



Neural Correlates, Visual Attention and Facial Expression during Social Interaction with Virtual Others

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Abstract

We present two recent studies which explore the biological basis of social interaction with virtual characters. Anthropomorphic virtual characters were presented which appeared moving on-screen and turned either towards the participant or towards a third party who is out of view. In dynamic animations, virtual characters then exhibited FACS-coded facial expressions, which were either socially relevant (i.e., indicative of the intention to establish interpersonal contact) or arbitrary. These four conditions thus established a two-by-two factorial design. This paradigm was developed for the purpose of a functional magnetic resonance imaging (fMRI) study and a study recording eye movements and facial muscle activity (EMG). Functional neuroimaging revealed that medial prefrontal activation is observed not only during one's own personal involvement in social interaction - as indicated by adequate facial expressions - but also during the experience of an interaction between the virtual character and a third other. Similarly, differential EMG activity was observed not only when the virtual characters smiled towards the human observer, but also when the smiles were directed towards someone else. In contrast, eye movements of human participants showed that the intensity of visual attention as manifested in visual fixation duration is specifically related to having eye-to-eye contact with a virtual other. In sum, the data from these two studies demonstrate a clear-cut difference between visual attention and neuro- and electrophysiological correlates depending upon the observer's personal involvement (i.e., adopting a secondperson perspective) versus being a passive by-stander (i.e., adopting a *third-person perspective*). We conclude with a discussion of the evolutionary significance of these results.

Introduction

Various disciplines have endeavoured to investigate how we understand other minds. *Social cognitive neuroscience* (Ochsner & Lieberman, 2001) in particular has begun to elucidate the neurophysiological substrates of the processes involved in social cognition. Despite significant efforts, there still is substantial debate about the nature of the underlying processes (Gallagher, 2001). Much research has focused on what is called *Theory of Mind* or *mentalizing* referring to the capacity to construct a metarepresentation to explain and anticipate the behavior of others. From our standpoint, however, it is unclear whether social understanding of others – particularly in everyday situations – does rely on inferential, *off-line* modes of meta-representation. Alternatively implicit, reflexive mechanisms constituting forms of personal involvement are suggested to be involved in understanding social situations (Lieberman, Gaunt, Gilbert, & Trope, 2002). This problem has been acknowledged by Frith and Frith (2003) who draw a distinction between *implicit* and *explicit* mentalizing corresponding to Theory of Mind *on-line* and *off-line*.

Functional neuroimaging (fMRI) studies have recently begun to target aspects of *on-line* interactions which require personal involvement in social communication (Gallagher & Frith, 2003). Thus far, however, the differential effects of self-involvement on the cerebral representation of *mentalizing* have not been investigated. This is emphasized by Ochsner (2004) who points out that a single common *mentalizing* ability might underlie understanding mental states of both self and other. Thus, it is an open question how far the biological mechanisms of perceiving social interactions are altered by being personally engaged (*on-line*) versus being a passive observer who watches others interact (*off-line*).

To address this question in an experimentally feasible way, forms of virtual reality are useful instruments. Mediated environments have the potential to elicit a sense of being there, a sense of presence in a virtual reality (Heeter, 1992; Steuer, 1992; Reeves & Nass, 1996; Ijsselsteijn & Riva, 2003). Furthermore, it has been demonstrated that virtual characters not only convey social information to human observers (Bente, Krämer, Petersen, & de Ruiter, 2001) but are also perceived as social agents evoking a sense of social presence, thus exerting social influence on human interactants (Bailenson, Blascovich, Beall & Loomis, 2003; Pertaub, Slater, & Barker, 2001; Biocca, Harms, & Burgoon, 2003). Consequently, this method has recently begun to be used in social and environmental psychological research (Blascovich, 2002; de Kort, Ijsselsteijn, Kooijman, & Schuurmans, 2003). As the character's morphology, outward appearance, and movements in space and time can be varied systematically, virtual characters and environments can be a powerful tool for experimental psychology overall (Loomis, Blascovich, &

Beall, 1999). This has also been recognized in *social cognitive neuroscience* which has recently begun to use virtual characters as stimulus material in fMRI studies (Adolphs, 2001; Pelphrey, Viola, & McCarthy, 2004)

In the studies reported here, anthropomorphic virtual characters are used to investigate the processes of *mentalizing* dependent upon whether the person who is deciphering someone else's mental state is either involved in social interaction with that other or not. For this purpose, we created a series of short video clips to set up an experimental situation in which test subjects were socially entrained by virtual others in a mediated scene. Within such a video clip, the observer could see a virtual character appearing on screen and exhibiting a dynamic facial expression resembling those found in real-life situations, thus, framing social interaction (Kendon & Ferber, 1973; Grammer, Schiefenhövel, Schleidt, Lorenz, & Eibl-Eibesfeldt, 1988).

In experiment I, we measured fMRI activity while participants watched the video clips described above. In experiment II we used the same paradigm as in experiment I, this time, however, recording eye movements and facial muscle activity.

Experiment I

Method

Participants Eighteen right-handed, healthy male volunteers (mean age 25.9 years \pm standard deviation 4.2 years) with no record of neurological or psychiatric illness participated in the fMRI study. All volunteers were naïve with respect to the experimental task and to the purpose of the study. Informed consent was obtained.

