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Why we interact: On the functional role of the striatum in the subjective experience of social interaction

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ABSTRACT

There is ample evidence that human primates strive for social contact and experience interactions with conspe- 15 cifics as intrinsically rewarding. Focusing on gaze behavior as a crucial means of human interaction, this study 16 employed a unique combination of neuroimaging, eye-tracking, and computer-animated virtual agents to assess 17 the neural mechanisms underlying this component of behavior. In the interaction task, participants believed that 18 during each interaction the agent's gaze behavior could either be controlled by another participant or by a 19 computer program. Their task was to indicate whether they experienced a given interaction as an interaction 20 with another human participant or the computer program based on the agent's reaction. Unbeknownst to 21 them, the agent was always controlled by a computer to enable a systematic manipulation of gaze reactions by 22 varying the degree to which the agent engaged in joint attention. This allowed creating a tool to distinguish neu- 23 ral activity underlying the subjective experience of being engaged in social and non-social interaction. In contrast 24 to previous research, this allows measuring neural activity while participants experience active engagement in 25 real-time social interactions. Results demonstrate that gaze-based interactions with a perceived human partner 26 are associated with activity in the ventral striatum, a core component of reward-related neurocircuitry. In 27 contrast, interactions with a computer-driven agent activate attention networks. Comparisons of neural activity 28 during interaction with behaviorally naïve and explicitly cooperative partners demonstrate different temporal 29 dynamics of the reward system and indicate that the mere experience of engagement in social interaction is 30 sufficient to recruit this system. 31

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37 Introduction

In the hierarchy of human needs, the need to affiliate with others has 38 been located directly after physiological and prior to egoistic needs 3940 related to self-actualization and esteem (Maslow, 1943). Accordingly, an intrinsic motivation for social interaction unique to the human 41 species has been proposed (Baumeister and Leary, 1995; Tomasello, 4243 2009). Over the last decade, multiple neuroeconomic studies have indeed found reward-related brain activity during social interactions 44 (Rilling and Sanfey, 2011). Two key regions of the reward system are 4546 the ventral striatum (VS) and the medial orbitofrontal cortex (mOFC) 47which have been implicated in the anticipation and consumption of re-48 wards (Berridge et al., 2009). While the VS has been specifically linked

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http://dx.doi.org/10.1016/j.neuroimage.2014.06.061 1053-8119/© 2014 Elsevier Inc. All rights reserved. to the anticipation of rewards and the computation of reward prediction 49 errors (Báez-Mendoza and Schultz, 2013; Daniel and Pollmann, 2014), 50 the mOFC appears to be involved in the subjective experience of reward 51 (Peters and Büchel, 2010) as well as value-guided decision making 52 (Noonan et al., 2012). While many studies indicate a link between social 53 interaction and the reward system (Krach et al., 2010; Rilling and 54 Sanfey, 2011), the application of economic games to study social 55 interaction typically involves high-level concepts such as trust, fairness, 56 cooperation, or competition (Fehr and Camerer, 2007). As a conse- 57 quence, the claim that experiencing engagement in interaction with 58 others per se is rewarding has never been put to the test. 59

An understanding of the neural mechanisms underlying human 60 sociality has recently been argued to require measurements of brain 61 activity during active participation in naturalistic social interactions 62 rather than detached observation of social stimuli (Hari and Kujala, 63 2009; Schilbach et al., 2013). Accordingly, there is growing consensus 64 that "it is in engagement with other people rather than in thought 65 that people normally and fundamentally know other people" (Reddy 66

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and Morris, 2004, p. 657). The relative paucity of studies of naturalistic 67 68 social interactions can be explained by the difficulty of designing experimental paradigms which allow experimental control while participants 69 70 subjectively experience engagement in social interaction. Up to date, the most natural social interactions have been studied using EEG 71 hyperscanning while participants perform spontaneous motor coordi-72nation tasks (e.g. Dumas et al., 2010; Tognoli et al., 2007), engage in 73 74joint attention (Lachat et al., 2012) or play games together (Astolfi 75et al., 2010; Babiloni et al., 2007). However, the types of interactions 76are too complex for application in fMRI studies - either due to the involvement of excessive movements or due to the inherent complexity 77 in the case of spontaneous motor coordination tasks (Pfeiffer et al., 782013; Schilbach et al., 2013). 79

The aim of the present study was to investigate the function of the 80 reward-system during naturalistic interactions. To this end, we ad-81 dressed the neural mechanisms supporting the subjective experience 82 of being engaged in social interaction by examining neural activity 83 while participants actively participated in gaze-based interactions. 84 Gaze was selected because it constitutes a crucial domain of everyday 85 social encounters and has the advantage that it can be implemented 86 inside an MRI scanner due to the minimal involvement of body 87 movements (Pfeiffer et al., 2013). Gaze behavior was visualized via 88 89 computer-animated agents in real-time (e.g. Fox et al., 2009). The combination of neuroimaging, eye-tracking and virtual reality techniques 90 allowed implementing realistic but basic social interactions while main-91taining experimental control (Bohil et al., 2011; Pfeiffer et al., 2013). 92

The interaction task applied in the present study was designed to 93 94create situations in which the gaze-based interaction with a virtual 95agent induced either the subjective experience of being engaged in 96 human social interaction or the subjective experience of being in a 97 non-social interaction - i.e. with a computer program. To this end, 98each block of the interaction task comprised five trials in which the 99 agent would engage either in joint or non-joint attention with the participant (Figs. 1A/B). Joint attention was chosen as a building block of 100

the interaction task because it is a core component of naturalistic social 101 interactions (Mundy and Newell, 2007). Participants believed that dur- 102 ing each block the agent was either controlled by a computer algorithm 103 or a human interaction partner. In fact, the interaction partner was a 104 confederate and the agent's gaze behavior was always controlled by 105 the algorithm to permit systematic manipulation. This was accom- 106 plished by varying the proportion of joint attention trials from zero to 107 five out of five, thereby modifying behavioral contingency over a 108 block. Participants' task was to decide on the nature of their interaction 109 partner based on the agent's reactions during each block. Thereby, the 110 decision between human and computer emerged during the course of 111 the interaction, while other studies explicated this distinction a priori 112 as an independent variable (Gallagher et al., 2002; McCabe et al., 113 2001; Sanfey et al., 2003). This allowed assessing the neural mecha- 114 nisms underlying the subjective experience of being engaged in 115 human social interaction (Pfeiffer et al., 2011). 116

Unconstrained as well as cooperative interaction contexts were 117 established in two phases in which the interaction partner was either 118 introduced as naïve to participants' task, or as an explicit cooperator 119 (e.g. Taborsky, 2007) helping them to identify human interactions. 120 Based on the claim that social interaction is per se rewarding, we 121 hypothesized that the reward component inherent to cooperative 122 contexts would already be present in unconstrained interactions. 123 Furthermore, we predicted that the striatum would encode reward 124 components related to a motivation to interact, whereas the orbitofrontal cortex was expected to encode the rewarding experience. 126

Materials	and	methods
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Participants

32 right-handed volunteers participated in the study, which was approved by the ethics committee of the Medical Faculty of the University 130 of Cologne. 12 participants were excluded due to excessive movements 131

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Fig. 1. Task structure and behavioral results. (A) Each interaction block comprises five gaze trials. At the end of each block participants indicate whether they experienced this interaction as social ('human') or non-social ('computer'). This block exemplifies a 3/5 condition in which the agent engages in joint attention three out of five possible times. (B) In each of five trials of an interaction block, participants initiate an exchange of gaze shifts. (C) In the naïve context, the mean proportion of 'human' ratings correlates with increased congruency of gaze reactions. (D) In the cooperative context, the mean proportion of 'human' ratings correlates with the mere contingency of the agent's gaze reactions. Error bars indicate 95% confidence intervals.

