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# Understanding Events

*From Perception to Action*

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Thomas F. Shipley and Jeffrey M. Zacks

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## 14

## Animacy and Intention in the Brain: Neuroscience of Social Event Perception

ANDREA S. HEBERLEIN

While many movements look animate because they are derived from actual biological motion (as discussed in Chapters 11, 12, and 13), some movements are perceived as animate even when the moving objects are geometric objects or blobs. Further, these moving objects may not look merely alive; in many instances, they look like intentional agents, with goals, emotions, and personality traits. Viewers make such anthropomorphic attributions despite being fully aware that the shapes to which they are ascribing these anthropomorphic qualities are animated geometric objects: the impression that the shapes are alive and social is so compelling that it is not amenable to top-down information, as in classic perceptual illusions. When people make these social attributions, a suite of brain regions is recruited, including structures known to be important for processing cues related to people and to emotional information: the amygdala, the fusiform face area (FFA), the temporo-parietal junction (TPJ), and both ventral and dorsal medial prefrontal cortices (VMPFC and DMPFC; Fig. 14.1; also see color insert). Though some of these structures have roles that extend considerably beyond processing social information, this circuit has been dubbed the “social brain” (Adolphs,

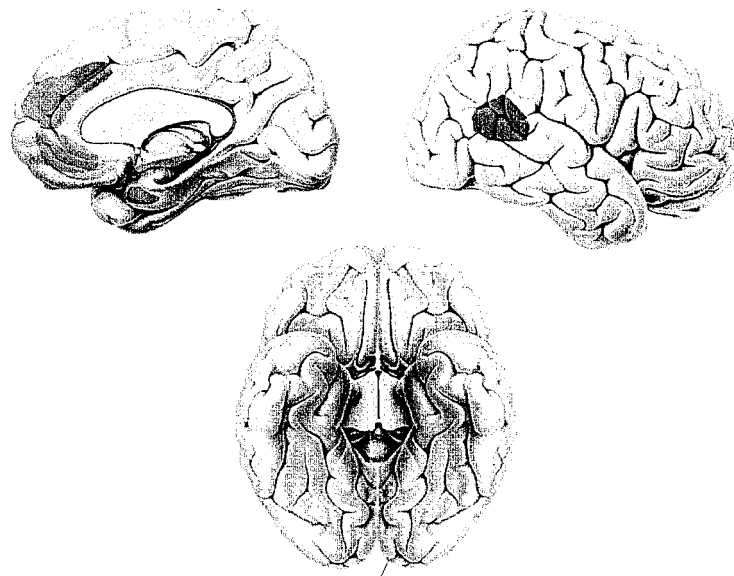


FIGURE 14.1. Brain regions involved in perceiving social events, in three views: medial (upper left), dorsal (upper right), and ventral (bottom). Two regions of medial prefrontal cortex, one more ventral and one more dorsal; the amygdala (shaded region in lower-middle portion of the upper-left figure), buried deep in anterior medial temporal cortex; cortices around the temporo-parietal junction (shaded region in upper-right figure); and the fusiform gyrus (lower left region of bottom figure). Note that in most cases these structures are implicated bilaterally, but here they are indicated only in the right hemisphere.

2003; Brothers, 1990; Skuse, Morris, & Lawrence, 2003) because its components are implicated across a wide variety of social processes.

In this chapter I will explore a set of related concepts, including judgments of animacy, judgments of agency or intentionality, and anthropomorphizing, focusing on the functional neuroanatomy of each process. Anthropomorphizing can be thought of as an illusion: stimuli possessing certain features appear to automatically elicit attributions of mental states and other qualities associated with people, in the face of declarative knowledge that the stimuli are not only not human but, in many cases, inanimate. Studies of illusions are particularly useful in revealing the organization of perceptual processes. Thus, I will focus on studies of anthropomorphizing—that is, the attribution of personhood and person-related features such as emotions, intentions, personality traits,

and beliefs to inanimate objects. I will focus especially on the neural circuitry underlying social attributions based on the kind of minimal stimuli described above, relating these findings to other social processes in which the same neural regions have been implicated. Finally, I will propose a framework relating judgments of animacy, agency or goal, and emotion.

### Social Judgments from Ambiguous Motion Stimuli: Animacy and Anthropomorphizing

Working separately in the early 1940s, Michotte (1946/1963) and Heider and Simmel (1944) examined the movement features that lead to attributions of psychological traits to simple geometric objects. Michotte, extending his work on physical causation, showed that different patterns of movement are interpreted as physically caused versus psychologically caused. For example, if one moving object contacts a second object which then immediately begins moving in the same direction as the initial moving object, the event is interpreted as a transfer of momentum—as physical causation. In contrast, if the second moving object begins moving after a pause, the event is interpreted as being caused by something internal in the second object (i.e., as psychological causation)—the second object moved of its own accord, having *decided* to move, perhaps because it was *convinced* to do so by the first object, or because it was *trying* to escape the other object.