Stimuli Using the software package Poser 4 (Curious Labs, Santa Cruz, California), dynamic video animation clips were designed to depict virtual characters that exhibit different facial expressions serving as social cues. Condition-specific dynamic changes in face morphology were obtained by choosing and manipulating polygone groups on a 3D-mesh, which makes up the character's facial structure which were comparable to the Action Units as described in the Facial Action Coding System (FACS) (Ekman & Friesen, 1978). Ten different facial expressions/movements were used. Pilot studies indicated that five of these were reliably classified as socially relevant (SOC) and five other as arbitrary (ARB), see Table 1. Animation of facial motion was realized by linearly interpolating images between the neutral and condition-specific facial expressions or movements. In the AVI video clips only head and shoulder of the virtual character were presented, as can be seen in Figure 1. The temporal order of each video clip adhered to a standardized pattern of 7.5 seconds, see Figure 2 (bottom row).

FACS code Description Winking 46 1+2+5B Facial Evebrow flash expressions Smile 12C+25 (SOC) Eyebrow flash + smile 1+2+5B+12B 12C+46 Smile + winking «ooh» (lipspeech 22+25 configuration) Facial Lip biting 26 movements Lip contraction 18 (ARB) Lip thrusting 23 AD 33 + 34 Blow up cheeks

Each sequence began with the entrance of a virtual character (*walk in*), followed by positioning (*turn*) either towards the observer or towards a third party who is out of view. Of crucial importance in eliciting the cognitive target state was the time-window from 2500 ms until 5500 ms (*social interaction*). This *window of action* was presented at precisely the same time across all four conditions and included all facial expressions or movements. Thereafter the virtual character turned away and walked out of the screen frame (*turn & walk off*). The virtual characters appeared either from the left or right side of the screen and were always presented against a light grey background (Figure 1).



Figure 1: Snapshots from the video clips: A virtual character directed at the observer (left) or aside (right).



Figure 2: Snapshots of exemplary video clips depicting all experimental conditions (top row: self-directed behavior; mid row: other-directed behavior; bottom row: temporal order in ms).

Across all video clips, the following factors were systematically varied and counterbalanced: appearance on

Table 1: Facial expressions/movements & FACS codes.

the screen (from left, right), direction of gaze (left, right, at the observer), hair color (4 different colors), haircut style (4 different styles) and gender (female, male) of the virtual character. The animations were not designed to explore special racial or ethnic issues. The left example in Figure 1 shows a male virtual character directed at the observer, demonstrating a social expression (evebrow *flash* and smile), whereas the right example shows a female virtual character directed at a imagined third person to the right of the observer, demonstrating a facial movement perceived as arbitrary (lip contraction). The facial morphology of the virtual characters was varied randomly while trying to assemble a neutral and homogenous group of characters. All video clips were coded and rated by an independent, qualified, and licensed FACS coder (Frank Schwab, Saarbrücken, Germany).

Apparatus The fMRI was carried out using echo planar imaging (EPI) with whole brain coverage and a 1.5 T MRI system (Siemens Sonata, Erlangen, Germany) with the standard head coil. An echo planar imaging sequence with the following parameters was employed: repetition time (TR) = 3020 ms, echo time (TE) = 66 ms, field-of-view = 200 x 200 mm², $\alpha = 90^{\circ}$, matrix size = 64 x 64, voxel size $= 3 \times 3 \times 4 \text{ mm}^3$. Using a mid-sagittal scout image, 30 axial slices (0.4 mm inter-slice gap) were positioned to cover the whole brain. In addition, anatomical wholebrain images were obtained by using a T1-weighted, 3D gradient-echo pulse sequence (MP-RAGE, magnetizationprepared, rapid acquisition gradient echo) with the following parameters: TR = 2200 ms, TE = 3.93 ms, 15° flip angle, FOV = 256 x 256 mm², matrix size = 200 x 256, 128 sagittal slices with 1 mm thickness.

Procedure Participants received standardized instructions on the computer screen. They were told to be part of a virtual 3D scene (ME, Figure 3) with two virtual others (OTHER, Figure 3). Throughout each video clip a fourth person would appear in this setting expressing mimic behavior (virtual character, Figure 3). The virtual other on either the right or left side (OTHER) could not be seen from the participant's point of view (ME). Virtual characters could either be turned towards the human observer directly (Figure 1, left) or towards one of the virtual others who were out of view (Figure 1, right) at an angle of approximately 30 degrees.

The facial expressions of the virtual character could, henceforth, be directed towards the human observer himself (ME) or towards another virtual other (OTHER). After each video clip, the participant was asked to answer two questions each of which was indicated by a signal word appearing on the screen: (1) whether the agent had looked at the participant directly or at a virtual other (WHO?) and (2) whether the participant had felt that the agent had tried to initiate social interaction with whom it had looked at (CONTACT?). The WHO question had to be answered using two buttons with the left hand (ME or OTHER) and the CONTACT question by indicating the level of contact on a four-point scale with the right hand (1 = strong feeling of contact - 4 = no feeling of contact). Subjects were instructed to respond as quickly as possible after the display of each signal word.

