low closeness ratings and therefore left hand responses we do not interpret the resulting motor-related activity (primary motor cortex, premotor cortex, supplementary motor cortex, cerebellum).

The random-effects analysis of the contrast compatible $>$ incompatible revealed activation in mOFC (0, 42, -14; BA 11) and vmPFC (-4, 53, 0; BA 10). The reversed contrast (incompatible $>$ compatible) yielded significant activation in bilateral DLPFC (35, 35, 39; -39, 35, 42; BA 46) and bilateral bilateral superior temporal gyrus (STG) extending into the posterior superior temporal sulcus (STS) in the left hemisphere (61, -26, 14; -67, -49, 4; BA 22/42) (Figure 3A).

In order to test the assumption that the activation found in mOFC and vmPFC is related to positive emotional states

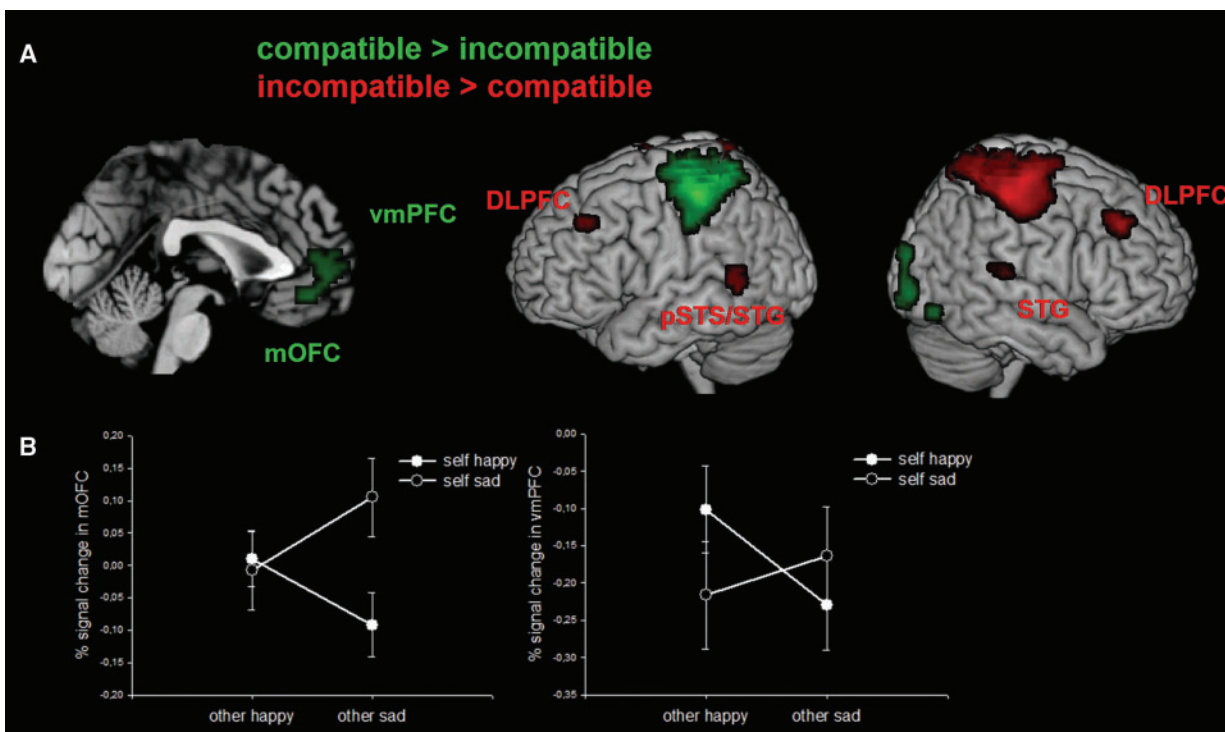


Fig. 3 (A) Brain activity in the compatible compared to the incompatible emotion condition (green depicts the contrast compatible > incompatible; red depicts incompatible > compatible). Activation map averaged over 16 subjects ($P < 0.001$, cluster > 22 voxels) mapped onto a T1 weighted MNI single subject template (colin27). The labelling is restricted to structures that are not part of the motor system and are not mirror-symmetric in both contrasts. (B) Percent signal changes in mOFC and vmPFC.

we contrasted the brain activation during the 10 s instruction screen that told participants to retrieve the happy emotion with the screen prompting the sad emotion. The brain regions found in this contrast were indeed overlapping with the vmPFC activation found in the compatible > incompatible contrast.