In contrast to these very simple movements, Heider and Simmel's (1944) 2.5-minute-long<sup>1</sup> movie depicts the movements of three geometric objects: a large triangle, a smaller triangle, and a circle. These three objects move around and in and out of the outline of a rectangle, circling and bumping into each other in nonrandom patterns. With very few exceptions, viewers of this movie interpret it as the interactions of three people moving in and out of a house, and include intentions, emotions, personality traits, gender, and relationships in their spontaneous descriptions of the movie. For example, the big triangle is frequently

1. Oddly, successive studies using, allegedly, the original movie have described it as anywhere from 90 seconds to 2.5 minutes long (e.g., Berry et al., 1992; Heberlein & Adolphs, 2004). It is possible that when the original movie was converted to VHS, it was somehow shortened.

described as a *bully* who *intimidates* both of the other characters; the other two are *friends* (or a *couple*) who finally manage to *escape*.

Many studies have followed up both the initial Michotte studies and the Heider and Simmel paper (reviewed in Scholl & Tremoulet, 2000). Studies in the Michotte tradition have primarily attempted to determine which stimulus features lead to perceptions of animacy and agency. In contrast, studies in the Heider and Simmel tradition have focused more on studying the attribution of personality traits and of representational mental states, such as theory of mind. Though the two processes are related, the distinction is a significant one and parallels distinctions that have been made in both developmental and neuroimaging studies of mental state attribution (e.g., Saxe, Carey, & Kanwisher, 2004). In this section, I will first review psychological studies of animacy and agency perception and then discuss studies of anthropomorphizing, or attributing representational mental states based on similar kinds of motion stimuli.

Studies of single objects moving (e.g., Stewart, 1982, summarized in Gelman, Durgin, & Kaufman, 1995; Tremoulet & Feldman, 2000) have illuminated some features that influence animacy judgments. The necessity for a hidden energy source appears to play some role, though only some animations that would require this inference are seen as animate (Stewart, 1982); environmental and/or contextual cues also play some role, so that animacy percepts might be seen as arising from interactions between certain movement patterns and specific environmental cues (Gelman et al., 1995), and very simple featural cues, such as the local orientation of the moving objects, or combinations of velocity and direction changes, influence judgments of animacy (Tremoulet & Feldman, 2000).

Stimuli that contain two or more moving objects often appear more compellingly animate than those depicting only one object, perhaps because each object provides a more rich and variable "context" for the other. Several variations of this have been explored by Bassili (1976), Dittrich and Lea (1994), Opfer (2002), Blythe, Todd, and Miller (1999), and Zacks (2004). Proposing a role for observable goal-directedness before many of the above studies of single moving objects were performed, Bassili showed that temporal contingencies between the movements of two objects influenced whether the objects were perceived as animate (and interacting) or not. Further, the relative directions of the

contingently moving objects influenced the kinds of interactions that were perceived, especially whether the interactions were seen as intentional (chasing, following) or not. When movement paths converged with temporal contingency between movements, both objects, and especially the following object, were seen as intentional, but when movement paths diverged or were random, temporal contingency had less of an effect in creating impressions of agency (Bassili, 1976). Looking specifically at the effect of "following" or pursuit movements, Dittrich and Lea showed subjects movies of multiple moving objects, in which all but one object moved randomly. The nonrandomly moving object followed one of the randomly moving objects, and, as in Bassili's study, the degree to which its movement was seen as animate was affected by variables relating the movement of the "chaser" to the randomly moving objects, especially how closely it tracked its target (Dittrich & Lea, 1994). Opfer (2002) developed two sets of stimuli that were identical in their depiction of a moving "blob" but differed in that one set had moving goal objects that the blob appeared to pursue. Adults and children as young as 5 years old consistently rated the goal-directed objects as more animate than the autonomously moving but not goal-directed blobs. Interestingly, adults and older children did not assign more psychological capacities to the blobs, implying that goal-directed movement is a better cue for animacy than for intentionality (Opfer, 2002).

In contrast to these three studies focusing on animacy from agency or goal-directedness cues, Blythe and colleagues (1999) attempted to parameterize the movement-specific cues that enable judgments of not just animacy but specific interaction intentions from the movements of pairs of objects. Their movement stimuli were created by having two subjects each control a cursor on a computer screen and interact according to assigned roles, including not only chaser/chased but also two individuals playing, fighting, or courting. Many of these displays were identifiable by a separate group of subjects in forced-choice settings, and furthermore they could be categorized correctly by an algorithm based on just a few motion parameters (Blythe et al., 1999). In contrast to Opfer's conclusions, then, Blythe et al.'s findings appear to show that sufficiently complex movement interactions—dependent perhaps on having two self-propelled moving objects, both of which are moving in goal-directed ways—convey not just biological but also psychological content. However, the primary response measure in this study was

forced choice, leaving open the possibility that subjects would not have spontaneously inferred such high levels of intentionality. Zacks (2004) used a different method to explore the effects of movement features on viewers' interpretations of animated objects: viewers were asked to segment activity at "meaningful event boundaries," or the beginnings and ends of parts of a dynamic stimulus, in this case a short movie of two moving geometric objects. The timing of viewers' marked boundaries correlated highly with movement features when the stimuli were created randomly, but less well when the stimuli were created by people following scripts like those used by Blythe and colleagues, such as "chasing" or "fighting." This is particularly interesting because participants showed this pattern of response even when they were given no cues as to the intentions behind these nonrandom stimuli, and, further, even when they were not told that some of the stimuli were goal-directed. Zacks (2004) concluded that while movement features play a major role in how people perceive events, inferences about the goals of the moving objects (or of the agents moving the objects) interact with the information contained in movement features.