Taken together, the two factors (i) *social interaction* (SOC vs. ARB) and (ii) *self-involvement* (ME vs. OTHER) constitute a two-factorial design (Table 2).



Figure 3: Virtual scene as shown in instructions.

Behavioral Study during fMRI Scanning During fMRI measurements 100 video clips were shown in 4 consecutive runs. Scanning was performed continuously over one run and re-started for the subsequent three runs. All runs consisted of equivalent numbers of condition-specific video clips, which were shown in completely randomized order. The sequence in which runs were presented to test subjects was also randomized. After removing responses in which the first question was answered incorrectly, the condition-specific mean response scores of all subjects were compared by non-parametric analyses of all experimental runs using SPSS 11 (SPSS Inc., Chicago, Illinois).

Table 2: Experimental design.

	SOCIAL INTERACTION			
SELF-INVOLVEMENT	SOC	ARB		
ME	SOC_ME	ARB_ME		
OTHER	SOC_OTHER	ARB_OTHER		

Image Processing and Analysis Image processing and analysis including realignment, unwarping and normalization, and statistical analysis was performed using Statistical Parametrical Mapping (SPM2, Wellcome Department of Imaging Neuroscience, London, UK) implemented in MatLab 6.5 (Mathworks Inc., Sherborn, Massachusetts). Analyses were carried out using the General Linear Model and a boxcar waveform convolved with the haemodynamic response function. A high pass filter (128 sec) removed subject-specific, low-frequency drifts in signal changes. Global signal changes were treated as a covariate of no interest. The mean activity of each voxel throughout the whole experiment was used as

a dependent variable. Specific effects for each voxel were tested by applying appropriate linear contrasts to the parameter estimates for each condition, resulting in a tstatistic for every particular voxel, thus constituting a statistical parametric map of the t-statistic (SPM $_{(t)}$). This was subsequently transformed to the unit normal distribution (SPM $_{\{z\}}$). Statistical inferences were based on the theory of random Gaussian fields (Friston, 1995). A random effects model with a height threshold of p = 0.001(uncorr.) and an extent threshold of 20 voxel throughout was used. To determine the increases in neural activity common to all four conditions a one-sample *t*-test with appropriate contrast images for each single subject was calculated. For a given contrast, t-tests with appropriate contrast images for each subject were calculated separately. The following contrast images were calculated for every subject: relative activation during SOC [(SOC ME plus SOC OTHER) relative to (ARB ME plus ARB OTHER)], relative activation during ARB [(ARB ME plus ARB OTHER) relative to (SOC ME plus SOC OTHER)], relative activation during ME [(SOC ME plus ARB_ME) relative to (SOC OTHER plus ARB_OTHER)], and relative activation during OTHER [(SOC_OTHER plus ARB_OTHER) relative to (SOC ME plus ARB ME)]. In order to find the main effects of the factors, the appropriate contrast images were analyzed in a one-sample t-test on a second level, thus allowing inference to the general population. The latter procedure was also applied to test for statistical interactions between the main effects (relative activation for SOC x ME and relative activation for SOC x OTHER).

Stereotactic MNI (Montreal Neurological Institute) coordinates of the voxels of local maximum significant activation were determined within regions of significant relative activity change associated with the different tasks. The anatomic localization of local maxima and other activated voxels was transformed in Talairach coordinates, assessed by reference to the standard stereotactic atlas (Talairach & Tournoux, 1988), and superposition of the respective SPM K map on the mean anatomical image of each subject (which had undergone the same anatomical stereotactic transformation).

Results

Behavioral Data During fMRI Scanning Dependent variables were the percentage of correct answers to the first question (WHO?) and mean response scores to the second question (CONTACT?) averaged over all events for each particular condition. One test subject was removed from the analysis as he had consistently failed to answer the questions correctly. The mean score for all remaining subjects on the first question was 97.35% (N = 17, SD = 1.95, SEM = 0.46). Mean response score for SOC_ME condition was 1.54 (N = 17, SD = 0.18, MIN = 1.12, MAX = 1.88), for SOC_OTHER 1.72 (N = 17, SD = 0.26, MIN = 1.16, MAX = 2.28), for ARB_ME 3.23 (N = 17, SD = 0.43, MIN = 2.58, MAX = 4.00) and for ARB_OTHER 3.36 (N = 17, SD = 0.34, MIN = 2.94, MAX = 4.00). When comparing

these responses to the four experimental conditions significant differences are found in non-parametric comparisons between ratings of SOC_ME and ARB_ME (Z = -3.724, p < .001) and between SOC_OTHER and ARB_OTHER (Z = -3.726, p < .001). Additionally, there was a significant difference in how socially relevant behavior was rated depending upon whom it was directed at (SOC_ME vs. SOC_OTHER: Z = -3.195, p < .001).

Neural Correlates The main effects of *social interaction* (SOC) are shown in Figure 4 corresponding to Table 3. Figure 3 represents the SPM{z} map of all suprathreshold voxels as overlay image onto a 3D MNI template on sagittal, axial and frontal views.

Table 3: Neural correlates of all permutations of experimental design.