Next, we explored the relation between the subjective closeness ratings and brain activation in mOFC and vmPFC. In order to do this we correlated the difference in percent signal change in mOFC and vmPFC of the two congruent conditions ('self happy-other happy', 'self sad-other sad') and two incongruent conditions ('self happy-other sad', 'self sad-other happy') with the same condition differences of closeness reported on the pictorial Inclusion of Other in the Self scale. The difference of activation in mOFC between the compatible conditions and the incompatible conditions was significantly correlated with the equivalent difference in subjective closeness scores across participants [$r(15) = 0.054$, $P < 0.05$]. This indicates that participants with stronger differences in mOFC activation between the compatible compared to the incompatible condition showed a higher difference in judged closeness to the interaction partner. The same analysis on the percent signal changes in vmPFC did not reach significance [$r(15) = 0.27$, $P = 0.29$]. We are aware that these correlations would not survive Bonferroni correction, but nevertheless they suggest a stronger relationship between mOFC and closeness ratings compared to vmPFC.

In order to address the question whether the frontomedian activation in the compatible emotion condition is due to the compatible happy emotion, or also elicited by the situation in which the other person and oneself feel sad we carried out a signal change analysis in mOFC and vmPFC (Figure 3B). The mOFC and vmPFC ROIs were created based on the peak voxels taken from the contrast compatible vs incompatible emotions of the random effects analysis. The analysis revealed higher brain activity in both conditions, when self and other are both in a happy as well as in a sad emotion. An ANOVA on the signal change in mOFC reveals a significant interaction of the factors self and other [$F(1,15) = 19.40$, $P < 0.01$]. *Post hoc* tests reveal significant differences between seeing a happy or sad face when experiencing a happy emotion [$t(16) = 3.40$, $P < 0.01$] and when experiencing a sad emotion [$t(16) = -3.00$, $P < 0.01$]. The same holds true for the vmPFC [$F(1,15) = 21.51$, $P < 0.001$, *post hoc* self happy: $t(16) = 4.28$, $P < 0.01$; self sad: $t(16) = -3.0$, $P < 0.01$]. There were no main effects for own or others emotion in mOFC ($P > 0.24$) or own emotion in vmPFC ($P = 0.63$) but a main effect in others emotion in vmPFC [$F(1,15) = 6.4$, $P < 0.05$].

To test whether there are different brain areas involved in synchrony in sorrow compared to synchrony in happiness we compared the conditions self sad-other sad and self happy-other happy directly with one another. This contrast revealed no differences.

DISCUSSION

Our results demonstrate a significant interaction between the perception of emotionally expressive faces and the performance and experience of emotions and their accompanying facial movements. We observed several systematic effects: Having the same emotion as a person one is confronted with (be it happy or sad) leads to higher closeness ratings. This emotional synchrony leads to higher brain activation in mOFC and vmPFC compared to situations of emotional asynchrony and the activation in mOFC is correlated with the closeness ratings. Most interestingly, not only experiencing a happy emotion, but also experiencing a sad emotion simultaneously produces higher activity in mOFC and vmPFC, brain areas that have been associated with reward processing. Emotional asynchrony on the other hand leads to higher brain activation in DLPFC and posterior STG/STS that have been shown to be related to conflict processing.