Affective information can also be derived from similar animations. Rimé, Boulanger, Laubin, Richir, and Stroobants (1985) used simple Michotte-esque stimuli consisting of two moving dots and asked subjects to rate the level of each of several affective states or traits associated with one of the two dots for each stimulus. Though their conclusion that the stimuli *evoke* emotional perceptions may not be warranted given the constrained nature of the responses, ratings demonstrated a high degree of consensus, including between European and U.S. raters, consistent with the interpretation that the stimuli lend themselves easily to emotional interpretation. Interestingly, when identical stimuli with simple human-like silhouettes were presented instead of dots as the moving objects, consensus between raters was markedly lower than for the dot stimuli (Rimé et al., 1985). People's ability to identify emotions based on fairly minimal movement stimuli is also shown in studies using point-light stimuli, including of both whole bodies (Dittrich, Troscianko, Lea, & Morgan, 1996) and, strikingly, of just single limbs (see Chapter 11 in this volume).

In summary, though autonomous motion itself is not a particularly strong cue for animacy, autonomous movements that appear goal-directed with respect to background contexts, especially when those

contexts are themselves moving objects, are robustly perceived as animate by both adults and children.<sup>2</sup> This suggests that goal-directedness, or agency, is a kind of perceptual primitive and may itself underlie attributions of animacy (Dittrich & Lea, 1994; Scholl & Tremoulet, 2000; Tremoulet & Feldman, 2000). Some of the studies reviewed here, especially Blythe et al.'s (1999) study of different types of interaction, presage the next section on more complex movement stimuli, in which the movements of simple geometric objects elicit attributions not just of animacy but of intentionality and representational mental content as well.

As noted above, Heider and Simmel's original (1944) movie was much longer than Michotte's stimuli, and given the contributions of contextual elements to animacy judgments it should not be surprising that the objects in this movie are robustly seen as animate. The shapes are not merely animate, or goal-directed, however: in contrast to descriptions of the simple Michotte-esque stimuli explored by Opfer (2002), descriptions of Heider-esque stimuli appear to include both psychological and biological attributions (Hashimoto, 1966; Heberlein & Adolphs, 2004; Heberlein, Adolphs, Tranel, & Damasio, 2003; Heider & Simmel, 1944). These attributions appear to be due to movement features or changes in location over time, and not the difference in the objects' shapes: versions of the movie in which the movement information is disrupted via a strobe-like effect were not described in anthropomorphic terms, whereas versions in which the shape information is disrupted by blurring were described much like the original movie was (Berry, Misovich, Kean, & Baron, 1992). Similar stimuli are anthropomorphized in other cultures (Barrett, Todd, Miller, & Blythe, 2005; Hashimoto, 1966; Morris & Peng, 1994), though the specific content of attributions may differ markedly

2. Note that developing concepts of animacy and the cues that elicit animacy and agency categorizations in infants, toddlers, and preschoolers are a rich field of study. Infants under 1 year of age categorize moving objects in terms of their goal-directedness, use other animacy cues such as the presence of eyes and the contingency of behavioral responses to categorize objects as agents, and also appear to reason with regard to teleological intention. Furthermore, supporting the distinction inherent in the present chapter, there are distinct time courses for the development of reasoning about goals as compared to reasoning about representational content such as in theory of mind. I will not review this literature here; instead I point readers toward just a few of the many excellent recent reviews: Csibra, 2003; Johnson, 2003; Mandler, 1992; Rakison & Poulin-Dubois, 2001; and Saxe, Carey, & Kanwisher, 2004.

(Morris & Peng, 1994), and watching them one is struck by the seemingly automatic and obligatory nature of the anthropomorphic impression. Despite knowing that one is watching two-dimensional depictions of simple shapes, the feeling that the shapes have complex intentions, emotions, and personality traits is unsettlingly strong. It has been challenging, however, to devise satisfactory methods for measuring the content and nature of such impressions. Hashimoto (1966) told one group of subjects that the movements they were viewing were of inanimate entities and instructed them to describe them that way. His subjects nevertheless described the movie in anthropomorphic terms, and this has been interpreted as evidence for the automaticity and obligatoriness of this percept. However, this paper not only lacked a systematic coding scheme to assign ratings of levels of animacy but also apparently lacked any effort to blind the experimenter as to the condition in which participants' descriptions were elicited.