Region	X	у	Z	k-size	Z
a) Common activations of social i	nteracti	on (SC	DC>AI	RB)	
Ventromedial frontal gyrus	0	42	-10	119	4.04
Right cuneus	2	-82	20	72	3.97
Left medial frontal gyrus	-6	58	6	59	3.95
Right precentral gyrus	48	-16	58	50	3.86
Right superior frontal gyrus	18	-20	60	25	3.69
Right cerebellum, post. Lobe	42	-72	-28	46	3.62
Left cerebellum, post. Lobe	-12	-86	-16	26	3.62
Left middle frontal gyrus	-22	28	56	55	3.52
Right cerebellum, post. Lobe	22	-80	-24	20	3.45
b) Common activations of arbitra	ry facia	l mov	emen	ts (ARB>	50C)
Left inferior temporal gyrus	-52	-68	2	122	4.14
Fusiform gyrus	-38	-54	-16	56	3.78
Right middle temporal gyrus	52	-58 -36	4 4	130 45	3.75 3.49
Right middle temporal gyrus	54				
Right middle frontal gyrus	50	20	22	57	3.37
c) Common activations of <i>self-inv</i>	olvemer	ıt (MF	C>OTH	IER)	
Left cerebellum (post. lobe)	-24	-74	-26	143	3.90
Right MPFC	4	54	20	226	3.88
Right cerebellum (post. lobe)	16	-78	-26	24	3.79
Left insula	-34	8	-10	24	3.40
d) Common activations of other-r	elated a	nctivit	у (ОТ	HER>ME)
Left precuneus	-34	-70	38	881	5.38
Precuneus	0	-58	50	1319	5.05
Right precuneus	10	-68	24	339	4.48
Left superior temporal gyrus	-58	-48	14	83	4.23
Left temporo-occipital junction	-50	-74	12	45	4.22
Left lingual gyrus	-18	-64	4	34	4.19
Right inferior parietal lobule	56	-38	28	95	3.84
Right precuneus	34	-76	36	76	3.81
Left cuneus	-12	-80	16	70	3.72
Right medial frontal gyrus	6	2	56	38	3.57
e) Common activations of the stat	istical i	ntera	ction 8	SOC x ME	
Left parahippocampal gyrus	-24	-32	-8	92	3.71
Right superior temporal gyrus	42	-44	20	26	3.59
Right MPFC	6	46	-6	21	3.57
f) Common activations of the stat	istical in	nterac	ction S	SOC x OTI	HER
Lett interior parietal lobule	-40	-56	46	689	5.46
Right superior parietal lobule	36	-68	50	106	4.26
Left precuneus	-6	-62	52	113	4.04

Differential activity was found in the ventromedial prefrontal cortex (vmPFC), right cuneus, left medial frontal gyrus, the right precentral gyrus, right superior frontal gyrus, the posterior lobe of the right and left cerebellar hemisphere and left middle frontal gyrus. The reverse contrast, that is the main effects of the perception of arbitrary facial movements (ARB), showed differential activation in the left inferior temporal gyrus, fusiform gyrus, right middle temporal and right middle frontal gyrus (see Table 3).



Figure 4: Main effects of SOC (principally activated voxel in vmPFC: x = 0, y = 42, z = -10).

The main effects of *self-involvement* (ME) are tantamount to differential activations in left posterior cerebellar lobe, medial prefrontal cortex (mPFC), left posterior cerebellar lobe and left insular cortex (Figure 5, Table 3). The reverse contrast (OTHER) showed differential activations in the precuneus, the left superior temporal gyrus and temporo-occipital junction, left lingual gyrus, right inferior parietal lobule, the left cuneus and premotor areas (Table 3).



Figure 5: Main effects of ME (principally activated voxel in right mPFC: x = 4, y = 54, z = 20).

Effects of the statistical interaction of SOC x ME were found in the left medial basotemporal lobes, the right superior temporal gyrus, and the right medial prefrontal cortex (Table 3). The second interaction, that is SOC x OTHER showed activation in the left inferior parietal lobule. Additionally, there was an interaction in the homologue area on the right, the right superior parietal lobule, and in the left precuneus (Table 3).

Experiment II

In the second experiment we applied the paradigm from the previous experiment to address possible differences in parameters of behavior. Therefore, eye movements and muscular activity of the face were recorded.

Methods

Participants Twenty-three right-handed, healthy male volunteers (mean age 23.4 years \pm standard deviation 2.4 years) with no record of neurological or psychiatric illness participated in this EMG and eyetracking study. All of them were naïve as to the purpose of the experiment. All the participants had normal or corrected-to-normal vision. Informed consent was obtained. All subjects were paid for participation.

Stimuli The material used in this study was the same as in experiment I. The movies subtended 25.6° horizontally and 13.3° vertically.

Apparatus Eye movements were recorded at 250 Hz using an EyeLink eye tracking system (SR Research Ltd., Toronto, Canada) with on-line detection of saccades and fixations.

