Why do I like you when you behave like me?

Neural mechanisms mediating positive consequences of observing someone being imitated

Simone Kühn^{1,2}, Barbara C. N. Müller³, Rick B. van Baaren³, Anne Wietzker¹, Ap Dijksterhuis³ & Marcel Brass¹

¹Ghent University

Faculty of Psychology and Educational Sciences, Department of Experimental Psychology and
Clinical Experimental Psychology
Ghent Institute for Functional and Metabolic Imaging

Henri Dunantlaan 2, 9000 Gent Belgium

² Department of Psychology
Max Planck Institute for Human Cognitive and Brain Sciences
Stephanstr. 1A, 04103 Leipzig
Germany

³Behavioural Science Institute
Radboud University of Nijmegen
P.O. Box 9104, 6500 HE Nijmegen
Netherlands

Corresponding authors: Simone Kühn and Marcel Brass e-mail: simone.kuhn@ugent.be & marcel.brass@ugent.be

Abstract

Social psychological and developmental research revealed that imitation serves a fundamental social function. It has been shown that human beings have the tendency to automatically mirror the behaviour of others – the so called chameleon effect. Furthermore, it has been demonstrated that being imitated leads to positive feelings towards the imitator. But why do we feel more positive about someone who imitates us? In the current fMRI study we aimed at exploring the neural correlates of the positive consequences of being imitated by means of an observation paradigm. Our results indicate that being imitated compared to not being imitated activates brain areas that have been associated with emotion and reward processing, namely medial orbitofrontal cortex/ ventromedial prefrontal cortex (mOFC/vmPFC, GLM whole-brain contrast). Moreover mOFC/vmPFC shows higher effective connectivity with striatum and mid-posterior insula during being imitated compared to not being imitated.

142 words

Introduction

Certainly everybody knows the following situation: While being involved in an interesting conversation with a friend or colleague one suddenly finds oneself displaying the same behaviour as the interaction partner, such as crossing the hands behind the head. This tendency to automatically mirror the behaviour of others – the so called chameleon effect – has been shown for gestures and mannerisms (Chartrand & Bargh, 1999), accents (Giles & Powesland, 1975), speech rhythm (Cappella & Panalp, 1981) and moods (Neumann & Strack, 2000). Some authors have conceptualized this behavioural matching mechanism as a by-product of pre-existing rapport (Scheflen, 1964), whereas others have argued for the reverse causal direction, namely that mimicking the behaviour of others increases attachment (Chartrand & Bargh, 1999; La France, 1982) and acts as "social glue" (Lankin et al., 2003). In any case, imitating others has positive social effects for the imitator and is therefore used as an implicit or explicit strategy to exert social influence in communicative situations. In psychotherapeutic settings, the so called "pacing" is even used as a technique. It includes not only matching the client's body posture, but also his voice tone or language use (e.g. Catherall, 2004).

It has been demonstrated that counselors who mimic the body position of their clients, are perceived by the clients as having a greater level of empathy (Maurer and Tindall, 1983). In a more day-to-day situation, van Baaren and colleagues (van Baaren, Holland, Steenaert, & van Knippenberg, 2003) assessed the effect of verbal mimicry on tipping in restaurants and found that waitresses mimicking their customers increased the tip amount significantly. Furthermore it has been demonstrated that mimicry does not only have proximal consequences in favour of the person mimicking (receiving more tip, getting help after being mimicked). It has also more distal

effects due to an increase in general prosocial orientation (donating more money to a charity after being mimicked; van Baaren, Holland, Kawakami, & van Knippenberg, 2004; Ashton-James, van Baaren, Chartrand, Decety & Karremans, 2007).