More recent studies examining subjects' descriptions of the original Heider and Simmel movie or similar stimuli have utilized a range of dependent measures to operationalize anthropomorphizing, from counting the instances of several categories of anthropomorphisms, such as actions, traits, and social roles (Berry et al., 1992), through very detailed analysis of specific types of anthropomorphic content, such as the percentage of propositions in the total description that contain affective content (Klin, 2000). In a recent study, my colleagues and I (Heberlein, Scheer, McGivern, & Farah, 2006) extended Hashimoto's finding using a more objective measure of anthropomorphizing: a computerized text analysis program known as Linguistic Inquiry and Word Count (Pennebaker, Francis, & Booth, 2001). This program counts words in 74 categories and thus provides an objective measure of the extent to which subjects are including references to or descriptions of anthropomorphic or animate content. Though it is not sensitive to context in the way that human-rater indices are, it has the twin advantages of very high speed and perfect replicability. Replicating Hashimoto (1966), we found that people who had been told before viewing that the movie depicted inanimate objects still included some anthropomorphic content in their descriptions; few described the movies in asocial, inanimate terms. However, relative to subjects given a neutral instruction, they used significantly fewer words in three categories that index such content: Affective and Emotional Processes (e.g., happy, evil), Social Processes (e.g., he,

hers, talk, friend), and Insight (e.g., want, try). In contrast, they did not differ in their use of words in a control category, Motion (e.g., move, go). We tested a more stringent instruction focusing on the description (as compared with the perception) of the stimulus, explicitly forbidding subjects from anthropomorphizing or using language "implying that the shapes have emotions, intentions, or mental states." In this condition, we hypothesized that the percept of intentionality would be strong enough to leak through in verbal responses, despite subjects' efforts to describe it in inanimate terms. Indeed, we found that while subjects were successful to some extent in regulating their word use—they anthropomorphized significantly less than subjects given a completely neutral instruction—they regularly failed, implying that their percepts of animacy and anthropomorphism were too strong to fully override. Furthermore, the rate of speech in subjects given the instruction not to anthropomorphize is significantly slower than that of subjects given a neutral instruction (Heberlein et al., 2006). In summary, movement cues can create percepts of intentionality that are so strong that it is difficult to override them with instructions given before viewing or before describing the movements, supporting the idea that such processes are both stimulus-driven and modular.

I will turn now to an examination of the neural substrates subserving animacy perception and anthropomorphizing from movement cues, but will return to a discussion of the bottom-up and top-down contributions to these processes at the end of the chapter.

### Functional Neuroanatomy of Animacy Perception and Anthropomorphizing

Functional neuroimaging studies have examined the neural circuitry subserving both animacy perception and the attribution of intentionality to simple moving objects. Notably, many of the structures involved in perceiving and interpreting these stimuli are also implicated in a variety of other social cognitive tasks. These structures principally include cortices along the posterior superior temporal sulcus (pSTS) and the temporoparietal junction more broadly, as well as bilateral amygdala, temporal poles, ventral occipital regions including the fusiform gyrus, and ventral and medial prefrontal cortices (see Fig. 14.1; also see color insert). This list overlaps to a striking degree with those regions proposed by Brothers

(1990) to make up the primate social cognitive brain, which she defined as a network of brain regions more or less specialized for perceiving and processing behavioral cues that are relevant for inferring mental states and predicting behavior based on them. Based primarily on neurophysiological studies in nonhuman primates, Brothers' social brain included orbitofrontal cortices, the temporal poles, amygdala, and STS cortices. An area in humans that appears to be homologous to macaque anterior STS, the posterior section of human STS (Logothetis, Guggenberger, Peled, & Pauls, 1999), has revealed regions responsive to the visual perception of human bodies (Downing, Jiang, Shuman, & Kanwisher, 2001); to representations of both whole-body movement and the movement of specific body parts such as mouths, eyes, and hands (reviewed in Allison, Puce, & McCarthy, 2000; also see Chapter 13 in this volume); and to the perception of animacy, goal-directedness, and intentionality.

In functional imaging studies of human subjects, participants have been scanned while viewing or making judgments about animate movements as depicted by simple geometric objects such as triangles or small dots. Because, as noted in the previous section, goal-directedness is a robust cue for animacy, the stimuli in many of these studies appear goal-directed. Brain regions implicated in animacy perception were isolated in contrasts of goal-directed movements as contrasted with physically random (J. Schultz, Imamizu, Kawato, & Frith, 2004), physically but not psychologically causal (Blakemore et al., 2003; Castelli, Happé, Frith, & Frith, 2000), or geometrically patterned movements (Castelli et al., 2000). Activations elicited by viewing such animations partly overlap with those elicited by viewing obviously human goal-directed movements, as contrasted with non-goal-directed movements (Decety et al., 1997; Pelphrey, Morris, & McCarthy, 2004) or with emotional movements (Bonda, Petrides, Ostry, & Evans, 1996). Notably, static animacy cues such as faces or human forms are also processed in a different set of overlapping brain regions; I will return to this point below. Some functional imaging studies did not distinguish between animate, goal-directed movement and intentional<sup>3</sup> movement, the interpretation

3. I use "intentional" in the sense of higher-order levels of intentionality; in the case of movement stimuli, one or more of the moving objects appears to take the intentional stance or, in other words, to attribute mental states to others, not just to have goal-directedness itself.

of which requires the attribution of mental states (i.e., mentalizing); still others focused specifically on mentalizing based on moving object stimuli. Perhaps not surprisingly, the brain regions implicated in this type of anthropomorphizing largely overlap those implicated in attributing mental states to unambiguously human targets.