In line with our previous study on the neural correlates that mediate the positive consequences resulting from being imitated (Kühn *et al.*, 2010) we found that being in the same emotional mood and performing the same facial movements leads to higher BOLD responses in the mOFC and vmPFC. Especially mOFC has been shown to be involved in positive affect (Kringelbach, 2004) as well as pleasant touch (McCabe *et al.*, 2008), and pleasant taste (Grabenhorst and Rolls, 2008). Moreover, a distinction between lateral and medial orbitofrontal cortex has been suggested with medial parts representing the pleasantness and lateral parts the unpleasantness of stimuli (Olsson and Ochsner, 2008). The vmPFC (or the dorsal ACC as the authors call it) has been demonstrated to be responsive to social feedback and to signal social acceptance (Somerville *et al.*, 2006). VmPFC has been shown to be involved in self-referential processing (for an overview: Northoff *et al.*, 2006); therefore one might speculate that being imitated increases self-consciousness by seeing the own expression being reflected in the other person.

The present results show that the rewarding effects of mimicry as shown in Kühn *et al.* (2010) extend to situations of emotion synchrony and onto a context in which participants are actively involved instead of observing an interaction passively. This underlines the validity of our previous findings. Moreover, the study extends the previous findings by demonstrating a correlation between the difference in closeness ratings and the difference in mOFC brain activity between the compatible and incompatible condition (but not in vmPFC) suggesting the in particular mOFC is related to the positive affect that accompanies mimicry situations.

In line with the predictions of the liking effects in mimicry (Chartrand and Bargh, 1999; Kühn *et al.*, 2010) we find mOFC/vmPFC activation and higher subjective closeness ratings only when the self and other are in the same emotion. Interestingly the content of the behaviour mimicked does not seem to play an important role. We find high levels of activity

in mOFC and vmPFC whenever the own emotion matches with the emotion displayed by the face that is observed, regardless of whether this emotion is positive or negative. Since activity in mOFC has been associated with reward processes this suggests that sharing a sorrow indeed halving it.

In contrast to our findings theories of emotion contagion would have predicted activation in brain areas that have been associated with sadness and negative affect such as lateral orbitofrontal cortex, insula or anterior temporal pole (Eugene *et al.*, 2003; Olsson and Ochsner, 2008). Based on a meta-analysis of PET and fMRI studies Phan and colleagues (2002) suggested that brain activity in the subcallosal cingulate cortex (SCC, BA 25) is related to sadness. But these brain areas were not activated during the congruent sorrow situation when compared to the congruent happiness situation. Unfortunately there is little consistency among studies on the neural correlates of sadness (Eugene *et al.*, 2003) and some studies even report overlap in the vmPFC or mOFC during the experience of happy as well as sad emotions (e.g. Damasio *et al.*, 2000). But nevertheless it is suggestive that we find no difference between the situation in which the person on the photo and the participant are both happy or are both sad, but find a considerably different pattern of activation when emotions do not match as predicted by the notion of mimicry.

When the emotion felt is different from the emotion observed we find conflict-related brain areas, namely DLPFC and STG/STS and less subjective closeness. This extends the findings of our previous study in which we found no conflict related brain activity. Most likely active involvement in the interaction (in contrast to passive observation) is necessary for conflict related brain activity to occur. Since participants were only watching the interaction passively in the previous study those activations might have been obscured.

The conflict monitoring theory suggests that the ACC plays a role in detecting conflict in tasks and the DLPFC engages in resolving the conflict (Botvinick *et al.*, 2004; Carter and van Veen, 2007). In our task context DLPFC might be recruited in order to prevent imitation of the incompatible facial emotion triggered automatically by emotion contagion. Previous studies have shown increased fMRI responses in the posterior superior temporal sulcus (STS) during tasks requiring responses to facial emotions compared to those to facial identity, so that it can be considered as a marker for processing of emotion-related facial information (Narumoto *et al.*, 2001; Vuilleumier *et al.*, 2001; Winston *et al.*, 2004). This could imply that experiencing an emotional asynchrony elicits an increase in attentional focus onto the facial emotion. Moreover it has been suggested that STS contains mirror neurons, many of which respond to the same degree for other and own movement but some of which discharge only to visual information of other's movement (Keysers and Perrett, 2004). These viewpoint-other mirror cells allow the brain to resolve the

issue of identity of the actor and provide an automatic sense of agency or ownership,

Furthermore, STS has not only been suggested to be involved in realizing others' goals and intentions, a capacity that has been subsumed under the term theory of mind (e.g. van Overwalle, 2009 for review), but on a lower level STS has been implicated in the perception of human motion (Allison *et al.*, 2000).