After each block, participants indicated whether they believed they had been interacting with the other participant or a computer algorithm by button press within a response window of 1500 ms. The response

Procedure

Participants received detailed written instructions covering the in- 227 teraction task. Before they were led to the scanner, they were briefly in- 228 troduced to the confederate, who was seemingly being instructed at the 229 same time. Upon calibration of the eye-tracker, scanning commenced 230 with a practice session of eight blocks. The ensuing experiment had 231 two phases, each consisting of two 10-minute runs that were preceded 232 by a re-calibration of the eye-tracker. The experiment started with the 233 naïve phase. After the second run, there was a break of 3 min. During 234 this break, participants were instructed that their interaction partner 235 received additional instructions and that a cooperative phase was now 236 beginning. After the first and third runs there was a short break. In 237 each run, all conditions were repeated thrice in a randomized fashion. 238 After the experiment, participants completed a questionnaire (Fig. 2). 239 Among other questions, this questionnaire contained the question, 240 how pleasant participants experienced interactions with humans and 241 computers, respectively. Following this question, they had the chance 242 to note down any comments they had with respect to the study. People 243 who uttered disbelief in the cover story were later excluded from the 244 analysis. Upon completion of data acquisition, participants received an 245 email debriefing them in detail regarding the cover story and the exper- 246 iment. They were then asked explicitly whether they had believed to be 247 interacting with another human participant in some of the interaction 248 blocks. This served as the final manipulation check and determined 249 whether participants entered data analysis or not. 250

Behavioral data analysis

Prior to analysis, an arcsine transformation was performed to correct 252 for violations of normality (McDonald, 2009). The effects of the factors 253

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Visual stimulation and eye-tracking 135

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The paradigm is an fMRI adaptation of the 'non-verbal Turing test' 136which has recently been validated behaviorally (Pfeiffer et al., 2011) 137138and used the same male virtual agent displaying a neutral facial expression as has been used in previous studies to ensure comparability 139140(Pfeiffer et al., 2011, 2012; Schilbach et al., 2010). Stimuli were presented using a thin-film-transistor liquid crystal display (TFT-LCD) screen 141 attached at a distance of 100 cm from the end of the scanner (viewing 142143angle: $14^{\circ} \times 18^{\circ}$ horizontal \times vertical). They were displayed to participants via a mirror on the head coil. Participants' gaze was monitored via 144 the same mirror using an EyeLink 1000 eye-tracking system (SR 145 146 Research, Mississauga, Canada). Gaze data were collected at a sampling rate of 500 Hz on the EyeLink host computer and made available to 147 Presentation[™] (Neurobehavioral Systems, Albany, CA) for interactive 148 stimulus presentation (Wilms et al., 2010). 149

(n = 4), technical problems with the eye-tracker (n = 5), and disbelief

in the cover story (n = 3). 20 participants (9 female/11 male, M =

27.75 years, $SD \pm 6.44$) were included in the analyses.

Interaction task 150

151 Participants interacted with a virtual agent in a series of interaction blocks (Fig. 1A). They believed that in each block the gaze reactions of 152the agent were controlled by either another participant or a computer 153algorithm. In fact, the other participant was a confederate and the 154155agent's reactions were always computer-controlled to allow for systematic variation. Each block (Fig. 1A) comprised five trials (Fig. 1B) in 156which the agent engaged in joint (JA) or non-joint attention (NJA). 157Systematic variation resulted in six experimental conditions (0/5, 1/5, 1/5)1581592/5, 3/5, 4/5, and 5/5 times of JA) and a control condition in which the agent closed its eyes on each trial. Each of these seven conditions was 160161repeated six times in each interaction context, thus yielding 42 blocks 162per context. In the control condition, participants disengaged from the actual task and were only required to watch the face and press one of 163the two buttons after the end of the block. The rationale was to improve 164165 the model in the fMRI analyses by including a regressor relating for taskunspecific perceptual and motor aspects. Similar control conditions 166 were used in previous studies of live interactions (e.g. Redcay et al., 167 2010, 2012; Schilbach et al., 2010). The trial-by-trial variation of gaze 168 169 behavior thereby induced a variation of behavioral contingency, which increased the more often the agent displayed the same reaction during 170 one block. An agent engaging in IA in each trial (positive contingency) 171 therefore behaved as contingently as an agent engaging in NJA in each 172173trial (negative contingency).

174At the beginning of a trial, participants established eye contact with the agent within 1000 ms. Upon eye contact, two objects appeared, one 175of which participants had to fixate within 1500 ms. If participants fixat-176ed an object earlier than 1500 ms, the remaining time was added to the 177 jittered break at the end of the trial in order to keep average trial length 178179at 4000 ms. If there was no fixation within these time limits, trials were 180 aborted and the block registered as invalid. Selected objects were marked in blue to provide participants with feedback about successful 181 gaze registration. They were informed that their initial gaze shift to 182183the object was transmitted to an agent on the other participant's screen 184 in real-time, and that they would likewise see the other's gaze reaction as visualized on their screen. With a jittered latency of 400-600 ms 185 (Pfeiffer et al., 2012), the agent followed participants' gaze or looked 186 to the other object, thereby establishing JA or NJA. This reaction was 187 displayed until trial duration of 3500 ms was reached. Before the next 188 trial started, a blank screen was presented for 500-1000 ms plus the 189remaining time of the object fixation phase. 190

191 192193 window was followed by a jittered break of 5000 to 7000 ms before 194 the next block began. 195

Interaction contexts

The experiment consisted of two phases to distinguish unconstrained 197 from cooperative interactions. In the first phase, the confederate was in-198 troduced as naïve to participants' task. Participants were told that their in- 199 teraction partner had been instructed to react to each of their gaze shifts 200 by looking at one of the objects without any additional information. This 201 was supposed to provide an unconstrained interaction context in which 202 participants had no a priori assumptions about the other's behavior. In 203 the second phase, the other was introduced as cooperative in order to as- 204 sess neural activity while participants engage in the same type of interac- 205 tion in a cooperative context. They were told that the other's task was 206 now to react to them in such a way that would facilitate the distinction 207 between human- and computer-controlled interactions. It was not speci- 208 fied in which exact way the interaction partner would do this. 209

The order of the two phases was not randomized because the naïve 210 condition required participants to assume that the other did not have 211 any knowledge about their task and reacted in an unconstrained fash- 212 ion. Specifically, we wanted to prevent activation of the high-level con- 213 cept of cooperation before participants engage in naïve interactions 214 because this could have primed expectations leveling out effects of 215 mere interactivity in the second phase. To prevent habituation and nov- 216 elty effects, participants engaged in a practice session of 5 min before 217 the first run. During this session, the experimenter monitored their be- 218 havior to provide additional instruction if necessary. As noted above, the 219 design is a within-subject adaptation of a behavioral study (Pfeiffer 220 et al., 2011). Behavioral results replicate those of the between-subject 221 version (see Fig. 2 of Pfeiffer et al., 2011). Moreover, participants' 222 responses in the debriefing questionnaires did not indicate differences 223 between the within- and between-subject version (compare Fig. 2 of 224 the present study and Figure S1 of Pfeiffer et al., 2011). 225

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Fig. 2. Participants' responses to post-experiment questionnaires. (A) Results indicate that the decision was more difficult in the naïve than in the cooperative context. (B) In the naïve context, the decision was not based on strategic thinking and explicit decision criteria, but on intuitive processes. (C) Participants preferred grounding their decision on considerations about human behavior rather than about the functionality of a computer program. (D) Interactions experienced as social interactions with another human participant were experienced as more enjoyable than non-social interactions.