EMG activity was measured using bipolar placement of miniature surface Ag/AgCl-electrodes filled with electrode paste, attached according to the guidelines by Fridlund and Cacioppo (1986) at the zygomaticus major muscle sites on the left side of the face. A third reference electrode was attached to the left earlobe. The skin of the subjects was cleaned before attaching the electrodes. EMG were recorded with a LabLinc V75-04 Bioamplifier (Coulbourn Instruments, L.L.C., Allentown, Pennsylvania), digitized at 1000 Hz and stored on a laboratory computer. Pictures were displayed using a GeForce2 MX card and a CRT display (19-inch Iiyama Vision Master 451) at 1024 x 768 pixels at a refresh rate of 100 Hz.

Procedure Subjects received the same instruction as in the fMRI experiment. After restating the instruction subjects performed a nine-point calibration routine. Calibration was repeated if any fixation point was in error by more than 1° or if the average error for all points was above 0.5° . Subjects were given initially two study trials in order to get acquainted with the task. Calibration was repeated after every second movie and each presentation was preceded by a drift correction. The experiment consisted of four blocks of trials with 25 dynamic video animation clips each. The experiment lasted

approximately one hour, with a short break between the blocks.

Data analyses Although the experimental setup and the procedure were similar to experiment I, two modifications concerning data analyses were undertaken and should be explained here. (1) Following the research literature on face perception, the classification for male or female seems to be an important factor (e.g. Ito & Urland, 2003; Mouchetant-Rostaing & Giard, 2003), thus the gender of virtual characters was additionally included into statistical analyses. (2) Parameters of eye movements are shown to react very quickly and are sensitive to stimulus modifications (Pannasch, Dornhoefer, Unema, & Velichkovsky, 2001). In particular, fixation duration and pupil size effects are expected within a rather fine time scale. Analyses over the whole video sequence might reveal lower effects for these parameters. Hence the dynamic scenes were compared frame by frame and divided into the three categories mentioned in Experiment I: walk in, turn and social interaction. Along with this classification, assumptions were made concerning relevant differential aspects: In the walk in section $(400-1500 \text{ ms})^1$ the virtual character enters the scene. Within this section only the gender of the virtual other can be discriminated and is therefore included as the only factor. Regarding the turn section gender and selfinvolvement were taken into account. And finally, in the social interaction sequence, the facial expression is displayed. Therefore, all three factors, gender, selfinvolvement and interaction, are included in statistical analyses.

EMG data sets were visually inspected and data sequences with artifacts were excluded from subsequent analysis. EMG data of six subjects had to be excluded because of technical difficulties and artifacts in the data stream. EMG signals were highpass filtered (50 Hz), rectified, and integrated with a 30 ms time constant. Area under the curve values were calculated for the relevant time windows of each movie. Subsequently, values of each subject were z-transformed and then used for further statistical analyses.

According to the literature, a delay of 200-400 ms of facial muscle responses to a virtual character's facial expression or movement can be expected (Dimberg, 1997a). Similar to the temporal sequences for eye movement data, we used an interval ranging from 600-800 ms (equals *walk in*) when the virtual other's head was fully visible. The interval 2100-2300 ms (equals *turn*) matches the sequence 200 ms after the character has finished turning its head. Finally, we used the interval 3500-3700 ms (equals *social interaction*) matching the interval 200 ms after the apex of the interactive gesture.

Owing to technical problems with the recording device, one subject had to be discarded from further analysis of eye movement data. Furthermore, fixations shorter than 40 ms were excluded as well as fixations outside of the presentation screen. In sum, 1.6% of all fixations were discarded by this trimming process.

Results

EMG For the *walk in* sequence no significant differences for the *gender* of the virtual character were observed. Within *turn* neither *gender* nor *self-involvement* revealed significant effects. During *social interaction* we obtained a significant main effect for *interaction*, F(1,16) = 6.03, p < .05, showing a differential plus in EMG activity for SOC vs. ARB.

Eye Movements and Pupil Size In a first analysis we compared the fixation duration and pupil size following the classification and the time scaling of experiment I. *Self-involvement* (ME vs. OTHER) and *interaction* (SOC vs. ARB) were compared over all video clips. Additionally, following our theoretical assumptions the third factor *gender* (FEMALE vs. MALE) was investigated. The application of a three-way repeated measures ANOVA for both parameters revealed no significant effects for fixation durations. However, for pupil size, significant effects for *gender*, F(1,21) = 96.40, p < .001, and *self-involvement*, F(1,21) = 5.87, p = .025, were obtained. Moreover, the interactions of *gender* x *self-involvement*, F(1,21) = 15.39, p < .001, and *gender* x *interaction*, F(1,21) = 5.53, p = .029, reached significance, too.

Table 4: Results for eye movement and EMG parameters
according to three-factorial design.

	Gender		Self-Involvement		Interaction	
	FEMALE	MALE	ME	OTHER	SOC	ARB
Fixation						
Duration [ms]						
Al	1 270	264	270	268	269	269
Walk Ir	n 277	247***				
Turr	n 249	251	256	251**		
Social Interaction	n 275	283	279	278	274	284
Pupil Size						
Al	1 2115	1980***	2031	2064*	2040	2056
Walk Ir	n 2056	1989***				
Turr	n 1988	1891***	1947	1932		
Social Interaction	n 2139	1996***	2043	2092**	2063	2072
EMG Activity						
[z-scores]						
Walk Ir	n036	054				
Turr	n040	052	040	052		
Social Interaction	<u>1033</u>	061	018	075	.007	102*

Note: Cells contain mean values of the different parameters and level of significance is indicated as follows: *** p < .001; ** p < .01; * p < .05.

