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Animated brain: A functional neuroimaging study on animacy experience

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A B S T R A C T

Previous research used animated geometric figures to investigate social cognitive processes involved in ascribing mental states to others (e.g. mentalizing). The relationship between animacy perception and brain areas commonly involved in social cognition, as well as the influence of particular motion patterns on animacy experience, however, remains to be further elucidated. We used a recently introduced paradigm for the systematic variation of motion properties, and employed functional magnetic resonance imaging to identify the neural mechanisms underlying animacy experience. Based on individual ratings of increased animacy experience the following brain regions of the "social neural network" (SNN), known to be involved in social cognitive processes, were recruited: insula, superior temporal gyrus, fusiform gyrus, parahippocampal gyrus and the ventromedial prefrontal cortex bilaterally. Decreased animacy experience was associated with increased neural activity in the inferior parietal and inferior frontal gyrus, key constituents of the human "mirror neuron system" (hMNS). These findings were corroborated when analyses were based on movement patterns alone, irrespective of subjective experience. Additionally to the areas found for increased animacy experience, an increase in interactive movements elicited activity in the amygdala and the temporal pole. In conclusion, the results suggest that the hMNS is recruited during a low-level stage of animacy judgment representing a basic disposition to detect the salience of movements, whereas the SNN appears to be a high-level processing component serving evaluation in social and mental inference.

Introduction

Humans like most other animals equipped with visual senses are very sensitive to detect biological motion in their environment. The attribution of liveliness in humans leads to inferences about the perceived intentions, emotions and social relations of others often subsumed under the headings of "mentalizing" and "Theory of Mind" (ToM). These social cognitive capacities are assumed to be a uniquely human capacity (Tomasello et al., 2005). Phenomenologically, biological motion constitutes a complex perceptual input conveying information about physical properties of the moving object (e.g. anatomy, size, and weight), its interrelation to the physical and social environment (e.g. gravity, responses to barriers, approach and avoidance), its behavioural capacities (e.g. sophistication and efficiency in performing motor tasks) and potentially also about psychological processes or mental states (e.g. thoughts, intentions, emotions, etc.). Previous research could amply demonstrate that movement properties as attached to graphically reduced object representations, such as point-light-walkers, are sufficient to perceive an object as alive, to extract various types of information (e.g. the action and identity of the agent) and to make meaningful inferences (Blake and Shiffrar, 2007; Johansson, 1973).

Research on the experience of animacy has put forward the notion that different variations of movement influence our ability to attribute mental states to moving objects independently of their structure or form (Abell et al., 2000; Barrett et al., 2005; Heider and Simmel, 1944; Rochat et al., 1997; Santos et al., 2008; Tremoulet and Feldman, 2006). This ability to perceive and understand others' socially meaningful movements relies on the integration of information into relevant motion cues, leading to ascriptions of mental states to others. Thereby, the perception of animacy requires a type of motion able to trigger the impression that an entity is alive, and that it also possesses some degree of "mind", whether very simple goal-directed (e.g. moving to reach an apple) or complex mental states like mentalizing. Thus, it is our interpretation of other entities as having a mind that ultimately leads to a perception of animacy (Santos et al., 2008; Tremoulet and

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Feldman, 2006). Movement features contributing to animacy perception include self-propelled motion, such as initiation of movement without an external cause (Leslie, 1984; Stewart, 1984), motion contingency (spatial and temporal synchrony) between objects (Bassili, 1976; Blakemore et al., 2003; Johnson, 2003; Johnson et al., 2001), and responsiveness to the motion by the environment (Abell et al., 2000; Blakemore et al., 2003, 2001; Castelli et al., 2000; Leslie, 1984; Michotte, 1946; Rochat et al., 1997; Santos et al., 2008; Schlottmann and Surian, 1999; Schultz et al., 2005; Springer et al., 1996; Tremoulet and Feldman, 2006). In our own study, participants experienced an increase in animacy perception whenever the animations displayed a combination of movement cues (e.g. break of a smooth movement trajectory, approach of one object to the other, and responsiveness from the addressed object to the actively moving object) (Santos et al., 2008).