Context (naïve vs. cooperative) and *Gaze contingency* (JA trials/block) on participants' ratings were analyzed using repeated-measures ANOVAs. Planned polynomial contrasts were applied for trend analyses. All results were Greenhouse–Geisser corrected. Effect size was calculated as ω^2 (Cohen, 1988): small effects: $\omega^2 < .006$; moderate effects: $\omega^2 < 0.15$; large effects: $\omega^2 > 0.15$.

To examine how participants' decision-making process unfolded 260 over time, we assessed how the blocks' rating was influenced by the 261 262 occurrence of JA or NJA on each of its five trials. The rationale behind these analyses is that we sought to obtain an implicit measure of how 263264trial information was integrated in the two different interaction contexts. This was necessary because post-experiment questionnaires 265can only provide explicit, introspective and therefore subjectively bi-266ased information about decision-making. Initially, we performed three 267logistic regressions with *Rating* (computer = 0, human = 1) as depen-268269dent variable using the 'Forward' method, in which predictors are added 270consecutively – starting with the strongest, and adding predictors with 271decreasing strength until adding a new predictor fails to explain more variance. The first analysis was performed over both contexts (naïve 272and cooperative) and included ten predictors: five Trial predictors for 273the agent's reactions on each of the five trials (NJA = 0, JA = 1), 274and five $Trial \times Context$ (naïve = 0, cooperative = 1) predictors. Subse-275quently, we performed two separate logistic regressions for each 276context (naïve vs. cooperative), in which only the agent's reactions on 277the five trials were entered as predictors. 278

279 Functional data acquisition

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Scanning was performed on a Siemens Trio 3-T scanner (Siemens
 Medical Solutions, Erlangen, Germany). A T2*-weighted gradient echo

planar imaging (EPI) sequence with the following parameters was 282 used: TR = 2200 ms, TE = 30 ms, 36 axial slices, slice thickness = 283 3.0 mm, in-plane resolution = 3.0×3.0 mm, and field of view = 284 200.0×200.0 mm. In each run, 280 images were acquired. The first 285 five images of each run were discarded to eliminate saturation effects. 286

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Functional data preprocessing

Images were processed using SPM8 (Wellcome Department of 288 Imaging Neuroscience, London, UK). Motion correction was completed 289 by an affine registration procedure (Ashburner and Friston, 1999). 290 Images were then realigned to the first image of the time series and 291 subsequently to the mean of these images. Next, the mean EPI was com-292 puted for each participant and spatially normalized to the MNI single 293 subject template (Collins et al., 1994) using the unified segmentation 294 function of SPM8 with a $2 \times 2 \times 2$ mm isotropic resolution. The ensuing 295 deformation was applied to individual EPI volumes. Spatial smoothing 296 of the normalized images was performed using an 8-mm FWHM 297 Gaussian kernel.

Functional data analysis

Data were analyzed using a General Linear Model as implemented in 300 SPM8. The following general specifications apply to all conducted anal-301 yses, each of which will be described in detail thereafter. Low-frequency 302 signal drifts were removed using a high-pass filter with a cutoff of 128 s 303 (Macey et al., 2004). At subject level, experimental conditions were 304 modeled by a boxcar reference vector convolved with the canonical 305 hemodynamic response function. Invalid blocks were modeled on a 306 distinct regressor. Each experimental condition was contrasted against 307

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308 the implicit baseline by weighting the regressor of interest with 1 and 309 the remaining regressors with 0, and the resulting contrasts were fed into a flexible factorial design (as provided by SPM8) with factors 310 311 Subject and Condition using a random-effects model for group level comparisons (Worsley et al., 1996). Here, all effects were thresholded 312 at p < .05 at cluster-level, family-wise-error-corrected for multiple 313 comparisons ($p_{FWE-corr} < .05$), with an underlying voxel-level threshold 314of p < .001, uncorrected. Version 1.8 of the SPM anatomy toolbox 315316 (Eickhoff et al., 2005) and the brain atlas of Duvernoy (Duvernoy, 317 1999) were used for anatomical localization. Activation maps were 318superimposed on an SPM canonical T1-weighted image. Error bars of the parameter estimates indicate 90% confidence intervals. 319

The present study design allows multiple different analyses, which 320 made it necessary to select a strategy for data analysis which allows 321addressing the main questions of our study. The first major question 322 concerned the neural mechanisms of the experience of being actively 323 engaged in social interaction (i.e. 'human'- versus 'computer'-rated 324 blocks) and a possible modulation of these mechanisms by interaction 325context. The second key question addressed the temporal integration 326 of behavioral cues (i.e. gaze reactions) depending on interaction 327 context. Study design therefore justified three major lines of analysis: 328

329 (1) Analysis based on participants' ratings (analyses 1–3). The first three analyses were guided by participants' responses to exam-330 ine activity differences between interactions rated as 'human' 331 (hum) and 'computer' (com). At the subject level of the first 332 analysis, blocks rated as 'human' and 'computer' were modeled 333 334 on distinct regressors, separately for the two contexts. Stimulus 335events were defined from block onset to block end (defined 336 by the response window, total duration of 20,000 ms). At group 337 level, we tested for effects of the rating both collapsed across 338the two contexts (hum_{all block} > com_{all block} and com_{all block} > 339hum_{all block}), as well as separately for the naïve and the coopera-340tive context (hum_{naïve block} > com_{naïve block}, com_{naïve block} > hum_{coop block}, hum_{coop block} > com_{coop block}, com_{coop block} > 341 hum_{coop block}). Two further analyses were informed by the 342 343 output of the regressions performed on the behavioral data. In the second analysis, early components of decision-making 344 in blocks rated as 'human' and as 'computer' were analyzed 345 by confining stimulus events to the first two trials (8000 ms) 346 of a block. Group level contrasts were: humnaïve_early > 347 348 $com_{naïve_early}$, $com_{naïve_early} > hum_{naïve_early}$, $hum_{coop_early} >$ com_{coop_early}, and com_{coop_first} > hum_{coop_first}. In the third analy-349 350 sis, the effect of trial progression was modeled by using linear parametric modulation of the BOLD response by trial position, 351 separately for blocks rated as 'human' and 'computer' and for 352353 naïve and cooperative contexts. By doing so, we isolated brain regions in which activity increased with increasing trial position. 354This resulted in the following group level comparisons: 355 hum_{naïve_param} > com_{naïve_param}, com_{naïve_param} > hum_{naïve_param}, 356 hum_{coop_param} > com_{coop_param}, and com_{coop_param} > hum_{coop_param}. 357 358

(2) Analysis based on gaze contingency (analysis 4). Driven by the manip-359 ulation of gaze contingency across proceeding trials within each block, the fourth analysis tested for linear increases of neural activity 360 with increasing positive and negative contingency. At subject level, 361 blocks with different conditions of contingency (0/5, 1/5, 2/5, 3/5, 362 363 4/5, and 5/5 times of JA) were modeled as distinct regressors, separately for the naïve and the cooperative context. At group level, we 364 applied differentially weighted contrasts in order to test for effects 365 of increasing positive contingency (naïve_{increase_IA} and coop_{increase_IA}: 366 -3-2-1123), and for effects of increasing negative contingency 367 (naïve_{increase_NJA} and coop_{increase_NJA}: $3 \ 2 \ 1 - 1 - 2 - 3$). 368

369 (3) Event-related analysis of joint attention (analysis 5). In the final anal 370 ysis we compared how JA and NJA trials were processed in the naïve
 371 and cooperative contexts irrespective of the experimental condition
 372 in which they occurred. Notably, JA and NJA constitute complex

events comprising multiple steps such as the establishment of 373 mutual gaze, a gaze shift to one of the objects and a gaze reaction 374 by the agent. Nonetheless, they can be used in such a fashion 375 because they only differ in one crucial aspect – i.e. the congruency 376 of the agent's gaze reaction which either follows participants' gaze 377 or averts its gaze to the other object, thereby engaging in JA or 378 NJA, respectively (e.g. Materna et al., 2008; Redcay et al., 2012; 379 Schilbach et al., 2010). For this analysis, stimulus events were 380 defined at subject level from trial onset to the trial end defined by 381 the appearance of the blank screen, thereby amounting to a length 382 of 3500 ms. JA and NJA trials were modeled on distinct regressors, 383 separately for the naïve and the cooperative contexts. At group 384 level, the following contrasts were computed: $JA_{naïve} > NJA_{naïve}$, $JA_{naïve} > NJA_{coop} > NJA_{coop} > NJA_{coop}$.