Following the rationale described above, data were further analysed within the three categories *walk in, turn* and *social interaction*. In the *walk in* part, significant differences for *gender* were found. The appearance of

¹ The start of this section was defined by the first frame where 50% of the head of the virtual character was visible. This condition was true for all movies 400 ms after the onset.

virtual females caused significantly longer fixations, F(1,21) = 21.98, p < .001, and larger pupil sizes F(1,21) =22.89, p < .001. In the *turn* sequence *gender* had no influence on the duration of fixations, but pupil sizes were again larger for virtual females, F(1,21) = 17.52, p < .001. The analysis for self-involvement revealed only significant differences for fixation durations, F(1,21) = 6.02, p = .023, but not for pupil sizes. For pupil sizes significant interactions were obtained for gender x self-involvement, F(1,21) = 13.17, p = .002. In the *interaction* section, no significant influences of gender, self-involvement and interaction on fixation duration were found. Again, gender showed significant influence on pupil sizes, F(1,21) = 71.19, p < .001. Concerning self-involvement, larger pupil sizes were found if virtual characters turned to someone who was apparently beside the subject, F(1,21) =10.46, p = .004. gender had no influence on the duration of fixations, but pupil sizes were larger for virtual females, F(1,21) = 71.19, p < .001. Also self-involvement had no influence on fixation durations, but larger pupil sizes were found if virtual characters were turned to someone beside the subject, F(1,21) = 10.46, p = .004. interaction had no influence on either fixation duration or on pupil size. For pupil size, significant interactions were also obtained in this sequence for gender x selfinvolvement, F(1,21) = 13.17, p = .002. Mean values and significance level for the main effects of eye movements and EMG activity are listed in Table 4.

Discussion

Our results show that using virtual characters can be a well-functioning tool to address different aspects of neural and cognitive functioning during dyadic interactions.

Neuroimaging Results Behavioral ratings during fMRI measurements show that socially relevant behavior exhibited by virtual others is judged differently depending upon whether it is self-directed or other-directed. Analyses of the neural activations revealed that the perception of social interaction (indicated by adequate facial expressions regardless towards whom they were directed [SOC]) modulates activity primarily in ventral medial prefrontal cortices (VMPFC). This finding agrees with our hypotheses based upon the literature that there is a specific role of MPFC in emotional processing and social cognition. For example, neuroimaging studies have indicated the involvement of this region in representations of self and other (Vogeley, Kurthen, Falkai, & Maier, 1999; Seger, Stone, & Keenan, 2004). Likewise, the involvement of VMPFC has similarly been implicated in joint attention (Williams, Waiter, Perra, Perret, & Whiten, 2005) the ontogenetic development of which has been said to depend upon social reward (Dawson et al., 2002). Consistent with this line of thought VMPFC has been implicated in anticipating positive or negative consequences of actions (Knutson et al., 2003), thereby guiding approach and withdrawal (Paulus & Frank, 2003) as well as behavior directed toward the attainment of goals. Furthermore, it has been demonstrated that MPFC contributes to autonomic responses to stimuli possibly being part of a dynamic between exteroceptive and interoceptive deployment of attention (Nagai et al., 2004). Frontopolar activity has also been related to the evaluation of internally generated information (Christoff & Gabrieli, 2000).

The perception of meaningless facial movements devoid of any specific social meaning and regardless of the addressee [ARB] correlated with activity in middle temporal cortex and fusiform gyrus. As predicted, the neural processes appear to be restricted to visual motion perception reflected by activity increases in motion-sensitive middle temporal gyrus (Beauchamp, Lee, Haxby & Martin, 2003). The fusiform gyrus is known to be involved in face perception (Gorno-Tempini & Price, 2001).

Intriguingly MPFC was also activated when subjects were gazed at directly by the virtual characters regardless of the kind of facial expressions that were shown [ME]. MPFC activations have, indeed, been described as selfreferential neural processing (Fossati et al., 2003). On the other hand, comparable activations have been reported for adopting the intentional stance in order to decipher someone else's mental states (Gallagher & Frith, 2003). As a consequence, MPFC has been suggested to participate (with anterior cingulate cortex) in a network of conscious self-regulation which is particularly important for integrating proprioceptive (e.g. self-action) and exteroceptive (e.g. facial expressions by others signaling behavior changes) information in social cognition (Mundy, 2003). Kampe et al. have presented similar activations for a paradigm investigating ostensive signals which help to initiate interpersonal communication (Kampe, Frith & Frith 2003). Decety and Sommerville (2003) likewise contend that right prefrontal cortex activation can be part of a shared representations network which plays a special role in interpersonal awareness. In concordance with our findings this may suggest that MPFC functions as an important relay in establishing interpersonal contact. In our experiment MPFC activation self-involvement associated with [ME] was complemented by a (mainly) contralateral left posterior cerebellar activation. These data support the notion of cerebello-frontal pathways through which the cerebellum might contribute to and modulate (social) cognitive processes in prefrontal areas (Preston & de Waal, 2002), particularly those which give rise to the capacity for empathic intersubjectivity (Eslinger, 1998; Critchley et al., 2000, Velichkovsky, 1994, 1999, 2002).