Both brain areas, DLPFC and STG/STS, correspond to regions that have been reported in controlling emotional expressions (Lee *et al.*, 2008). The authors asked participants to view movie clips showing different intensities of happy and angry facial expressions and after watching this, participants were instructed to frown or smile. In the incompatible response situation brain activity in inferior frontal gyrus, right anterior insula and STS was observed. Unfortunately, the authors only focus on the interference related activity and do not report brain activity related to the situation in which participants perform the same facial expression as the face seen shortly before. Further research is needed in order to clarify whether the motor part of the facial expression as explored by Lee and colleagues suffices in order to increase subjective liking and elicit reward related mOFC and vmPFC activity in mimicry situations, or whether it is necessary to involve both the emotional and motoric pathways in order to observe the described mimicry effects.

Although the present study involves a social and an emotional aspect at the same time, our previous study suggests that the social aspect itself suffices to increase liking typical for behavioural mimicry as well the associated brain activity in mOFC/vmPFC. The present study extends this previous finding by showing that even an emotion that is negative in valence results in increased mOFC/vmPFC activity, previously related to reward processing, when being mimicked in a social context. An interesting idea for future research would be to present words (e.g. 'smile', 'frown') that communicate an emotion in order to test whether congruency without any social context is sufficient produce mimicry effects.

A drawback of the current study design was that our contrasts contained motor-related activity due to the strong congruency effects observed on the subjective judgement of closeness. This could be avoided in a follow-up study by switching the response mapping after the first half of the experiment.

In conclusion, we have shown that emotional mimicry situations are accompanied by brain activation in mOFC and vmPFC and that differences in subjective feelings of closeness between mimicry and non-mimicry situations are correlated with mOFC activity. This activation that has been interpreted as resulting from reward processing is not restricted to situations in which participants and the face were experiencing a happy emotion, but extends to experiences of sorrow as well. Emotional asynchrony, on the other hand, lead to higher brain activation in areas involved in conflict processing (DLPFC, STG/STS).