Results

Behavioral

Effect of gaze contingency and context on participants' decisions

Blocks containing invalid trials (naïve context: 6.67%, cooperative 390 context: 6.11%) were excluded from the analysis. In the remaining 391 blocks, results demonstrated a main effect of gaze contingency on 392 participants' ratings, F(2.45, 46.55) = 13.19, p < .001, $\omega^2 = .23$, and a 393 significant interaction between instruction and contingency, F(3.13, 394) $(59.35) = 11.19, p < .001, \omega^2 = .08$. This interaction was scrutinized 395 by separate analyses of ratings in the naïve and the cooperative context. 396 In the naïve context (Fig. 1C), there was a significant main effect of 397 gaze contingency on participants' ratings, F(2.76, 52.38) = 3.55, p = 398.023, $\omega^2 = .03$. Planned polynomial contrasts revealed that this effect 399 was characterized by a significant linear trend, F(1, 19) = 7.84, p = 400.011, $\omega^2 = .29$, thereby indicating that the proportion of blocks and 401 the proportion of 'human'-rated blocks were positively correlated 402 with the number of joint attention trials per block. This means that 403 'human' ratings increased with increasing numbers of joint attention 404 trials and thus argues for a particular importance of congruent reactions 405 during unconstrained interactions. In the cooperative context (Fig. 1D), 406 contingency also had a significant effect on participants' ratings, F(2.79, 407 $(52.95) = 21.79, p < .001, \omega^2 = .27$. This was characterized by a signifi- 408cant linear trend, F(1, 19) = 20.21, p < .001, $\omega^2 = .19$, and a quadratic 409 trend, F(1, 19) = 36.63, p < .001, $\omega^2 = .39$, which indicates that 410 'human' ratings were more closely related to the general contingency 411 of reactions. This suggests that any consistent behavior over an entire 412 block was taken as indicative of a human counterpart and replicates 413 the findings of a behavioral between-subject version of the present 414 task (Pfeiffer et al., 2011). 415

Temporal integration of information

The results of the logistic regression over both interaction contexts 417 are listed in the top half of Table 1. The final three trials showed up as 418 main effects across both contexts, with the fourth trial weighing in the 419 heaviest: if on this trial the agent engaged in joint attention, the chances 420 of rating 'human' are over 1.59 times higher than when the agent looks 421 the other way. Most importantly, however, the second trial loaded only 422 in interaction with condition. The second and third logistic regressions, 423 for the naïve and cooperative contexts respectively, confirmed the per- 424 sistence of the main effects for the final three trials in both contexts 425 (Table 1, bottom half). In the naïve context, already the second trial 426 had a significant influence on the final rating, with 'human' becoming 427 1.38 times more likely than 'computer' if the agent engaged in joint 428 attention on that trial. Such an early component was absent in the 429 cooperative context where the second trial did not load at all. In sum, 430 there is an early influence of trial type in the naïve context, which is 431 absent in the cooperative context, where the integration of information 432 related to decision-making is approximately linear. 433

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t1.1 Table 1

t1.2 Regression coefficients for the logistic regression models.

t1.3		Coeff	SE	Wald	Odds ratio	95% CI
t1.4	Naïve $+$ coop: main effect of trials and interaction of trials	* condition				
t1.5	2nd trial (NJA vs JA) * condition (naïve vs coop)	0.284	0.087	10.70**	1.33	[1.12-1.58]
t1.6	3rd trial NJA vs JA	0.293	0.079	13.63***	1.34	[1.15-1.57]
t1.7	4th trial NJA vs JA	0.464	0.08	34.08***	1.59	[1.36-1.86]
t1.8	5th trial NJA vs JA	0.309	0.08	15.02***	1.36	[1.17-1.59]
t1.9 t1.10	Naïve: main effect of trials					
t1.11	2nd trial NJA vs JA	0.32	0.113	8.07**	1.38	[1.10-1.72]
t1.12	3rd trial NJA vs JA	0.255	0.114	4.98*	1.29	[1.03-1.62]
t1.13	4th trial NJA vs JA	0.432	0.114	14.32***	1.54	[1.23-1.93]
t1.14	5th trial NJA vs JA	0.264	0.115	5.31*	1.3	[1.04-1.63]
t1.15 t1.16	Coop: main effect of trials					
t1.17	3rd trial NJA vs JA	0.328	0.111	8.76**	1.39	[1.12-1.72]
t1.18	4th trial NJA vs JA	0.489	0.112	19.09***	1.63	[1.31-2.03]
t1.19	5th trial NJA vs JA	0.346	0.112	9.52**	1.41	[1.14–1.76]

t1.20 *** p < .001.

t1.21 ** p < .005.

t1.22 * p < .05.

434 Imaging

435 Neural correlates of active engagement in social interaction

Initial analysis of functional imaging data was driven by participants' 436 ratings. Irrespective of interaction context, blocks rated as 'human' 437 (hum_{all block} > com_{all block}) were accompanied by enhanced activation 438 439of the ventral striatum (VS) and the medial orbitofrontal cortex (mOFC; Fig. 3A, Table 2A). In contrast, during blocks rated as 'computer' 440 (com_{all block} > hum_{all block}) there was increased activation of a fronto-441 parietal attention network (FPAN, Corbetta and Shulman, 2002) includ-442 ing the inferior parietal cortex, precuneus, and the lateral prefrontal 443444 cortex (Fig. 3B, Table 2B). When considering only the naïve context, 'human'- versus 'computer'-rated blocks (hum_{naïve_block} > com_{naïve_block}) 445engaged the mesolimbic reward system (Berridge et al., 2009) including 446

the ventral tegmental area (VTA) and the VS (Fig. 4A, Table 2C), 447 while there were no significant results for the reverse contrast 448 (com_{naïve_block} > hum_{naïve_block}). Conversely, in the cooperative 449 context, there was increased activation of the FPAN during 'computer'- 450 rated blocks (com_{coop_block} > hum_{coop_block}, Table 2D), while no regions 451 were more active during 'human'-rated blocks (hum_{coop_block} > 452 com_{coop_block}). 453

Neural correlates of temporal integration of information

Further fMRI analyses (analyses 2 and 3) were driven by the behavioral finding of early versus linear integration of gaze reactions in the naïve and cooperative contexts, respectively. With respect to the early integration during the first two trials of blocks, VS activity during the first two trials of a block was predictive of participants' 'human' ratings 459

454



Fig. 3. Neural activity during blocks rated as 'human' and 'computer'. (A) The experience of interaction with another human participant recruits the ventral striatum (VS) and medial orbitofrontal cortex (mOFC). (B) The experience of an interaction as computer-driven is associated with activity in a fronto-parietal network including the inferior parietal sulcus (IPS), precuneus (PC), premotor cortex (PMC), and lateral prefrontal cortex (for all fMRI graphs: statistical threshold is *p* < .05 cluster-level-corrected for multiple comparisons; error bars depict 90% confidence intervals).