The observation of facial expressions or movements directed towards someone else [OTHER] correlated with extensive activations in dorso-medial parietal cortex. Differential activity of this region has been found in studies of mental transformations of one's own body (Bonda, Frey, & Petrides, 1996). As participants in our study had been instructed to imagine a spatial scene with themselves being positioned between two others, we suggest that the activations account for the participants' endeavor to reconstruct the virtual scenario. Differential activity in the parietal and frontal cortex could then be interpreted as contributing to the neural instantiation and transformation of an egocentric spatial reference frame relative to which the position of the third other is computed (Marshall & Fink, 2001). In good agreement with our findings, involvement of the right inferior parietal lobule has also been described by Ruby and Decety (2001) as being associated with third-person perspective-taking and involved in distinguishing selfproduced actions from those generated by others.

An interaction of the neural processes underlying SOC x ME was observed in the medial prefrontal cortex and the right superior temporal gyrus (STG). This replicates the results of a study in which participants were asked to imagine how they would act in a certain situation (Vogeley et al., 2001). As our task involved passive observation of stimuli, the obtained differential activity in STG is consistent with recent data which demonstrate that STG involvement can be triggered automatically by socially salient stimuli (Singer, Kiebel, Winston, Dolan, & Frith, 2004). Pelphrey, Viola and McCarthy (2004) have recently presented evidence for the involvement of right superior temporal sulcus in processing of social information conveyed by gaze shifts in an overtly social context. Furthermore, this interaction (SOC x ME) depicted activation of the left parahippocampal gyrus which may reflect the emotional valence of self-relevant, interactional stimuli giving the observer a feeling of what happens (Damasio, 1999). Medial temporal lobe activity has been ascribed to being part of an automatic core system for a Theory of Mind (Siegal & Varley, 2002). Leibenluft, Gobbini, Harrison and Haxby (2004) have found intriguingly similar activations in the anterior paracingulate, medial temporal, and posterior superior temporal areas for mothers' responding to pictures of their own children.

Wild, Erb, and Bartels (2003) have suggested that differential activity in medial basotemporal lobes is part of an implicit system for non-volitional emotional facial movements which occur naturally and play an important role in human communication. We suggest that these automatic reactions to facial expressions might be a source of embodied information contributing to the understanding of someone else's behavior and mental states.

It has been proposed that VMPFC and ventromedial temporal cortex might be connected to the sympathetic nervous system, thereby representing or producing changes in visceral sensations as present in affective states (Westerhaus & Loewy, 2001). Activations in these areas could, henceforth, be interpreted as contextual modulation of bodily arousal states thereby optimizing bodily readiness for any further behavior (Critchley, Elliott, Mathias, & Dolan, 2000). These findings converge with Klin et al.'s suggestion of an enactive approach to social cognition, which views cognition as bodily experiences accrued as a result of an organism's adaptive actions upon salient aspects of the environment (Klin, Jones, Schultz & Volkmar, 2003). Being affected by someone (even a virtual other, as suggested by our data) appears to be closely connected to sensing the bodily relevance of his/her presence to oneself bringing about changes in action readiness.

Similar to the main effect of OTHER, the interaction of SOC x OTHER revealed activation in dorso-medial and dorso-lateral parietal areas. This interaction reflects processes associated specifically with stimuli that present social signals being directed towards someone else. Our assumption is that reconstructing the spatial features of the scene in the mind's eye could have been more demanding than deciphering the social cues thereby leading to a relatively stronger neural effect in areas known to be involved in visuo-spatial cognition. In turn, this may have masked the subtle neural substrates of perceiving social cues.

In sum, the neural activations observed during task performance demonstrate that encounters with anthropomorphic virtual others involve differential neural activity in anterior medial prefrontal cortices that have been implicated in *mentalizing* and *enactive* social cognition. Intriguingly, MPFC was involved both in the perception of social communication (regardless of selfinvolvement) and in situations of personal involvement (regardless of the particular meaning being conveyed during the encounter). This suggests that understanding social interactions necessarily relies upon self-related neural processing as a point of reference.

EMG data EMG data suggest that the perception of smiling rated as a relevant social cue to initiate social interaction leads to increased differential activity in facial musculature, namely M. zvgomaticus major. This fact agrees with the literature, which describes unvolitional facial reactions in viewers (as indicated by EMG activity over specific muscles in the face) in response to faces exhibiting certain expressions (Lanzetta & Orr, 1986; Lang, Greenwald, Bradley, & Hamm, 1993; Esteves, 1994; Lundqvist, 1995; Dimberg, 1997b; Doherty, 1998). This form of 'facial mimicry' might represent a source of information, since facial reactions elicited by emotional stimuli are consistent with how subjects perceive the stimuli and their own emotions and might, thus guiding the selection of response patterns (Dimberg, 1982, 1988; Dimberg, Thunberg, & Elmehed 2000). Activity in M. zygomaticus major is generally considered to be indicative of positive affects (Cacioppo, Petty, Losch, & Kim, 1986).