REFERENCES

- Allison, T., Puce, A., McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, 4, 267–78.
- Aron, A., Aron, E.N., Smollan, D. (1992). Inclusion of other in the self scale and the structure of interpersonal closeness. *Journal of Personality and Social Psychology*, 63, 596–612.
- Brett, M., Anton, J.-C., Valabregue, R., Poline, J.B. (2002). Region of interest analysis using an SPM toolbox [abstract]. *Presented at the 8th International Conference on Functional Mapping of the Human Brain*, June 2–6, Sendai, Japan.
- Botvinick, M., Cohen, J.D., Carter, C.S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences*, 8, 539–46.
- Carter, C.S., van Veen, V. (2007). Anterior cingulate cortex and conflict detection: an update of theory and data. *Cognitive, Affective, Behavioral Neuroscience*, 7, 367–79.
- Chartrand, T.L., Bargh, J.A. (1999). The chameleon effect: the perception-behaviour link and social interaction. *Journal of Personality and Social Psychology*, 76, 893–910.
- Damasio, A.R., Grabowski, T.J., Bechara, A., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, 3, 1049–56.
- Dimberg, U. (1982). Facial reactions to facial expressions. *Psychophysiology*, 19, 643–7.
- Dimberg, U., Thunberg, M., Grunedal, S. (2002). Facial reactions to emotional stimuli: automatically controlled emotional responses. *Cognition & Emotion*, 16, 449–71.
- Doherty, R.W. (1998). Emotional contagion and social judgement. *Motivation and Emotion*, 22, 187–209.
- Eugene, F., Levesque, J., Mensour, B., et al. (2003). The impact of individual differences on the neural circuitry underlying sadness. *NeuroImage*, 19, 354–64.
- Grabenhorst, F., Rolls, E.T. (2008). Selective attention to affective value alters how the brain processes taste stimuli. *European Journal of Neuroscience*, 27, 723–9.
- Hatfield, E., Cacioppo, J.T., Rapson, R.L. (1992). Primitive emotional contagion. *Review of Personal and Social Psychology*, 14, 151–77.
- Hatfield, E., Cacioppo, J.T., Rapson, R.L. (1994). *Emotional Contagion*. Cambridge: Cambridge University Press.
- Keysers, C., Perrett, D.I. (2004). Demystifying social cognition: a Hebbian perspective. *Trends in Cognitive Sciences*, 8, 501–7.
- Kringelbach, M.L. (2004). Food for thought: hedonic experience beyond homeostasis in the human brain. *Neuroscience*, 126, 807–19.
- Kühn, S., Müller, B.C.N., van Baaren, R.B., Wietzker, A., Dijksterhuis, A., Brass, M. (2010). Why do I like you when you behave 'like me? Neural mechanisms mediating positive consequences of observing someone being imitated. *Social Neuroscience*, 12, 1–9.
- Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O. (1993). Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology*, 30, 261–73.
- Lee, T.-W., Dolan, R.J., Critchley, H.D. (2008). Controlling emotional expression: behavioral and neural correlates of nonimitative emotional responses. *Cerebral Cortex*, 18, 104–13.
- Lee, T.-W., Josephs, O., Dolan, R.J., Critchley, H.D. (2006). Imitating expressions: emotion-specific neural substrates in facial mimicry. *Social Cognitive Affective Neuroscience*, 1, 122–35.
- Lipps, T. (1903). Einfühlung, innere Nachahmung und Organempfindung. *Archiv Für Die Gesamte Psychologie. I. Band*, 185–204.
- Lundqvist, D., Flykt, A., Öhman, A. (1998). The Karolinska directed emotional faces—KDEF, CD ROM from Department of Clinical Neuroscience, Psychology section, Karolinska Institutet, ISBN 91–6307164–9.
- McCabe, C., Rolls, E.T., Bilderbeck, A., McGlone, F. (2008). Cognitive influences on the representation of touch in the human brain. *Social, Cognitive and Affective Neuroscience*, 3, 97–108.

- Narumoto, J., Okada, T., Sadato, N., Fukui, K., Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Brain Research: Cognitive Brain Research*, 12, 225–31.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J. (2006). Self-referential processing in our brain—a meta-analysis of imaging studies on the self. *Neuroimage*, 31, 440–57.
- Olsson, A., Ochsner, K.N. (2008). The role of social cognition in emotion. *Trends in Cognitive Sciences*, 12, 65–71.
- Oldfield, R.C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I. (2002). Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage*, 16, 331–48.
- Sato, W., Yoshikawa, S. (2007). Spontaneous facial mimicry in response to dynamic facial expressions. *Cognition*, 104, 1–18.
- Somerville, L.H., Heatherton, T.F., Kelley, W.M. (2006). Anterior cingulate cortex responds differentially to expectancy violation and social rejection. *Nature Neuroscience*, 9, 1007–8.
- Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Human Brain Mapping*, 30, 829–58.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*, 30, 829–41.
- Ward, B.D. (2000). Simultaneous inference for fMRI data. *AFNI AlphaSim Documentation*. Medical College of Wisconsin.
- 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 Research*, 102, 109–24.
- Wild, B., Erb, M., Eby, M., Bartels, M., Grodd, W. (2003). Why are smiles contagious? An fMRI study of the interaction between perception of facial affect and facial movements. *Psychiatry Research: Neuroimaging*, 123, 17–36.
- Winston, J.S., Henson, R.N., Fine-Goulden, M.R., Dolan, R.J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology*, 92, 1830–9.