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t2.1 Table 2

t2.2 Analyses based on participants' subjective ratings of the nature of their interaction partner ('human' versus 'computer').

Region	Cluster		Side	MNI coordinates			Т
	Size	p _{FWE-corr}		x	у	z	
Whole block							
A) $Hum_{all_block} > com_{all_block}$							
Nucleus accumbens (ventral striatum)	468	.000	R	8	4	-10	4.96
Nucleus accumbens (ventral striatum)			L	-6	10	-8	4.57
mOFC	326	.002	R	4	48	-16	4.61
mOFC			L	-8	42	-12	3.98
B) $Com_{all \ block} > hum_{all \ block}$							
Supramarginal gyrus	2919	.000	R	52	-42	36	4.88
Intraparietal sulcus			R	34	-60	44	4.88
Precuneus			R	10	-60	40	4.67
Intraparietal sulcus	1513	.000	L	-30	-48	32	5.63
Inferior frontal gyrus	1455	.000	R	40	56	-2	5.04
Lateral orbital sulcus			R	46	48	-12	4.93
Middle frontal gyrus			R	52	38	22	4 39
Middle frontal gyrus	1207	000	R	32	6	60	4 89
Superior frontal sulcus	1207	.000	R	22	14	42	4.03
Inferior frontal surcus	222	012	K I	22	14 EC	42	4.02
	552	.015	L	-30	50	2	4.59
) nullinaïve_block > Collinaïve_block	000	000	р	10	4	10	F 17
Nucleus accumbens (Ventral striatum)	836	.000	ĸ	10	4	-10	5.17
Medial orbitofrontal cortex			R	6	22	- 10	4.40
Putamen			R	24	20	0	4.14
Anterior cingulate cortex	299	.020	L	-8	32	6	4.54
Anterior cingulate cortex			R	10	28	16	3.75
Nucleus accumbens	248	.039	L	-10	2	-2	4.19
Putamen			L	-8	16	2	4.14
Medial orbitofrontal cortex			L	-8	28	-12	3.98
Substantia nigra/subthalamic nucleus	243	.043	L	-6	-6	-16	4.53
Ventral tegmental area			R	6	-24	-18	4.46
Ventral tegmental area			L	-6	-20	-18	4.07
) $Com_{coop_block} > hum_{coop_block}$							
Intraparietal sulcus	10,451	.000	R	36	-44	34	6.23
Precuneus			R	8	-58	42	6.11
Supramarginal gyrus			R	50	-44	36	6.03
Intraparietal sulcus			L	-32	-54	40	5.87
Inferior frontal sulcus	6743	.000	R	28	52	4	6.56
Inferior frontal gyrus			R	40	56	-2	6.29
Middle frontal gyrus			R	32	8	60	6.21
Middle frontal gyrus	936	.000	L	-50	24	34	6.47
Lateral orbital gyrus	868	.000	L	-35	56	-8	5.17
Inferior frontal gyrus			L	-34	48	2	4.98
First two trials of block							
E) Hum _{naïve_early} > com _{naïve_early}							
Nucleus accumbens (ventral striatum)	704	.012	L	-12	6	-6	4.35
Caudate nucleus (head)			L	-10	18	2	4.08
Putamen			L	-18	18	-8	3.92
Medial orbital gyrus			L	-22	14	16	3.93
05							
Parametric increase over block							
$Hum_{coop_param} > com_{coop_param}$							
Nucleus accumbens (ventral striatum)	719	.000	R	6	6	-4	4.49
Nucleus accumbens (ventral striatum)			L	-6	10	-8	4.45
Putamen			R	20	14	-10	3.84
G) Com _{coop_param} > hum _{coop_param}							
Angular gyrus	474	.001	R	42	-64	52	4.25
Angular gyrus			R	48	-64	34	4.07
Inferior frontal gyrus	201	.051	R	44	30	24	4.13

exclusively in the naïve context ($hum_{naïve_first} > com_{naïve_first},$ Fig. 4B, 460 Table 2E). On the contrary, only in the cooperative context, linear 461 parametric analyses including trial progression as a parametric regres-462 sor revealed an increase of VS activity with increasing trial progression 463 over the full length of blocks rated as 'human' (hum_{coop_param} > 464com_{coop_param}, Fig. 4C, Table 2F). Neural differentiation of social inter-465action therefore occurs early during naïve interactions while developing 466 over time during cooperative interactions. The latter finding explains 467 the lack of differential activity during the entire block for 'human'- versus 468 469 'computer'-rated blocks in the cooperative context, when activity during the entire block is compared ($hum_{coop_block} > com_{coop_block}$). 470

Neural processing of gaze in interaction

Finally, the agent's gaze behavior was used to analyze fMRI data 472 with respect to gaze contingency (analysis 4) and at the level of single 473 events (analysis 5). In the naïve context, single joint attention trials 474 (JA_{naïve} > NJA_{naïve}) recruited regions associated with the 'social brain 475 network' (Frith, 2007) involving the bilateral anterior cingulate cortex 476 (ACC), and the left amygdala, medial prefrontal cortex (mPFC), temporal pole, and superior temporal sulcus (Fig. 5, Table 3). However, the 478 analysis focusing on effects of gaze contingency (naïve_{increase_JA}) 479 revealed increases of activity in the bilateral paracentral lobule, but 480 not in social brain regions (Table 4A). In the cooperative context, 481

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Fig. 4. Modulation of reward processing by interaction context. (A) In the naïve context, blocks rated as 'human' recruit mesolimbic reward areas relative to 'computer'-rated blocks. This includes the ventral tegmental area (VTA) and the ventral striatum (VS). (B) The activity of the VS is predictive of participants' ratings already during the first two trials of a block. (C) In the cooperative context, activity in the ventral striatum (VS) unfolds over the time course of interaction blocks (i.e. with increasing trial progression) rated as 'human'.



Fig. 5. Event-related analysis of joint attention in the naïve context. Event-related analysis of single events of joint attention revealed activation in regions of the social brain network including the medial prefrontal cortex (mPFC), amygdala (Amy), and the anterior region of the superior temporal sulcus (aSTS). In addition, activity in the paracentral lobule (PL) was enhanced.

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t3.1 Table 3

t3.2 Event-related analyses of gaze reactions comparing JA with NJA trials.

t3.3	Region	Cluster	Cluster		MNI coordii	Т		
3.4		Size	$p_{FWE-corr}$		x	у	Z	
t3.5	$JA_{naïve} > NJA_{naïve}$							
t3.6	Precentral gyrus	3207	.000	R	26	-22	60	5.86
t3.7	Postcentral gyrus			R	32	-30	62	5.31
t3.8	Postcentral gyrus			L	-20	-40	56	5.05
t3.9	Middle cingulate cortex			R	12	-16	42	4.66
t3.10	Middle cingulate cortex			L	-8	-2	34	4.60
t3.11	Paracentral lobule			R	4	-24	48	4.57
t3.12	Paracentral lobule			L	-8	-24	48	4.56
t3.13	Amygdala	510	.001	L	-22	-6	-14	4.82
t3.14	Medial orbitofrontal cortex			L	-22	8	-22	4.28
t3.15	Putamen (ventral striatum)			L	-20	8	-6	3.80
t3.16	Thalamus	410	.003	L	-4	-18	14	4.66
t3.17	Superior temporal sulcus (anterior region)	398	.004	L	-46	-6	-8	4.59
t3.18	Temporal pole			L	-54	8	-14	3.93
t3.19	Ventromedial prefrontal cortex	364	.006	R	4	44	-16	5.17
t3.20	Anterior cingulate cortex			R	4	36	10	3.90
t3.21	Anterior cingulate cortex			L	-4	38	2	3.61

there was no differential activity at single-trial level ($JA_{coop} > NJA_{coop}$). Instead, results showed an increase of activity with increasing positive contingency (coop_{increase_JA}) in the dorsal striatum, the thalamus, the ACC and the mPFC (Fig. 6A, Table 4C). This indicates that the social brain network is recruited by behavioral consistency. Increasing negative contingency (coop_{increase_NJA}) recruited the FPAN (Fig. 6B, Table 4D).