Extending this position, Lundqvist and Dimberg (1995) have advanced the idea that automatic reactions in face muscle activity to certain perceived facial expressions might subserve *emotional contagion*, that is experiencing

an emotion similar to the one expressed by the stimulus (cf. also Bavelas, Black, Lemery, & Mullett, 1986; Laird, Alibozak, Davainis, & Deignan, 1994). In dyadic interaction this mechanism gains another dimension as an interactant's facial expression might highlight an emotional state referring to some (existing or imaginary) object, but might also be expressive on the assessment of the vis-à-vis' behavior or the process of interacting. Frijda and Tcherkassof (1997) spell out the idea that facial expressions are indicative of states of action readiness, thereby conveying important pragmatic information in communicative interaction. It is particularly interesting that a plus in EMG activity is found for all smiles exhibited by the virtual others in our experiments regardless of whether they were directed towards the human observer or towards someone else. This complements our fMRI findings which also reveal similar patterns of processing for socially relevant facial expressions regardless of whom they are directed towards. It will be a question of further research to elucidate whether these parallels in EMG and brain activity might be functionally connected.

We tentatively propose that the activity in *M. zygomaticus major* can be understood as a manifestation of *facial embodiment*, that is, an automatic, imitative response to salient aspects of the stimuli that predisposes us to process social cues and helps us to grasp them (Cole, 2001).

Evetracking data Our oculomotor and pupillometric data enhance the impression of a differential involvement of several dedicated functional systems in the processing the communicative episodes. The very fact that visual fixations were significantly prolonged only when the virtual characters were directed towards the observer indicates that a kind of domain-specific mechanism is at work here as well. The prolongation was again registered regardless of other circumstances, in the first line, independent of facial expression of the virtual other. Such an excessive prolongation of visual fixations has been found previously in conditions where states of joint attention have to be maintained as a prerequisite for dyadic collaborative actions (Velichkovsky, 1995). It may also result from mutual eye contact as a particularly important variant of joint-attention mechanisms involved in virtual collaboration (Vertegaal, Velichkovsky & van der Veer, 1997, see also Garau, Slater, Vinavagamoorhty, Brogni, Steed & Sasse, 2003, and Lee, Badler & Badler et al., 2002, for recent examples of studies of eye movements in dyadic interaction). An additional analysis of the spatial parameters of visual fixations can give the final answer to this question.

The next and final domain-specific mechanism discovered in our study is that of emotional arousal as manifested by a general increase of pupillary response to the gender of virtual characters. The response was apparent from the first appearance of the characters in the visual field, that is, well before the characters' communicative orientation (a 'second-person perspective' versus a 'third-person perspective') and their facial expressions could be computed by MPFC or any other structures of the cortex. Though somewhat elusive, the definition of pupillary reactions in the past has always been related to the affective conditions as, for instance, induced by sexually appealing pictures and stressful cognitive tasks (Janiss, 1977; Kahneman, 1973).

Therefore, the simple virtual characters appear to have demonstrated a surprisingly high degree of communicative realism and to have had an emotional effect on the human observers, as manifested by the complex pattern of changes in several physiological systems. Together with the data on the particular neuroevolutionary architecture of levels of social interaction, this represents the major finding of our study for further investigations of human interaction with virtual forms of life.

Conclusions

In sum, the results of the two experiments indicate that human observers can be socially, as well as physiologically entrained by virtual characters to which a communicative intention can be attributed.

We also discovered evidence for differential involvement of several functional systems in understanding and being involved in *on-line* social interactions with virtual others. These functional systems could be conceived as building a kind of hierarchy from relatively nonspecific mechanisms at lower levels to a more specific and higher-order mechanisms operating within MPFC.

(i) Emotional valences and arousal value of perceived characters seem to be dominated by their gender information and as reflected by pupillary dilation. These responses were quite unspecific to communicative orientation and the facial expression of virtual others.

(ii) Visual processing as measured by fixation duration appears to be correlated in distinguishing the self- or other-directedness of a virtual other's attention. Thus, it is obviously subserving basic mechanisms of joint-attention that are instrumental to all forms of direct collaborative activities, both in evolution at large and in developmental setting (Tomasello, 1999; Velichkovsky, 1995).

(iii) On the highest level, neuroimaging and EMG results converge in demonstrating that understanding social signs relies upon more elaborate mechanisms of social cognition. As processing of socially relevant facial expressions seems to rely on self-referential neural mechanisms, understanding social signs could be thought of as a 'self-othering' experience (Thompson, 2001; Lipps, 1907). This sheds light onto the dyadic nature of human self-consciousness.

We speculate that all the aforementioned mechanisms can be functional in a cascade-like evolutionary emergence of the meaningful space for common social actions. This relational information appears to be evaluated at the highest level of the hierarchy, that is, by the self-referential computations of prefrontal brain structures.

Acknowledgments

The authors thank Fiona Mulvey, Anke Karl, Tilman Hensch, Sven-Thomas Graupner, Markus Joos, and Constanze Liebers for participation in experiments and helpful advice. Support was provided by grants from the Deutsche Forschungsgemeinschaft (KFO 112 and VE 192) and the European Commission (NoE COGAIN).

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