While these positive consequences of imitation are well documented in the social psychological literature, the underlying functional and neural mechanisms are still poorly understood. We hypothesized two possible underlying mechanisms that could be the cause of the increased liking: (1) observing mimicry could trigger reward-related processing and therewith elicit positive affect or (2) observing antimimicry could trigger conflict-related processing and therewith elicit negative affect. The aim of the present study was to investigate whether being imitated acts like a rewarding stimulus (O'Doherty et al., 2001). This would lead to the prediction that being imitated should activate brain areas that have been shown to be involved in hedonic feelings such as sympathy and love (Bartels & Zeki, 2004; Decety & Chaminade, 2003; Kringelbach, 2004) encompassing the medial orbitofrontal cortex/ ventromedial prefrontal cortex (mOFC/vmPFC), the striatum and the insula.

On the other hand the observed increase in liking could be driven by the fact that antimimicry leads to conflict processing that is experienced as effortful and unpleasant. Dabbs (1969) for instance has shown that antimimicry can have negative effects in certain circumstances. According to simulation theory (Hesslow, 2002) observed behaviour is constantly simulated by activation of motor structures. Therefore a mismatch between the gestures planned and simulated for oneself (or the person seen from a first-person perspective) and the gestures simulated for the interaction partner might afford additional processing. This conflict hypothesis would therefore predict an enhanced involvement of brain areas related to conflict processing and negative effect including lateral orbitofrontal cortex (IOFC), anterior cingulate cortex (ACC) involved in detection of conflict, and dorsolateral prefrontal cortex (DLPFC) engaged to resolve the conflict

in the antimimicry condition (Buchel, Morris, Dolan & Friston, 1998; Carter & van Veen, 2007; Lee, Dolan & Critchley, 2008; Lee, Josephs, Dolan, & Critchley, 2006; O'Doherty et al., 2001; Small et al., 2001).

However, investigating natural imitation in the MRI scanner is difficult as participants are instructed not to move in order to avoid movement artefacts. Therefore, we used an observation paradigm in which participants did not overtly respond but viewed an interaction between two actors. One actor sat with the back to the camera in a pseudo-first person perspective while the interaction partner was seated vis-á-vis facing the camera. The interaction partners either mimicked or antimimicked the gestures of the first-person actor. On the basis of simulation theory (Hesslow, 2002) we assumed that this virtual-imitative situation should be highly similar to a real imitative situation because the observer puts himself in the shoes of the person who is being imitated. In particular functional imaging studies have shown similar patterns of brain activity in the premotor and in the posterior parietal cortices when subjects observe actions performed by another individual and when they actually perform or mentally simulate the same actions (e.g. Decety et al., 1997). This assumption was supported by a pilot study outside the scanner, in which we tested whether being imitated in a virtual-imitative context has the same consequences as being imitated in a real interactive context.

Pilot Study

Methods

Materials. We recorded 14 dyadic interaction sequences between female actors. One female actor played in the first-person perspective in all videos with the back to the camera so that mainly the lower body part and the arms were visible. The different interaction partners were facing the camera. For each of the interaction partners two video types were recorded. Respectively, one in

which the interaction partner mimicked the gestures of the person filmed from a first-person perspective and another, in which the gestures were not mimicked and another gesture was performed instead. Each video clip contained three different gestures: crossing legs, arranging hair, and folding hands. An example of a mimicry sequence would therefore be: first person crosses legs, then the interaction partner crosses legs; then the first person arranges her hair, then the interaction partner does the same and then the first person folds her hands and then the interaction partner folds her hands as well. Contrary to this a antimimicry sequence would for example contain: first person crosses legs, then the interaction partner folds her hands; then the first person arranges her hair and the interaction partner crosses legs, then the first person folds her hands and the interaction partner arranges her hair.

Pilot Study Task. In this pilot study we tested whether videos elicit an increased liking of the interaction partner when she imitates the gestures of the person who is filmed from a pseudo-first-person perspective. For that purpose 129 female participants saw each of 14 films (seven different actors once in a mimicry interaction, once in an antimimicry interaction) once. Half of the participants were explicitly instructed to take the perspective of the person filmed from a pseudo-first-person perspective whereas the other half received no perspective taking instruction. After each video participants had to evaluate the likability of the interaction partner in the video on a 7-point-scale ("I find the person in the video likable"; 1 = I completely disagree, 7 = I completely agree). Moreover, they were asked to indicate how close they felt towards the interaction partner by means of a 6-point-scale version of the Inclusion of Other in the Self (IOS) Scale (Aron, Aron & Smollan, 1992). On this pictorial measure of closeness participants select the picture that best describes their relationship from a set of six Venn-like diagrams each representing different degrees of overlap of two circles that represent the self and the other

person. Furthermore we administered the Interpersonal Reactivity Index (Davis, 1980) in order to assess empathy.