Social cognition involves the cognitive perceptual and conceptual processes, which helps us make sense of our social world. The amygdala, the orbital frontal cortex and the temporal cortex are considered part of the social brain since its original description by Brothers in 1990 (Brothers, 1990). Subsequently, a vast number of neuroimaging studies have contributed to our present knowledge of how social information is processed at the neural level. Although some debate exist to which brain areas constitute the what is now called "social neural network" (SNN), across different social researchers these include the ventromedial prefrontal cortex (vmPFC) (Adolphs, 2009; Amodio and Frith, 2006; Beer and Ochsner, 2006; Bifulco et al., 2006; Blakemore, 2008; Brothers, 1990; Frith, 2007; Skuse and Gallagher, 2009; Van Overwalle, 2009), the superior temporal sulcus (STS) and gyrus (STG) (Adolphs, 2003; Amodio and Frith, 2006; Beer and Ochsner, 2006; Blakemore, 2008; Frith, 2007; Gallese et al., 2004; Van Overwalle, 2009), the insula (Adolphs, 1999; Blakemore, 2008; Frith and Frith, 2006), the amygdala (Adolphs, 1999, 2001, 2003; Blakemore, 2008; Brothers, 1990; Frith, 2007; Pinkham et al., 2008; Skuse and Gallagher, 2009), the fusiform gyrus (FG) (Adolphs, 2003; Beer and Ochsner, 2006; Blakemore, 2008), and the anterior temporal poles (TP) (Amodio and Frith, 2006; Blakemore, 2008; Frith, 2007; Pinkham et al., 2003). Some of these brain areas are typically implicated in mentalizing processes, essential for social cognition, constituting the ToM neural network: the medial prefrontal cortex, the STS/STG, and the precuneus (Frith and Frith, 2003; Gallagher and Frith, 2003; Gobbini et al., 2007; Van Overwalle and Baetens, 2009). Observing animated movement patterns, independently of the characters shape and form, can elicit increased neural activation in brain areas that are part of the SNN (Blakemore et al., 2003; Castelli et al., 2002; Castelli et al., 2000; Chaminade et al., 2007; Gobbini et al., 2007; Martin and Weisberg, 2003; Schultz et al., 2005, 2004, 2003; Tavares et al., 2008; Wheatley et al., 2007), and in areas that are specifically related to the ToM network. Using animations similar to those developed by Heider and Simmel (1944), Castelli et al. (2000) in a PET study found increased activations in vmPFC and basal temporal regions (fusiform gyrus and TP), when comparing animations eliciting ToM with random motion animations (Castelli et al., 2000). More recently, it was demonstrated an increased activity in the anterior cingulate cortex (ACC), as part of the medial prefrontal cortex, both under the presentation of ToM stories and ToM animations, but not during the observation of simple point-light displays of human motion (Gobbini et al., 2007). In accordance with others (Walter et al., 2004) the authors proposed a crucial role of the ACC in the representation of the social intentions of actions. The STS has also been implicated in processing the kinematics of geometrical figures, in particular related to those properties that are strongly tied to animacy perception such as goal-directed motion (Schultz et al., 2004), contingency between objects (Blakemore et al., 2003) and interactivity (Schultz et al., 2005).

While most neuroimaging studies that have used animated stimuli aimed at evoking ToM in human subjects (Campbell et al., 2006; Castelli et al., 2002; Castelli et al., 2000; Gobbini et al., 2007; Horan et al., 2009; Kana et al., 2009; Russell et al., 2006; Salter et al., 2008), only few studies focused on the neural correlates of animacy experience (Wheatley et al., 2007) and the relation between animacy and social cognition (Martin and Weisberg, 2003; Tavares et al., 2008). Focusing on neural correlates of animacy perception, Wheatley et al. (2007) compared animations of the same object moving with different backgrounds in the absence of any social content, which either lead to interpretations of animacy (e.g. "ice-skating") or of inanimacy (e.g. "spinning-top") (Wheatley et al., 2007). The interpretation of the same motion as animated (depending on background) was sufficient to elicit activations throughout the SNN. Similarly, Tavares et al. (2008) manipulated the attended aspect of two animated circles by instructing the subjects to focus on either the social interaction between them or motion properties such as speed (Tavares et al., 2008). Viewing animations while attending to social cues in contrast to motion properties activated areas previously linked to the SNN, namely the fusiform gyrus, the STS, and the amygdala.

The present study investigates the neural correlates of animacy experience and the parallels between animacy experience and the SNN. In addition, we were interested in identifying movement patterns that strongly influence increases in animacy experience at the neural level. We employed a previously developed paradigm aiming at inducing an increase in animacy experience, which was confirmed behaviourally in our first previous study (Santos et al., 2008). The movies we used range from movies that could clearly be judged as animated to movies that could clearly be judged as least animated, while the majority was more ambiguous. This ambiguity, we believe, was fundamental to induce subjective ratings, so that judgments depended entirely on the individual subjective experience of animacy. The design involves systematic variations of motion parameters shown to successfully induce and parametrically vary the experience of animacy including the degree of interaction between two objects (e.g. approach and responsiveness) (Dittrich and Lea, 1994; Santos et al., 2008; Schultz et al., 2005) and the time delay one object spent in the vicinity of another object (Santos et al., 2008). Subjects saw three-dimensional (3D) animations of two spheres displaying different types of movement sequences, and were instructed to judge each animation as (i) physical, (ii) rather physical, (iii) rather personal or (iv) personal. This allowed a parametric analysis of fMRI data according to increased vs. decreased animacy, based on subjective experience and physical properties of the stimuli.

Materials and methods

Subjects

Fifteen male subjects (mean age $= 26.59 \pm 3.94$) without any past medical history with respect to psychiatric or neurological diseases participated in the study. All had normal or corrected-to-normal vision. Written informed consent was obtained and all participants were informed of the necessary safety precautions involving fMRI experiments prior to the scanning session. The study was approved by the local ethics committee of the Medical Faculty of the University of Cologne, Germany.

Stimuli and design

The stimuli consisted of 104 animations showing two 3D-spheres moving on a black background. The basic scenery comprised one sphere crossing the setting horizontally in the background (sphere1) and one static sphere in the foreground (sphere2). The following stimulus parameters were systematically varied: 1) the time sphere1 spent in the center of the screen: 0 (without break), 100, 200, 400, 600, 800 and 1000 ms ("time delay"); 2) whether the moving sphere1 did approach sphere2 or not ("approach"); 3) whether sphere2