489 Discussion

The present study aimed at unraveling the neural substrates of the subjective experience of engagement in social interaction with another person in real-time. We made use of an interactive eye-tracking paradigm in which participants indicated whether they experienced an interaction as human- or computer-mediated based on the gaze

t4.1 Table 4

t4.2 Analysis based on the contingency of the agent's gaze behavior. The number of joint
 attention (JA) trials per interaction block was used as a parametric regressor. Both the
 contrasts referring to increasing numbers of JA and increasing numbers of non-joint atten tion (NJA) trials were reported to obtain information about the neural integration of
 positive and negative contingencies of gaze reactions.

t4.7	Region	Cluster		Side	MNI coordinates		es	Т
t4.8		Size	$p_{\rm FWE-corr}$		x	у	z	
t4.9	A) Naïve _{increase_JA}							
t4.10	Paracentral lobule	217	.002	R	4	-32	54	3.89
t4.11	Paracentral lobule			L	-2	-22	58	3.63
t4.12 t4.13	R) Naïve							
t4.10	Superior occipital gyrus	277	009	R	30	-78	20	4 09
t4.15	Middle occipital gyrus	2	1000	R	30	-72	32	3.97
t4.16 t4.17	C) COODimension 14							
t4.18	Caudate nucleus	3048	.000	L	-16	14	-6	5.38
t4.19	Anterior cingulate cortex			R	2	20	22	5.15
t4.20	Caudate nucleus			R	22	20	4	5.02
t4.21	Putamen			L	-18	14	0	4.98
t4.22	Thalamus	495	.000	R	18	-16	12	4.20
t4.23	Thalamus			R	0	22	6	3.98
t4.24 t4.25	D) Coop _{increase NIA}							
t4.26	Precuneus	2493	.000	R	10	-58	48	6.20
t4.27	Intraparietal sulcus			R	40	-46	44	5.53
t4.28	Superior parietal lobule			R	36	-60	62	5.09
t4.29	Supramarginal gyrus			R	46	-36	40	4.96
t4.30	Middle frontal gyrus	932	.000	R	50	24	34	5.91
t4.31	Middle frontal gyrus			R	36	12	60	4.49
t4.32	Intraparietal sulcus	878	.000	L	-36	-56	40	4.77
t4.33	Inferior frontal gyrus	869	.000	R	32	60	8	5.10
t4.34	Lateral orbital gyrus			R	44	48	-14	4.68

behavior of a virtual agent (Pfeiffer et al., 2011). Behavioral judgments 495 of humanness and the accompanying neural activations were influ- 496 enced substantially by the interaction context. When participants 497 interacted with a naïve-interaction partner, the congruency of gaze 498 reactions provided the major cue to humanness of the partner. When 499 the interaction partner was explicitly cooperative, general contingency 500 as compared to mere congruency of gaze reactions was interpreted as 501 indicative of being in interaction with another human being. These re- 502 sults constitute a within-subject replication of an extensive between- 503 subject pilot study (Pfeiffer et al., 2011), thereby implicating a universal 504 difference in mindset between unconstrained and cooperative interac- 505 tions. In-depth regression analyses of the influence of trial type with 506 increasing trial progression revealed that there was an early influence 507 of trial type (i.e. whether a trial was a JA or an NJA trial) in the naïve 508 context, whereas there was an increasing influence of trial type in the 509 cooperative context. This strongly suggests fundamental differences in 510 the integration of information as a function of interaction context. This 511 is complemented by neuroimaging results showing that the subjective 512 experience of being engaged in social interaction is predicted by early 513 ventral striatal activation in the naïve context. In contrast, during coop- 514 erative interactions, activity in this region increased differentially with 515 increasing trial position in those interaction blocks rated as human. 516 Taken together, these findings provide first-time evidence that the 517 mere subjective experience of social interaction with another human 518 is sufficient to recruit the mesolimbic reward system, including the 519 VTA, the VS, and the mOFC (Alcaro et al., 2007). Furthermore, they 520 argue for different functions of the reward system during unconstrained 521 and cooperative social interactions. 522

The rewarding nature of social interactions

523

The present results provide a fundamental extension of previous 524 studies on social rewards. In addition to the more general observation 525 that inert social stimuli recruit the VS similar to monetary rewards 526 (Izuma et al., 2008; Spreckelmeyer et al., 2009), neuroeconomic studies 527 have demonstrated an involvement of both mOFC and ventral striatum 528 in social interactions. For instance, Rilling et al. (2002) scanned participants playing a Prisoner's Dilemma Game with another person or a 530 computer. In each round, players could choose to defect or to cooperate, 531 with cooperation representing the riskier choice in terms of monetary 532 outcome. Mutual cooperation generally led to increased activity in the 533 anterior cingulate cortex, the mOFC, and the VS. However, the VS was 534 not activated during cooperation with a computer, thus suggesting 535 that activity in this area is specifically related to positive reinforcement 536 by mutual cooperation with a human conspecific. Using multi-round 537

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Fig. 6. Temporal integration of gaze reactions in the cooperative context. (A) Parametric increases of activity with increasing numbers of joint attention trials per block in the caudate nucleus (NC), the putamen (Put), the thalamus (Thal), the anterior cingulate cortex (ACC), and the medial prefrontal cortex (mPFC). (B) Parametric increases of activity with increasing numbers of non-joint attention trials per block in the FPAN including the precuneus (PC), intraparietal sulcus (IPS), and regions of the IFG and MFG corresponding to the dorso- and ventrolateral prefrontal cortex. Parameter estimates are only shown for the maxima of the largest clusters.

trust games, it has accordingly been demonstrated that both the intention to trust someone (King-Casas et al., 2005) and another person's
reputation for positive reciprocity are encoded in the striatum (Phan
et al., 2010).

While these findings suggest a role of reward-related processes dur-542ing human social encounters, they rely on static social stimuli or com-543plex economic interactions and do not answer the question whether 544the experience of human social interaction per se recruits the reward 545system. Furthermore, in other studies employing a human-computer 546 distinction subjects were informed a priori whether they would be 547interacting with another person or a computer program (e.g. Decety 548et al., 2004; McCabe et al., 2001; Sanfey et al., 2003). This prevents an as-549550sessment of participants' phenomenological experience of an interaction as social (De Jaegher and Di Paolo, 2007). In contrast, the present 551 study required participants to determine the nature of their counterpart 552553via the interaction itself and hence focuses on the subjective experience.