Results

First, we analyzed the data from the pilot study in order to check whether the virtual-imitation setup produces behavioural results similar to the real imitation setup. The behavioural pilot study revealed that observing a video sequence where the third-person actor imitates the first-person actor leads to a more positive evaluation of the imitator than observing an third-person actor that does not imitate (liking: F(1,127) = 8.11, p < .01; feeling of closeness: F(1,127) = 11.87, p < .001). Furthermore, we found a significant interaction between perspective taking and the liking judgement (F(1,127) = 4.04, p < .05) indicating that instructing participants to take the perspective of the first-person actor enlarges the basic liking effect. From these pilot data we concluded that a) the virtual-imitation setup is suited to investigate affective consequences of being imitated in the scanner, b) that the instruction to take the perspective of the first-person actor increases the effects of being imitated.

fMRI study

Methods

Participants. Fifteen healthy women (age: mean = 20.7, ranging from 18 to 24) participated on the basis of informed consent. The study was conducted according to the Declaration of Helsinki, with approval of the 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 a handedness questionnaire (Van Strien, 1992; mean score = 9.5).

Materials. We recorded 42 new interaction sequences (with seven different interaction partners) in order to control for the transition between gestures which is important for the counterbalancing in fMRI experiments. For each interaction partner we recorded three videos with different sequences of the three gestures (crossing legs (C), arranging hair (A), and folding hands (F)), respectively for the mimicry and the antimimicry condition. The actors, who were blind to the hypothesis of the study, were instructed to behave neutrally while pretending to be engaged in a conversation and only perform the action we verbally announced. We selected the videos in a pseudorandom fashion from the six possible mimicry gesture sequences (CC-AA-FF, AA-CC-FF, FF-AA-CC, AA-FF-CC, CC-FF-AA, FF-CC-AA) and the twelve possible antimimicry gesture sequences (CF-AC-FA, CA-AF-FC, AC-CF-FA, AF-CA-FC, etc.). The gesture of the interaction partner took place approximately 5, 15 and 25 s after the onset of the video, each time approximately 2 seconds after the gesture of the person filmed from a first-person perspective. The length of each video was 30 s.

Behavioural Task in the scanning session. Participants were informed that they would watch interactions between a person and various interaction partners. They were instructed to take the perspective of the actor filmed from a pseudo-first-person perspective. In each trial first a fixation cross was presented on the centre of the screen for 500 ms and after a blank of 100 ms one of the videos was presented. The interaction partner as well as the imitative content of the video sequence was randomized. During each video sequence a small red square was presented for 2 s at a random location and a random time (5-20 s after video onset). Participants were encouraged

to find a pattern in the appearance of red squares and report the detected pattern at the end of the scanning session. Each trial started with a jitter of 0, 666 or 1333 ms to obtain an interpolated temporal resolution of 666 ms. Moreover we included null events of 22 seconds after each video trial in order to compensate for the overlap of the blood-oxygenation level-dependent (BOLD) response between adjacent trials. The experiment consisted of 3 runs, with 14 video trials each (7 mimicry, 7 anti-mimicry trials) and lasted approximately 45 min. After the scanning sessions we asked participants whether they recognized a pattern in the red squares. Furthermore we presented 14 videos of the ones used in the scanner (selected randomly but depicting all seven actors, once in a mimicry, once in an antimimicry interaction) and administered the questionnaires reported for the pilot study.