#### *Animacy and Agency Percepts: Superior Temporal Sulcus*

In a clever isolation of animacy perception from movement, Schultz, Friston, O'Doherty, Wolpert, and Frith (2005) created animations of two autonomously moving discs, in which one appears to chase the other while the "chasee" appears to evade capture. By continuously varying the cross-correlation of the discs' motions, the authors could capture the interactive nature of the movements in a single continuous variable and relate it to both viewers' percepts and their brain activity. Interactive movement stimuli were seen as significantly more animate than control stimuli created by decoupling the movements of the two object (thus replicating Bassili, 1976, and others discussed earlier), and rating of animacy increased with the degree of cross-correlation. Bilateral regions of posterior STS/STG were more active when subjects viewed the cross-correlated movements relative to the uncorrelated movement and activity in these regions increased parametrically with the increase in the relationship of the objects' movements. Notably, this was the case even when subjects were performing a task for which the relationship between the objects' movements was irrelevant (judging how fast both objects were moving), implying that this region is sensitive to animacy cues even in the absence of full attention to this feature (Schultz et al., 2005). However, though it may respond to animacy even with limited attentional resources, this posterior STS/STG region responds *more* to animate or goal-directed stimuli when attention is focused on this aspect of movement: instructing subjects to attend to the contingent nature of animate contingent animations (as opposed to physically contingent collision events and noncontingent animate and physical events) increased activity in posterior STS/STG (Blakemore et al., 2003), and instructing subjects to attend to the strategy employed by a chasing object (predict versus follow the target), as compared to attending to the outcome (success versus failure in catching it), had a similar effect (Schultz et al., 2004). These findings support the idea of a role for posterior STS/S'

in processing animacy cues from goal-directed motion. Also consistent with such a role is the finding that the same pSTS region that is activated in response to biological motion cues demonstrates activity correlated with the moments in a simple animated stimulus that participants code as event boundaries (Zacks, Swallow, Vettel, & McAvoy, 2006). Because these authors used a biological motion localizer, they were able to demonstrate that certain features in the motion of circles and squares elicit activity from the same region that responds to nonrigid, articulated, whole-body movements. Notably, the same region is involved in processing specifically goal-directed human movements (Pelphrey et al., 2004), including in the context of imitation (Decety, Chaminade, Grezes, & Meltzoff, 2002; Grezes, Armony, Rowe, & Passingham, 2003), which appears to be facilitated by attention to goals.

*Intentional and Anthropomorphic Attributions: pSTS, FFA, Amygdala, and mPFC*

Posterior STS/STG, along with several other structures, is also implicated in processing more complex social movements, such as those that are seen as not merely goal-directed but also intentional or representational. Castelli et al. (2000) compared brain activity in participants viewing three types of Heider-and-Simmel-like animations: random or physically constrained movements (e.g., bouncing, star pattern, billiard balls); goal-directed movements (e.g., chasing, fighting); and movements implying higher-level mental content, which they termed “Theory of Mind movements” (e.g., coaxing, mocking, seducing). Four regions—temporoparietal cortex corresponding to pSTS, medial prefrontal cortex, the fusiform gyrus on the ventral occipitotemporal surface, and extrastriate regions of lateral occipital cortex—were more active during viewing of the goal-directed stimuli versus the random stimuli, and all of these were also significantly more active during the theory of mind movies than during the goal-directed ones. In addition, activity in these areas correlated with subjects’ ratings of intentionality in the movies, regardless of the designated movie type (Castelli et al., 2000).

Two other studies employing similar stimulus contrasts have found largely complementary patterns of activation: viewing animated actions that look intentional and social (dancing, swimming, fishing, scaring) compared with objects that are not involved in any such actions

(a cannon, a paper shredder, billiard balls), movies depicting random motion, and static stimuli yielded greater activity in lateral fusiform, right amygdala, bilateral pSTS, bilateral anterior STS, and ventromedial prefrontal cortex (Martin & Weisberg, 2003). These differences are especially noteworthy given the authors’ report that subjects had to be actively prevented from attributing meaning to the random movement stimuli, as pilot testing showed that they would otherwise do so. This implies that some part of the activation difference observed is due to top-down effects, such as a dampening of response in the random movement case or in a ramping-up of response in the social case, or both; I will return to this issue shortly. In a similar study, subjects viewing animations of three interacting geometric objects while judging whether all the objects were “friends” showed greater activity in the fusiform gyrus, amygdala, temporal pole, medial PFC, and STS as compared to viewing somewhat different “bumper car” animations while judging whether all the objects weighed the same amount (Schultz et al., 2003). These experimenters focused particularly on a region of the fusiform cortex that has widely been reported to be critical for processing face information, the “fusiform face area” or FFA (Farah, Wilson, Drain, & Tanaka, 1995; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996). This region responds significantly more to visually presented faces than to any other visual stimulus, though it also responds to other visual stimuli with which the viewer has expertise, especially if processing of the said stimuli occurs holistically (Tarr & Gauthier, 2000). R. Schultz and colleagues localized the FFA on each subject’s brain and confirmed that the fusiform activation—which was also observed by both Castelli and colleagues (2000) and Martin and Weisberg (2003)—was in fact in the face-responsive part of the fusiform gyrus.