The results reported here raise the question whether the engage-554555ment in social interaction and the processing of rewards share common anatomical substrates. Intriguingly, a recent study revealed a significant 556correlation between social reward dependence - i.e. a measure of an in-557dividual's propensity to engage in social interaction - and gray matter 558density in the VS and the mOFC (Lebreton et al., 2009a). Another mor-559560phometric study found a positive correlation between mOFC volume 561and participants' capacity to infer intentions from stories describing social interactions (Powell et al., 2010). These studies suggest an overlap 562563between structural predispositions for the engagement and performance in social interactions and brain regions involved in the process-564565ing of rewards and thereby lend support to the major finding of this study. 566

While social affiliation is among our most basic needs (Baumeister 567and Leary, 1995), caution must be exercised because not any kind of so-568cial interaction is necessarily related to reward and positive affect. For 569example, studies using designs involving competition with a human 570counterpart have not found reward-related neural activations in situa-571tions of explicit competition rather than cooperation (Decety et al., 5722004; Polosan et al., 2011). Furthermore, it has long been known that 573574intergroup relations constitute an important determinant of the emotional valence of an interaction (Cikara and Bavel, 2014) — for ex- 575 ample, interacting with a member of an out-group might foster conflict 576 and negative emotions such as fear and disgust, while the interaction 577 with in-group members is related to positive emotions (e.g. Rilling 578 et al., 2008). 579

The 'wanting' and 'liking' of social interactions

The processing of rewards has been divided into 'wanting' and 581 'liking' components (Berridge et al., 2009). In the naïve context, striatal 582 activity during the first two trials reliably predicted that an interaction 583 will be rated as 'human'. Concordantly, post-hoc ratings revealed that 584 participants relied on their intuition in this context (Fig. 6B), and pre- 585 ferred thinking about the behavior of a human conspecific rather than 586 a computer when making the decision (Fig. 6D). There are two possible 587 interpretations of this finding. The first possibility is that the VS encodes 588 a prediction signal. It has been repeatedly shown that the VS is involved 589 in the prediction of rewards (e.g. Bromberg-Martin et al., 2010; Schultz 590 and Dickinson, 2000). Specifically, dopaminergic neurons of the nucleus 591 accumbens encode a reward prediction error which relates to the differ- 592 ence between a predicted reward and the reward which actually occurs 593 (Schultz et al., 1997). It is hence possible that the early activation of the 594 VS in human-rated blocks within the naïve context represents a reward 595 prediction signal. It has further been argued that neural activity related 596 to reward prediction should be involved in encoding the contingency 597 between a stimulus potentially predicting reward and the actual reward 598 (Schultz, 2006). In the case of our study, however, there is no measur- 599 able contingency between the second trial of a block and the continuing 600 trial progression because trial order is completely randomized. This 601 implicates that the VS should not be able to calculate a reliable reward 602 prediction error. 603

In other words, the agent's behavior during the first two trials is actually inconclusive regarding the nature of the counterpart. Therefore, it is possible that the early striatal activation in human-rated blocks in the naïve interaction context might relate to the 'wanting' component associated with the human need to interact (Baumeister and Leary, 1995). 608 Albeit speculative, this interpretation would be consistent with the 609

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610 previous observation that the VS conveys automatic incentive signals to 611 the mOFC during initial stages of impression formation (Kim et al., 612 2007). If such an association of the VS with the motivational drive for in-613 teraction could be confirmed in future studies, these results might con-614 tribute to a larger picture of the VS as an automatic valuation system 615 which encodes preferences irrespective of stimulus modality and task 616 demands (Lebreton et al., 2009b).

Although our results do not provide a direct proof of this idea, one 617 618 might speculate that if a need for interaction represents the 'wanting' 619 component, its fulfillment by the actual experience of engagement in in-620 teraction might correspond to reward 'liking'. Behaviorally, this idea 621 gains support by participants' post-experience ratings which indicate 622 that social interactions are experienced as more pleasant than non-623 social interactions (Fig. 2C). The subjective hedonic experience of rewards has been attributed to the mOFC rather than the VS (for recent re-624 views see Diekhof et al., 2012; Peters and Büchel, 2010). Interestingly, 625 the mOFC was active during blocks rated as 'human' irrespective of in-626 teraction context, which might possibly reflect a general 'liking' of 627 being engaged in interaction. Although task structure does not allow 628 any direct proof of this interpretation, post-experiment questionnaires 629 did not provide any hint to a difference in the perceived pleasantness 630 of naïve and cooperative human interactions. This might be interpreted 631 632 as evidence that neural activity related to the subjective experience of 633 reward should not be affected by the context of the interaction. Indeed, our results show that the interaction context exclusively modulates VS 634 function and thus implicate that activation of the mOFC - and not the 635 VS - might be related to the pleasantness of being in interaction with 636 637 another human. At present, however, explanations which address such detailed functional segregations must remain speculative. Future 638 studies involving carefully devised online interaction paradigms specif-639 ically aimed at differentiating the desire for human interaction and the 640 641 pleasure of being engaged in interaction are needed to confirm these 642 hypotheses.

In a more general framework, the concept that social interaction rep-643 resents a reward in itself is supported by previous studies indicating 644 that social exclusion - which can be regarded as an externally forced 645 disengagement from social interaction - is correlated with activity in 646 647 the pain network (Eisenberger et al., 2003). Specifically, novel social encounters create instant expectations regarding another person's behav-648 ior whose violation is correlated with activation of the anterior 649 cingulate cortex, an important component of this network (Somerville 650 et al., 2006). Moreover, the fulfillment of such expectations might re-651 cruit the reward system and thereby pave the way to the establishment 652of a prolonged relationship (Baumeister and Leary, 1995) which is con-653 sequently assigned with high reward-value in future interactions 654 655 (Fareri et al., 2012).

656 Accumulation of value in cooperative interactions

Importantly, there are ultimate as well as proximate definitions of 657 658 cooperation. The former relate to the survival value of a behavior, 659 whereas the latter relate to the underlying mechanisms (West et al., 2007). In its ultimate definition, cooperation is a behavior selected to 660 create mutual benefit for an actor and a recipient (e.g. Fehr and 661 662 Rockenbach, 2004). It often requires the actor to sacrifice an immediate 663 reward (i.e. reward discounting) in order to create a mutual, but delayed benefit for both actor and recipient (Axelrod, 1984). However, co-664 operation has also been described as a form of behavioral coordination 665 which is a proximate mechanism required for obtaining mutual benefit 666 (e.g. Noë, 2006; Taborsky, 2007). Obviously, the introduction of a coop-667 668 erative interaction partner in the present study is not directly related to evolutionary fitness but rather to behavioral coordination. Accordingly, 669 behavioral results (Fig. 1D) showed that - irrespective of overall con-670 gruency - coordinated behavior is judged as indicative of a human in-671 672 teraction partner. This replicates results of a behavioral pilot study which assessed naïve and cooperative interactions in a between- 673 subject design (Pfeiffer et al., 2011). 674

Neuroimaging data complemented these behavioral observations. 675 As expected, the cooperative context was also associated with reward 676 processing. Notably, however, there was no early activation of the VS 677 as in the naïve context, but a gradual increase of striatal activity with in- 678 creasing trial progression. Considering that the human interaction part- 679 ner allegedly facilitated participants' decisions, consistent behavior had 680 to be detected by an accumulation of information over time rather than 681 by trusting initial intuitions (Pfeiffer et al., 2011). The question arising 682 here is whether the differential increase of VS activity in blocks rated 683 as human relates to a general accumulation of evidence for a choice 684 (e.g. Heekeren et al., 2008) or to an accumulation of value inherent to 685 that choice (e.g. Rangel et al., 2008). In our opinion, the differential in- 686 crease of VS activity over cooperative interaction blocks rated as 687 human is reflective of value rather than evidence accumulation. The lat- 688 ter has mainly been investigated in studies on perceptual decision- 689 making and is considered to be an effortful and noisy process due to 690 fuzzy category boundaries (Ratcliff and McKoon, 2008). In contrast, 691 the decision criterion for social interaction during cooperation is com- 692 paratively straightforward because only behavior that is highly contin- 693 gent is taken as evidence for the agent being controlled by another 694 human 695