Scanning Procedure. Images were collected with a 3T Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany) using an 8-channel radiofrequency head coil. First, high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 2530ms, TE = 2.58ms, TI = 1100ms, acquisition matrix = $256 \times 256 \times 176$, sagittal FOV = 220 mm, flip angle = 7° , voxel size = $0.86 \times 0.86 \times 0.9$ mm³). Whole brain functional images were collected using a T2*-weighted EPI sequence sensitive to BOLD contrast (TR = 2000ms, TE = 35ms, image matrix = 64×64 , FOV = 224 mm, flip angle = 80° , slice thickness = 3.0 mm, distance factor = 17%, voxel size $3.5 \times 3.5 \times 3$ mm³, 30 axial slices). 390 image volumes aligned to AC-PC were acquired per run.

fMRI Data Pre-processing and GLM Analysis. The fMRI data were analysed with statistical parametric mapping using the SPM5 software (Wellcome Department of Cognitive Neurology, London, UK). The first 4 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 datasets. 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 normalised to the Montreal Neurological Institute (MNI) template, and the normalisation parameters were applied to the EPI images to ensure an anatomically informed normalisation. During normalisation the anatomy image volumes were resampled to $1\times1\times1$ mm³. A commonly applied filter of 8 mm FWHM (full-width at half maximum) was used. Lowfrequency 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 (GLM). We modelled the point in time when the interaction partner started to move and either imitated (mimicry condition) or did not imitate (antimimicry condition) the person filmed from a pseudo-first-person perspective. We collapsed across the six possible mimicry gesture sequences and the twelve possible antimimicry gesture sequences. Vectors containing the event onsets (duration = 0) were convolved with the canonical haemodynamic response function (HRF) to form the main regressors in the design matrix (the regression model). The vectors were also convolved with the temporal derivatives and the resulting vectors were entered into the model. The statistical parameter estimates were computed separately for each voxel for all columns in the design matrix. Contrast images were constructed from each individual to compare the relevant parameter estimates for the regressors containing the canonical HRF. The group-level random effects analysis was then 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 structural image of a single subject and the coordinates reported correspond to the MNI coordinate system.

Effective Connectivity Analysis. Effective connectivity, also called psychophysiological interaction (PPI, Friston et al., 1997) analysis explores whether connections between brain areas are modulated by psychological factors. It assesses whether the effective connectivity between a seed region and all other voxels in the brain is changed by an experimental condition. We explored PPI for a volume of interest (VOI) in the mOFC/vmPFC. Individual VOIs were defined as 10 mm radius spheres, with the centre being the local maximum in the contrast of all conditions vs. null events closest to the peak voxel of the mOFC/vmPFC activation found of the main contrast mimicry vs. antimimicry (-7, 49, -7) within a radius of 12 mm falling within Brodmann's area (BA) 10/11.

The significance for the VOI extraction was set to p = 0.005, k = 5 (uncorrected). We had to exclude four participants because they did not show a significant activation close enough to the group peak voxel. The time-series data of the first eigenvariate of the VOI was extracted using SPM5. Then one vector containing the main effect of the contrasts of interest (P regressor, psychological variable) and a second vector representing the VOI time-course (Y regressor, physiological variable) and a third vector was generated contrasting the time-series of the estimated neural response for the conditions of interest (PPI regressor, interaction of the psychological and physiological variable). The PPI analysis convolves those regressors with the canonical hemodynamic response function to estimate the effects of the regressors. Brain sites receiving contextual influences of mOFC/vmPFC that were stronger during the mimicry

compared to the antimimicry condition were determined by a t-test. This second-level random effects analysis was thresholded at p = 0.001, with a more lenient extent threshold of 10 neighbouring voxels (uncorrected), because the analysis contained only eleven participants.

Results

In order to test which brain areas are involved in mediating the positive consequences of being imitated we compared the fMRI signal in the mimicry and antimimicry condition. The random-effects analysis of the contrast mimicry > antimimicry revealed an activation in the mOFC/vmPFC (-7, 49, -7; BA 10) (*Figure 2A*). The reversed contrast (antimimicry > mimicry) yielded no significant activation, even not when applying a more lenient threshold (p < 0.05, uncorrected).