There are at least two ways in which one might interpret FFA activity in a social judgment task not containing any faces: FFA might participate in social judgments even when those judgments are made based on nonface stimuli, or the FFA might be potentiated by input from a structure such as the amygdala, which might participate in the detection of socially relevant stimuli and the focus of attention by relevant visual cortices—including FFA and pSTS—onto such stimuli (Schultz et al., 2000). This latter view is consistent both with the finding of greater amygdala activity in two of the above studies (and both of



the two fMRI studies) and with a recent lesion study: a subject with complete bilateral amygdala damage describes the original Heider and Simmel (1944) movie in strikingly inanimate (and therefore also nonanthropomorphic) terms (Heberlein & Adolphs, 2004). As noted above, it is difficult for neurologically intact subjects to describe the movie without references to animacy or mental content, and yet, on two separate testing occasions, patient S. M. gave remarkably consistent inanimate descriptions. For example, her first spontaneous (oral) description of the movie is as follows:

OK, so, a rectangle, two triangles, and a small circle. Let's see, the triangle and the circle went inside the rectangle, and then the other triangle went in, and then the triangle and the circle went out and took off, left one triangle there. And then the two parts of the rectangle made like a [sic] upside-down V, and that was it. (Heberlein & Adolphs, 2004)

#### *Amygdala, TPJ, and mPFC: Roles in Other Social Cognitive Processes*

The amygdala is known to be important for a range of emotional and social processes, including fear conditioning (LeDoux, 1993; Phelps & Anderson, 1997); recognizing certain basic emotional facial expressions, most commonly fear (Adolphs & Tranel, 2000; Adolphs et al., 1999); processing facial cues relevant to trustworthiness ratings (Adolphs, Tranel, & Damasio, 1998; Winston, Strange, O'Doherty, & Dolan, 2002); and processing other-race faces (Cunningham et al., 2004; Hart et al., 2000; Phelps et al., 2000; but see Phelps, Cannistraci, & Cunningham, 2003). It receives visual information through both cortical and noncortical pathways, the latter via the superior colliculus and pulvinar nucleus of the thalamus (Jones & Burton, 1976), and projects widely, including extensive projections to visual and other sensory cortices, as well as to frontal and temporal regions (Amaral & Price, 1984). These projections are thought to reflect the amygdala's role in directing attention to salient environmental stimuli, including certain features of socially relevant stimuli such as emotional faces (Adolphs, 2002; Adolphs et al., 2005; Whalen, 1998; Whalen et al., 2004). Thus the amygdala's role in processing anthropomorphic movements may be related to the detection of specific movement features that communicate information about emotional or goal-directed content and the

direction of attention to facilitate further processing of the relevant stimuli by, for example, FFA, pSTS, and prefrontal regions. Amygdala damage has also been linked to impairments in difficult theory of mind tasks (i.e., those requiring more complicated levels of processing than simple false belief tasks; Fine, Lumsden, & Blair, 2001; Shaw et al., 2004; Stone, Baron-Cohen, Calder, Keane, & Young, 2003), though it appears to have an effect primarily when damage was acquired early in life, suggesting that its role in such processes lies in acquiring relevant social knowledge and not in representing mental content in an online fashion (Shaw et al., 2004).

As noted above, pSTS cortices (and cortices around the temporo-parietal junction more generally) have been implicated in a wide range of social cognitive tasks (Allison et al., 2000). Several authors have hypothesized that the implication of posterior STS regions in animacy perception, biological motion perception, body-form perception, and mental state attribution is due to a common process underlying these different behaviors (e.g., J. Schultz et al., 2004). However, studies directly comparing two or more such processes in individual subjects imply that they are in fact dissociable. For example, by comparing areas of maximal activation in individual subjects, Saxe and colleagues have dissociated regions of TPJ that are activated during the representation of other people's mental states (but not physical representations of people; Saxe & Kanwisher, 2003) and for viewing goal-directed action (but not merely articulated body motion; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). Note that both of these two regions are distinct from two other nearby regions: the extrastriate body area, which responds to representations of human body forms (Downing et al., 2001), and the pSTS region responsive to articulated biological motion (Grezes et al., 2001; Grossman et al., 2000; Servos, Osu, Santi, & Kawato, 2002). This distinction between attribution of goal states and theory of mind processes parallels a distinction seen in development, leading Saxe, Carye, and Kanwisher (2004) to conclude that these are not the same system at two levels of elaboration, but rather two distinct, and separately instantiated, cognitive systems. However, because these regions are very close together, they may not be distinct in group analyses, and thus it is difficult to compare the coordinates of regions activated across studies. Further careful comparisons across tasks focusing on animacy perception, goal attribution, and mental state attribution—to humans

in narratives, to physical representations of moving humans, and to minimal stimuli such as geometric objects—will help to elucidate the relationships among the underlying processes.