A recent study directly investigated whether VS activation during 696 decision-making is related to the accumulation of evidence in general 697 or the accumulation of value (Gluth et al., 2012). In a buying task, a 698 number of positive and negative ratings of a product were sequentially 699 disclosed to participants. The general disclosure of the ratings correlated 700 with activity in the pre-SMA and anterior insula. As this activity was in-701 fluenced neither by the valence of the ratings nor by the buying deci-702 sion, it was argued to reflect the accumulation of evidence. In contrast, 703 the VS specifically updated the representation of value when positive 704 ratings were disclosed. This can be directly compared to our study: In 705 each trial, novel information regarding the nature of the interaction 706 partner is revealed in the form of the agent's gaze reactions. Each trial 707 of an interaction block rated as 'human' during cooperative interactions 708 therefore must have been interpreted as positive evidence that the agent 709 is controlled by a human interaction partner. Furthermore, the specific-710 ity of striatal activation for 'human'-rated blocks argues against general 711 evidence accumulation. The differential linear increase of VS activity 712 with these trials thus reflects the accumulation of value rather than 713 evidence per se (Fig. 3C), which is consistent with the previously 714 described role of this region in encoding benefit signals during 715 decision-making (Basten et al., 2010). 716

Contextual modulation of gaze processing in social interaction

The contextual modulation of the neural processing of the agent's 718 gaze reactions allows a deeper understanding of the integration of infor-719 mation underlying reward-based decisions. First insights come from 720 event-related analyses of JA and NJA. In the naïve context, activity in 721 the mPFC and aSTS was confined to single joint attention trials. The in-722 volvement of these regions in the inference of mental states suggests 723 that the social salience of gaze behavior is processed in a trial-by-trial 724 fashion (Redcay et al., 2012; Schilbach et al., 2010). Furthermore, activa-725 tion of the reward system is confined to single events of joint, but not 726 non-joint attention (Gordon et al., 2013; Schilbach et al., 2010), thereby 727 indicating that making someone follow your gaze represents a reward 728 in itself. In contrast, in cooperative interactions, single events are only 729 indicative of a human counterpart when part of a contingent behavior. 730 Accordingly, positive contingency was processed by the dorsal striatum, 731 while negative contingency recruited the FPAN. Possibly, this interplay 732 of reward and attention networks reflects a distribution of cognitive re-733 sources required to ensure that joint attention is only considered as a so-734 cial cue in cases of high contingency. The dorsal striatum is also 735 recruited in iterated trust-games (King-Casas et al., 2005), which 736

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require participants to monitor cooperators' actions across multiple 737 738 rounds and demand similar temporal binding of contingent information as the present task (McCabe et al., 2001). Furthermore, it plays a role 739 740 whenever participants experience contingency between their actions and a reward (Tricomi et al., 2004). This is consistent with the recent 741 observation that successful initiation of joint attention results in an in-742 creased experience of agency (Pfeiffer et al., 2012), and hence suggests 743 that the reward value of cooperative interactions relies on the experi-744 745 ence of contextually meaningful contingencies between one's own 746 actions and another individual's behavior.

747 Limitations of the present study

Despite the novelty of our findings, there are several limitations with
 respect to study design and the interpretation of the results.

First of all, it must be emphasized that no interaction in our study is 750 an actual interaction with a real human interaction partner. It would 751 therefore be misleading to claim that the paper discusses the neural 752substrates of engagement in human social interaction. Instead, task 753 design elicited participants' subjective experience of being engaged in 754 interaction with a human counterpart. Although it is conceivable that 755756 the underlying neural mechanisms are similar, the distinction between 757 subjective experience and actual engagement must be kept in mind when interpreting the results. 758

Directly related to the first limitation, a more general limitation is 759 imposed by the interaction task itself. Although ecological validity and 760 761 behavioral realism of the interactive eye-tracking paradigm are high (e.g. Fox et al., 2009; Schroeder, 2002), the gaze-based interactions are 762 still comparably inflexible in contrast to everyday social interactions 763 764 which are rich in dynamics and sensory detail. However, while some 765EEG studies have investigated more dynamic interactions (e.g. Dumas 766 et al., 2010; Lachat et al., 2012; Tognoli et al., 2007), possibilities to do so are limited in MRI scanners which are required to detect activity in 767 subcortical structures related to motivational and reward processes 768(for a methodological discussion see Pfeiffer et al., 2013). For this rea-769 770 son, neuroimaging studies of real-time social interactions are currently 771 still limited by a trade-off between social realism and technical feasibility. To move towards even more naturalistic interactions, future gaze-772 based tasks could involve important modulators of our experience of 773 social interaction such as emotional expressions (Adams and Kleck, 774 7752005) or culture (Krämer et al., 2013).

Third, it must be noted here that the present study was not explicitly 776 designed to disentangle the neural mechanisms underlying the motiva-777 tional desire for social interaction on the one hand and the pleasantness 778 of being engaged in interaction on the other. To some extent, the corre-779 780 sponding discussion is thus speculative. More work is clearly needed to uncover the precise roles of the VS and mOFC in encoding the motiva-781 tional aspects of 'online' social interactions (Schilbach et al., 2013). 782 Such studies would also need to include refined behavioral measures 783 of the subjective pleasantness of social interactions which could then 784 785 be included in parametric analyses of functional imaging data. In 786 addition, it would be helpful to obtain indicators of participants' propensity to engage in social interaction, for example by assessing their 787 social reward dependence using Cloninger's Temperament and Charac-788 789ter Inventory (Cloninger et al., 1993).

790 Besides these conceptual issues, there are also some methodological caveats. The first concerns the lack of randomization of the order of in-791 teraction contexts due to the importance of keeping participants naïve 792 with respect to the task in the naïve context. Despite the fact that behav-793 ioral results replicate those of a between-subject study (Pfeiffer et al., 794 2011) and that participants were given an extended practice session 795 to prevent novelty and habituation effects, we cannot fully exclude 796 the possibility of sequence effects. Future studies should therefore use 797 designs allowing a more direct comparison of unconstrained and coop-798799 erative interactions.

The final methodological aspect relates to the limited number of 800 blocks per experimental condition (i.e. six), which decreases statistical 801 power and thereby prevents in-depth assessment of mechanisms relat- 802 ing to reward prediction and accumulation of evidence in general. As reward prediction plays an important role in virtually all decision-making 804 tasks (Berridge et al., 2009; Daniel and Pollmann, 2014), future studies 805 would have to be designed in such a way that the motivational and 806 learning-related aspects of VS function can clearly be disentangled. 807

Taken together, we believe that in light of the scarcity of studies in- 808 vestigating social encounters in real-time and despite the limitations 809 discussed above, the present study provides important insights into 810 the motivational mechanisms underlying the subjective experience of 811 engagement in social interaction (Becchio et al., 2010; De Jaegher 812 et al., 2010; Schilbach et al., 2013). 813

Conclusion

In sum, this study demonstrates how the neural systems possibly 815 sustaining the active engagement in social interaction can be examined 816 using a novel, interactive paradigm. It provides first evidence that the 817 social nature of human primates rests upon an urge to interact and 818 upon the rewarding nature of the active participation in social interac- 819 tions. The present results hence further endorse the proposal of a 820 human predisposition for cooperation (Tomasello, 2009) by suggesting 821 that a fundamental motive for cooperation could be the sustainment of 822 an interaction with another person. A final note concerns the potential 823 of the present study to foster our understanding of autism spectrum dis- 824 orders (ASD). It has recently been claimed that autism is primarily an 825 impairment of social motivation, with disturbances of both 'wanting' 826 and 'liking' of social rewards (Chevallier et al., 2012). Although first 827 studies support this idea by demonstrating hypoactivation of the nucle- 828 us accumbens during the anticipation of social rewards (Delmonte et al., 829 2012; Richey et al., 2014), there are no studies examining the brains of 830 persons with ASD while they are actively engaged in social interaction. 831 It is hence conceivable that the present paradigm could provide a tool to 832 test the social motivation hypothesis under ecologically valid but 833 controlled conditions. 834

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Conflict of interest

The authors declare no competing financial interests. 845

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