Because mOFC/vmPFC is considered to be part of a more widespread reward-related hedonic system we applied a PPI analysis to test whether the mOFC/vmPFC changes its functional connectivity to other components of this network depending on the condition mimicry vs. antimimicry. This was confirmed by a significant difference in effective connectivity to the striatum (left putamen; -28, -7, -7) and left mid-posterior insula (-42, -21, 4; -35 -4 -4) (*Figure 2B*).

Furthermore we also wanted to relate the fMRI data to behavioural changes caused by the mimicry – antimimicry manipulation. Due to a lack of statistical power and a wash out of the experimental manipulation caused by the repetitive presentation of the same video-sequences we did not expect any differences between mimicry and antimimicry in the averaged ratings that were collected after the scanning session. However, because inter-individual differences are sometimes more sensitive than averages across conditions, we correlated the difference in percent signal change (mimicry – antimimicry) with the degree of closeness reported on the pictorial

Inclusion of Other in the Self scale (Aron, Aron, & Smollan, 1992) in the mimicry condition. This correlation was significantly positive (r(14) = .54, p < .05), indicating that participants with stronger mOFC/vmPFC activation in the mimicry compared to the antimimicry condition judge the closeness to the interaction partner in the mimicry condition as higher.

Discussion

In the present experiment we set out to explore the neural mechanisms mediating positive consequences of being imitated. Two possible underlying mechanisms were proposed that could cause the increase in liking: (1) observing mimicry could elicit reward-related processing and therewith lead to positive affect or (2) observing antimimicry could elicit conflict-related processing and therewith lead to negative affect. When contrasting a condition, in which participants observed from a first person perspective someone being imitated they showed increased activity in mOFC/vmPFC compared to an antimimicry condition. The reversed contrast did not yield any significant activity. This clearly argues in favour of a reward based mechanism of the mimicry induced liking effect. Furthermore, a PPI analysis revealed increased functional connectivity of mOFC/vmPFC with the striatum and mid-posterior insula, both areas that have been previously related to positive affective states. Finally, we found a positive correlation between mOFC/vmPFC and a measure of closeness, suggesting that positive emotional consequences of being imitated are related to mOFC/vmPFC activity.

The involvement of mOFC/vmPFC in positive affective states

Our findings primarily point to a crucial role of mOFC/vmPFC regarding social consequences of being imitated. In the literature mOFC/vmPFC has consistently been associated with general

positive affect (Kringelbach, 2004) as well as pleasant touch (McCabe, Rolls, Bilderbeck & McGlone, 2008), pleasant taste (Grabenhorst & Rolls, 2008), winning money (O'Doherty et al., 2001), and attractiveness of faces (O'Doherty et al., 2003) in particular. 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 & Ochsner, 2008). In studies focussing on reward mOFC/vmPFC has been shown to be involved in reward expectation, often by using computationally derived regressors to estimate subjects' expectations (Behrens et al., 2008; Knutson & Cooper, 2005; Reuter et al., 2005; Tanaka et al., 2004). One might speculate that participants infer the chances that more intense contact with the interaction partner in the video might be rewarding. This interpretation is in line with results indicating that attributing traits to other people (Heberlein & Saxe, 2005; Mitchell et al., 2005, van Overwalle, 2009) as well as being socially accepted instead of rejected (Somerville, Heatherton, & Kelley, 2006) involves activation of vmPFC. Moreover, in a multitude of studies mOFC/vmPFC has been shown to be involved in self-referential processing (for an overview: Northoff et al., 2006). When comparing reported z-coordinates of studies on self-referential processing on the one hand and of studies focussing on reward processing and positive emotions on the other hand our coordinate seems to be slightly closer to studies exploring reward and positive emotions: the mean z-coordinate reported in studies on self-processing listed in the metaanalysis of van Overwalle (2009) is 1 whereas its -4 for studies on positive emotions and -12 for studies on reward processing. Moreover we did not apply an EPI sequence that was optimized for reducing artifacts in OFC, which may be why the z-coordinate is slightly more superior than the ones reported for reward processing.