The role of medial prefrontal cortices in mental-state attribution is similarly controversial. Substantial evidence exists supporting a role for mPFC in person-related cognition. However, interpretations differ as to its specialization, with data from some studies supporting a role in representing mental states (Amodio & Frith, 2006; Fletcher et al., 1995; Gallagher et al., 2000; Mitchell, Banaji, & Macrae, 2005a) and making trait judgments (Mitchell, Neil Macrae, & Banaji, 2005), as well as in making trait, emotion, and intention judgments relevant to one's self (den Ouden, Frith, Frith, & Blakemore, 2005; Gusnard, Akbudak, Shulman, & Raichle, 2001; Mitchell, Banaji, & Macrae, 2005b; Ochsner et al., 2004); in certain kinds of moral judgments (Greene & Haidt, 2002); and in semantic knowledge about people (Mitchell, Heatherton, & Macrae, 2002). However, bilateral lesions affecting medial prefrontal regions do not necessarily affect theory of mind abilities (Bird, Castelli, Malik, Frith, & Husain, 2004), implying that these cortices are not critical for mental state attribution. Consonant with this interpretation, Saxe and colleagues failed to find mPFC activation in a contrast between stories requiring theory of mind and stories containing physical descriptions of people, though a region in TPJ was robustly more active in this contrast (Saxe & Kanwisher, 2003); they interpret these findings to mean that mPFC is involved in representing people but not specifically mental states. The debate is far from settled, however: a recent paper by Mitchell, Banaji, and Macrae (2005a) found equivalent dorsal mPFC activity during a task requiring judgments of the applicability of psychological-trait words such as "friendly" (as compared to abstract concept adjectives such as "celestial") to people or to dogs. Judgments as to whether body parts were in fact present on people or on dogs (as compared to whether objects such as "bolt" were) did not yield a similar activation difference for either person or dog judgments. For the time being, one can summarize by saying that medial prefrontal regions appear to be important for many person-related judgments, especially but not consistently those requiring thinking about mental content such as beliefs or traits. Such a role is entirely consistent with the repeated finding of mPFC activity in interpreting the movements of geometric shapes in anthropomorphic terms, given that subjects imbue

the shapes with intentions, personality traits, and beliefs as they watch the stimuli. However, it does not address how or why certain stimuli appear to elicit such interpretations.

#### **Automaticity and Top-Down Versus Bottom-Up Contributions to Animacy and Intentionality**

As noted above, certain stimuli, such as the original Heider and Simmel (1944) movie, seem to automatically elicit judgments of animacy and intentionality, despite the difficulty of measuring this automaticity. Interestingly, reports of neuroimaging studies using such stimuli have referred to the difficulty of keeping participants from interpreting similarly complex stimuli in anthropomorphic terms. For example, R. Schultz et al. (2003) noted that they did not use the original set of social stimuli while asking nonsocial questions because pilot testing revealed that participants "were not able to consciously stop seeing the films as social stories" (p. 417). Castelli et al. (2000) noted that a substantial minority of participants anthropomorphized in their descriptions of even the "random" stimuli; furthermore, they found no difference in activation between a condition in which participants viewed each movie after having been told what each type was ("a random movement," "a simple interaction," or "an interaction with feelings and thoughts") as compared to one in which they did not receive such cuing. This implies that the stimuli were sufficiently different in the dimension described by the cues that participants did not differ in how they saw the stimuli, whether they were biased by the cues or not; the activation differences and associated differences in the level of intentionality in participants' descriptions were driven completely by stimulus features. Consistent with a limited role for instruction, as compared to movement features, in how participants perceive intentions from animated shapes, Zacks and colleagues (2006; Zacks, 2004) have reported similar segmenting behavior and neural activity when the same set of stimuli are described as either goal-directed or random in nature.

A recent study by Wheatley, Milleville, and Martin (in press) specifically addresses the question of stimulus-driven versus top-down contributions in anthropomorphizing animated geometric objects. Participants viewed the same animated geometric objects superimposed onto two different backgrounds, one that biased an animate interpretation and

one that biased an inanimate one. (For example, a spinning cone with a knob on top could look like an ice skater when spinning on a frozen pond but like a top when on a floor strewn with toys). The brain regions recruited more when visual contexts biased animate interpretations largely overlapped the social brain structures implicated in the interpretation of stimuli that look animate due to movement alone: lateral fusiform gyrus, STS, amygdala, insula, mPFC, and posterior cingulate cortex. Thus, top-down information affects the activity of these regions, and not just perceptual information. Wheatley and colleagues observed a similar pattern for merely *imagining* movements in the animate-biasing as compared to the inanimate-biasing background. They theorize that the social brain network may prime further social processing, such as attributions of emotions, personality traits, and mental states.

### Conclusion

The network of social brain structures implicated across all of these studies of anthropomorphic animations appears to be recruited by certain movement features, but also by conceptual knowledge about animacy and agents in the absence of any movement differences.

What are the stimulus features that lead to anthropomorphic or intentional attributions (and, presumably, the recruitment of the social brain components)? Agency or goal-directedness cues alone do not appear to be sufficient: as J. Schultz (Schultz et al., 2004, 2005) and Blakemore (Blakemore et al., 2003) both note, animations that are animate by virtue of being goal-directed (Blakemore's stimuli also appeared to imply perceptual tracking) do not elicit intentional or mentalistic processing or recruit mPFC and other brain regions frequently associated with such processing. Contextual cuing alone is also insufficient to explain the existing data, as robust animate and intentional percepts or interpretations can be elicited from objects moving on backgrounds including only a single rectangle, as in the original Heider and Simmel (1944) movie or Castelli's more recent ones (2000). One clue might come from the finding, discussed above, of reduced anthropomorphizing subsequent to amygdala damage (Heberlein & Adolphs, 2004). The original Heider and Simmel movie contains several prominent emotionally laden interactions: the big triangle and the small triangle "fight"; the big triangle "corners" the circle inside the house, "threatening" it; the two

