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

Introduction

In the hierarchy of human needs, the need to affiliate with others has been located directly after physiological and prior to egoistic needs related to self-actualization and esteem (Maslow, 1943). Accordingly, an intrinsic motivation for social interaction unique to the human species has been proposed (Baumeister and Leary, 1995; Tomasello, 2009). Over the last decade, multiple neuroeconomic studies have indeed found reward-related brain activity during social interactions (Rilling and Sanfey, 2011). Two key regions of the reward system are the ventral striatum (VS) and the medial orbitofrontal cortex (mOFC) which have been implicated in the anticipation and consumption of rewards (Berridge et al., 2009). While the VS has been specifically linked to the anticipation of rewards and the computation of reward prediction errors (Báez-Mendoza and Schultz, 2013; Daniel and Pollmann, 2014), the mOFC appears to be involved in the subjective experience of reward (Peters and Büchel, 2010) as well as value-guided decision making (Noonan et al., 2012). While many studies indicate a link between social interaction and the reward system (Krach et al., 2010; Rilling and Sanfey, 2011), the application of economic games to study social interaction typically involves high-level concepts such as trust, fairness, cooperation, or competition (Fehr and Camerer, 2007). As a consequence, the claim that experiencing engagement in interaction with others per se is rewarding has never been put to the test.

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

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

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

The interaction task applied in the present study was designed to create situations in which the gaze-based interaction with a virtual agent induced either the subjective experience of being engaged in human social interaction or the subjective experience of being in a non-social interaction — i.e. with a computer program. To this end, each block of the interaction task comprised five trials in which the 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 the interaction task because it is a core component of naturalistic social interactions (Mundy and Newell, 2007). Participants believed that during each block the agent was either controlled by a computer algorithm or a human interaction partner. In fact, the interaction partner was a confederate and the agent's gaze behavior was always controlled by the algorithm to permit systematic manipulation. This was accomplished by varying the proportion of joint attention trials from zero to five out of five, thereby modifying behavioral contingency over a block. Participants' task was to decide on the nature of their interaction partner based on the agent's reactions during each block. Thereby, the decision between human and computer emerged during the course of the interaction, while other studies explicated this distinction a priori as an independent variable (Gallagher et al., 2002; McCabe et al., 2001; Sanfey et al., 2003). This allowed assessing the neural mechanisms underlying the subjective experience of being engaged in human social interaction (Pfeiffer et al., 2011).

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

Materials and methods

Participants

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

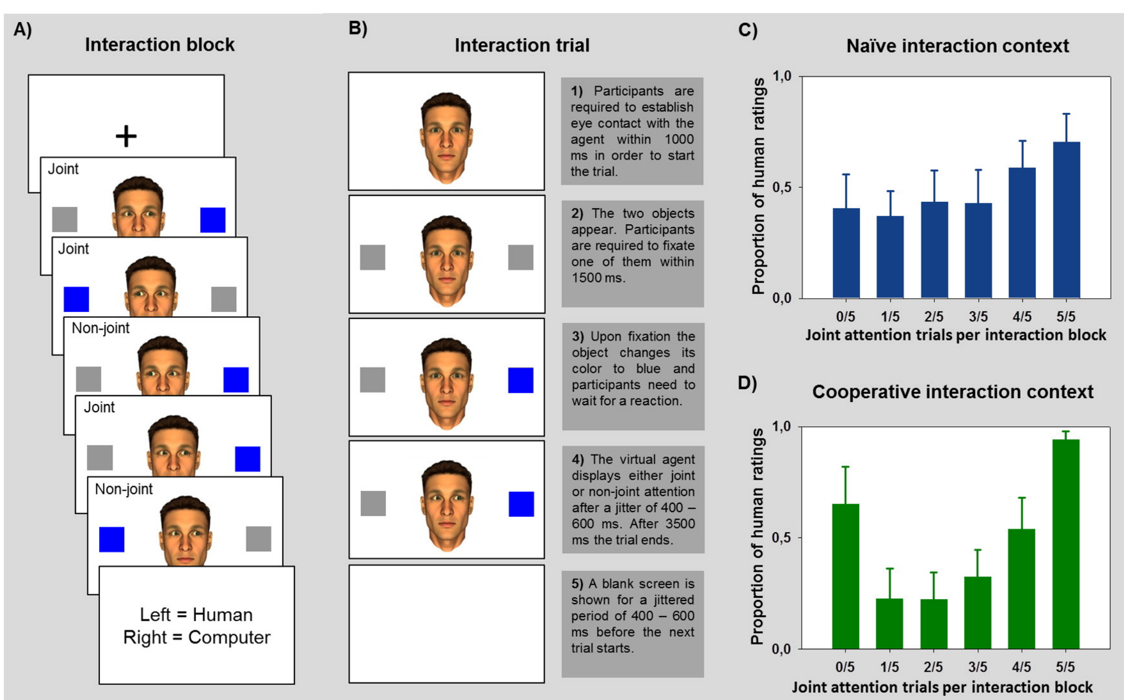

Fig. 1. Task structure and behavioral results. (A) Each interaction block comprises five gaze trials. At the end of each block participants indicate whether they experienced this interaction as social ('human') or non-social ('computer'). This block exemplifies a 3/5 condition in which the agent engages 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.