According to our reasoning these different functions ascribed to mOFC/vmPFC flow together when assuming that participants judge the mirroring interaction partner is a friendly contemporary and appreciate the interaction.

The correlation between the closeness judgement of the mirroring interaction partner and the increase in mOFC/vmPFC in the mimicry condition further substantiates the notion that the mOFC/vmPFC mediates the "social glue" effect elicited by mimicry (Lankin et al., 2003). We conducted an effective connectivity analysis to obtain supporting evidence that the mOFC/vmPFC activation found in the whole brain contrast should indeed be interpreted in the light of reward rather then self-referential processing. In the former case we hypothesized a higher connectivity with regions being part of the reward network, whereas the later case would suggest increased connectivity with brain areas that are usually reported in studies of self-processing as e.g. precuneus. The finding of higher effective connectivity between mOFC/vmPFC with left striatum and mid-posterior insula in the mimicry condition compared to the antimimicry condition seems to support our claim that the observation of behavioural matching leads to increased liking by involvement of the reward system. Both connected regions have been implicated in processing of emotional or reward-related stimuli as well such as monetary reward (Elliot, Newman, Longe, & Deakin, 2003) or romantic love (Aron et al., 2005).

Investigating social consequences of being imitated with brain imaging

Brain imaging research in the domain of imitation has primarily focussed on the neural correlates of imitating rather than being imitated (for an overview see Brass & Heyes, 2005). To our knowledge, this is the first brain imaging study that investigates the consequences of being imitated in a communicative context. Decety and colleagues (2002) explicitly investigated being imitated with positron emission tomography. However, this seminal experiment by Jean Decety

rather investigated object-related actions, than the social consequences of imitation in a communicative situation. Besides, an 'online' imitation procedure was applied, in which the movement was simultaneously imitated by the experimenter. This might be the reason why Decety and colleagues did not identify brain areas related to positive affect when comparing an imitative situation with a non-imitative situation.

The main reason why social imitation has not been investigated with functional MRI is presumably that it is very difficult, if not impossible to create a situation in an MRI environment that corresponds to a social communicative situation where social imitation naturally occurs. We have circumvented this problem by creating a virtual-imitative context. While we are quite aware that this is not the perfect solution, our behavioural pilot study and the fMRI results suggest that our approach is nevertheless a fruitful way to investigate social imitation.

Conclusion

Taken together our results imply that the neural correlates of chameleon-effect-induced liking are to be found in emotion- and reward-related brain areas, namely mOFC/vmPFC and the functionally connected striatum and mid-posterior insula. Interestingly, this network is very similar to brain networks activated when we receive primary reward (e.g., while eating chocolate, Small et al., 2001). The fact that similar brain areas have been shown to be involved in romantic, maternal love and friendship (Bartels & Zeki, 2000, 2004; Güroglu et al. 2008) might indicate that mimicking the behaviour of people around us is a good way to make friends and to signal social acceptance (Somerville, Heatherton, & Kelley, 2006). This might also explain why imitation plays such a crucial role in early development (Heyes, 2001; Jones, 2007; Meltzoff & Moore, 1977) and therewith promotes bonding between individuals and prosocial behaviour on a more general level (van Baaren et al., 2004). Furthermore, it explains why imitation is such a

powerful strategy when trying to create a short-term social relationship and is therefore used in a number of professional contexts such as psychotherapy.

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Figure captions

Figure 1: Cut-out of a mimicry interaction

Figure 2: A) Increased activity in the mimicry compared to the antimimicry condition. Activation map averaged over 15 subjects (p < 0.001, cluster-thresholded) mapped onto a T1 weighted MNI single subject template (colin27). Sagittal plane showing activity in the medial orbitofrontal gyrus/ ventromedial prefrontal cortex (-7, 49, -7) of the contrast mimicry > antimimicry; B) axial plane showing regions depicting significant changes in effective connectivity (mimicry > antimimicry) between the seed region (mOFC/vmPFC) and striatum (-28, -7, -7) and midposterior insula (-42, -21, 4) (p < 0.001, k = 10).





Figure 2