smaller shapes "escape" and run away; the big triangle becomes angry and destroys the house. Note that most of these emotional events are negative ones: the sole positive interaction event is when the smaller triangle helps the circle escape from the house, and the two smaller shapes spin around one another, touching tenderly. Though most participants describe it as "kissing," "high-fiving," or "celebrating" when asked about this event, few participants include the interaction in their spontaneous oral descriptions; in contrast, the negative events, especially the fight and the destruction of the house, are almost always included (Heberlein et al., 2006). Negative events thus seem more salient, and in fact may prompt or bootstrap a social interpretation of the movie. Consistent with this interpretation, damage to the amygdala, a structure important for processing emotionally salient stimuli and especially threat-related cues, may lead to reduced anthropomorphizing in response to the Heider and Simmel (1944) movie because of abnormally low sensitivity to the emotional significance of certain movement features. It remains to be seen whether a similar deficit would be observed in responses to anthropomorphic movement stimuli in which the salient emotional events were positive; such studies are underway.

A general lack of sensitivity to emotional cues also affects spontaneous interpretations of the Heider and Simmel movie: patients with damage to right somatosensory cortices—a region known to be important for emotion recognition from tasks such as labeling or rating faces, vocal prosody, and body movements—not only use fewer emotional words in their descriptions of the Heider and Simmel (1944) movie but also use fewer words in other categories indicative of anthropomorphizing, such as gendered pronouns and social role words (Heberlein et al., 2003). However, the descriptions given by these patients are not as inanimate as that given by patient S. M., perhaps because their brain damage was incurred in adulthood, allowing normal development of social knowledge, or because their intact amygdalas allowed some awareness of the negative events of the movie to proceed and to bring online other social cognitive processing.

The existence of a negativity bias in agency attribution has recently been documented in studies of neurologically intact participants: Morewedge (2006) recently showed that negative outcomes are more likely to bias judgments of intentionality. For example, participants were more likely to believe that a person and not a computer was behind

an unusually selfish offer in an ultimatum game, while unusually generous offers were thought to be generated by a computer. Similarly, unexpected negative outcomes were more likely to lead to anthropomorphisms of computers and cars than unexpected positive outcomes (Morewedge, 2006; we curse our computers for crashing, after all, but do not thank them for remembering to auto-save). Such a negativity bias makes sense given an influential theory for humans' evolved predisposition to anthropomorphize: humans and proto-humans who were biased to interpret rustles in the forest as predators and react accordingly, and to respond to approaching conspecifics as though they had (potentially aggressive) intentions, would be, in the long run, more successful, despite the potential costs associated with overinterpretation (such as positing forest elves and sacrificing to weather gods; Guthrie, 1995). Given this account, it may be unsurprising that negative events draw more social-attributional attention than positive ones; the costs associated with failing to detect potential benefactors are presumably less than those associated with failing to detect agents with the intent to end one's existence. This theory accounts for the observations of experimenters, noted above, that it is difficult to dissuade subjects from interpreting even random movements as inanimate; unless an obvious mechanical interpretation can be found, we seem curiously predisposed to attribute animacy and intention to ambiguous objects.

In conclusion, emotional cues, and possibly primarily negative emotional cues, may be featural primitives. Like agency or goal-directedness cues, we may automatically detect the presence of certain emotion-relevant features from static as well as dynamic cues, a process in which the amygdala would be hypothesized to play a critical role. Taking this into account, an account of how we perceive and interpret social events from motion might run something like this<sup>4</sup>: In parallel, the cortical

4. Note that it is never simple to ascribe a cognitive process to a given brain region, and in this case the levels at which I am specifying cognitive processes are likely to be far too complex. Given the non-social-cognitive tasks that engage these same, or largely overlapping, neural regions and the level of resolution at which we are discussing both neuroanatomy and cognitive process, any framework that attempts to lay out how a complex stimulus such as a social event is interpreted will doubtless be subject to considerable revision. With this major caveat, I'll still make an attempt at such a framework here.

and subcortical visual processing streams process movement and form information. More specialized extrastriate cortical regions respond to stimulus features normally associated with animate entities, which include pSTS regions for movement that appears biological by virtue of its path or its articulation and FFA for face-like configurations. Amygdalar responses to both static and dynamic cues could serve to direct attention, via projections to these and other cortical regions, to objects possessing emotion-relevant features like large sclera (Adolphs et al., 2005; Whalen et al., 2004) or, perhaps, certain movement features. By feed-forward mechanisms, conceptual information about mental-state contents and person-related features could be accessed and related to perceived behaviors via some combination of medial prefrontal cortices, TPJ, and other cortical regions. In cases of contextual cuing, activation of such information could prime pSTS, FFA, and amygdala by feedback mechanisms. In summary, the combined detection of emotional content and goal-directed agents may engage social attention for the perception and attribution of intentions, relationships, and social narratives—the complex and richly interwoven fabric that supports our daily social interactions.

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## Section 2 Segmenting Events