

# NeuroImage

www.elsevier.com/locate/ynimg NeuroImage xx (2005) xxx - xxx

# **Dissociation between emotion and personality judgments: Convergent evidence from functional neuroimaging**

Andrea S. Heberlein<sup>a,b,\*,1</sup> and Rebecca R. Saxe<sup>c,d,1</sup>

<sup>a</sup>Children's Hospital of Philadelphia, PA 19104, USA

<sup>b</sup>Center for Cognitive Neuroscience, University of Pennsylvania, 3720 Walnut St., Philadelphia,

PA 19104, USA

<sup>c</sup>Brain and Cognitive Sciences, MIT, MA 02139-4307, USA

<sup>d</sup>Department of Psychology, Harvard University, MA 02138, USA

Received 5 November 2004; revised 14 June 2005; accepted 21 June 2005

Cognitive neuroscientists widely agree on the importance of providing convergent evidence from neuroimaging and lesion studies to establish structure-function relationships. However, such convergent evidence is, in practice, rarely provided. A previous lesion study found a striking double dissociation between two superficially similar social judgment processes, emotion recognition and personality attribution, based on the same body movement stimuli (point-light walkers). Damage to left frontal opercular (LFO) cortices was associated with impairments in personality trait attribution, whereas damage to right postcentral/ supramarginal cortices was associated with impairments in emotional state attribution. Here, we present convergent evidence from fMRI in support of this double dissociation, with regions of interest (ROIs) defined by the regions of maximal lesion overlap from the previous study.

Subjects learned four emotion words and four trait words, then watched a series of short point-light walker body movement stimuli. After each stimulus, subjects saw either an emotion word or a trait word and rated how well the word described the stimulus. The LFO ROI exhibited greater activity during personality judgments than during emotion judgments. In contrast, the right postcentral/supramarginal ROI exhibited greater activity during emotion judgments than during personality judgments. Follow-up experiments ruled out the possibility that the LFO activation difference was due to word frequency differences. Additionally, we found greater activity in a region of the medial prefrontal cortex previously associated with "theory of mind" tasks when subjects made personality, as compared to emotion judgments. © 2005 Elsevier Inc. All rights reserved.

*Keywords:* Simulation; Social cognition; Mentalizing; Personality attribution; Emotion recognition; Double dissociation; Lesion overlap; Pointlight walkers; Biological motion

Available online on ScienceDirect (www.sciencedirect.com).

# Introduction

In everyday reasoning about other minds, observers frequently appeal to both the target's emotional states ("she smiled because she was happy") and her enduring personality traits ("she smiled because she's friendly"). These processes share some apparent similarities: both emotion recognition and personality attribution depend on serial processes, with both rapid, relatively automatic components and more effortful, conscious components (Fiske, 1993; Gilbert, 1998; Macrae and Bodenhausen, 2000; Adolphs, 2002). However, results from developmental psychology suggest that these two processes rely on distinct psychological mechanisms. Emotions are among the first mental states that young children attribute to other people (Wellman and Bartsch, 1988), with 2-year-olds able to correctly select an appropriate facial expression for a character in a vignette (Wellman and Woolley, 1990). In contrast, children do not appear to understand the relationship between personality traits and typical behaviors before age 5 (see review by White, 1995).

Two processes may develop sequentially and yet come to rely on the same psychological and neural mechanisms in the adult mind and brain. However, a recent lesion overlap study (Heberlein et al., 2004) suggests that in this case, the processes remain at least partially distinct into adulthood. Heberlein et al. showed that different neural regions are critically involved in attributing emotional states vs. personality traits: lesions in a region overlapping right postcentral and supramarginal gyri produced abnormalities in attributing emotions, whereas lesions around the left frontal operculum led to deficits in attributing personality traits, based on the same body movement stimuli.

Normal adult observers can reliably make both emotion judgments and personality trait judgments based on static or brief dynamic stimuli depicting nonverbal behavior (Ekman

<sup>\*</sup> Corresponding author. Center for Cognitive Neuroscience, University of Pennsylvania, 3720 Walnut St., Philadelphia, PA 19104, USA. Fax: +1 215 898 1982.

E-mail address: heberlei@psych.upenn.edu (A.S. Heberlein).

<sup>&</sup>lt;sup>1</sup> These two authors contributed equally to this work.

<sup>1053-8119/\$ -</sup> see front matter  ${\odot}$  2005 Elsevier Inc. All rights reserved. doi:10.1016/j.neuroimage.2005.06.064

and Friesen, 1971; Scherer, 1986; Ambady and Rosenthal, 1992; Wallbott, 1998). One form of nonverbal cue, body movement, can be minimally portrayed using point-light walkers, created by affixing small lights to an actor's body and filming him moving in the dark (Johansson, 1973). From the movements of 8–12 such moving dots, observers readily recognize biological motion (the characteristic articulated motion of a human body), and can also recognize gender (Kozlowski and Cutting, 1977), the identity of familiar individuals (Cutting and Kozlowski, 1977; Loula et al., 2005), emotion (Dittrich et al., 1996; Makeig, 2001; Pollick et al., 2001), and even personality traits (Gunns et al., 2002; Heberlein et al., 2004).

Most investigations of the neural substrates of biological motion have focused on the recognition of biological motion per se (e.g., Grossman et al., 2000; see review in Allison et al., 2000), or on the perception of intentional actions (Bonda et al., 1996), rather than on the attribution of higher-level social and emotional information. In the current study, we sought converging evidence from fMRI for the findings of Heberlein et al. (2004), i.e., that emotion and personality trait judgments from body movement cues rely on at least partly distinct neural circuitry. We examined the neural activity in neurologically normal subjects making, by turns, emotion and personality trait judgments about the same set of point-light walker stimuli. This study is, to our knowledge, the first attempt to use fMRI to distinguish the neural substrates of two different kinds of social attributions based on the same biological motion cues.

#### Materials and methods

#### Subjects

Seven healthy right-handed adults (5 women) participated for payment. All subjects had normal or corrected-to-normal vision and gave informed consent to participate in the study as approved by the local Internal Review Board.

# Stimuli

# Construction of point-light stimuli

12 small lights were attached to the major joints and the head of a male actor. He was filmed moving in a dark room, while portraying specific emotions and personality traits (see examples at http://ccn.upenn.edu/farahlab/andrea/). Twelve stimuli were chosen that had been used in the prior lesion study, and that elicited strong inter-subject reliability on both emotion and personality attribution tasks. Stimuli were edited so that all were 6 s long, by looping shorter stimuli and cropping the beginning and end of longer stimuli as needed. They were played in pseudorandom order, counterbalanced across subjects.

## Task

Subjects were first told about the two types of judgments they would be asked to make: emotions and personality traits. They were then trained on the probe words: four emotion words (happy, sad, angry, afraid<sup>2</sup>) and four personality trait words

(trustworthy, outgoing, friendly, adventurous<sup>3</sup>), and learned threeletter codes for each. While being scanned, subjects first saw a cue telling them what judgment they were to make, then a single 6-s point-light walker stimulus, and finally the three-letter code for the probe word (e.g., "hap"). During the presentation of the three-letter code, subjects were asked to rate the fit of the emotion or trait word to the stimulus they had just seen on a 4point Likert scale, corresponding to four buttons on a button box. Each trial, consisting of the task cue, stimulus, and probe, was treated as a block. All movies were rated in both task conditions, and task conditions alternated, interleaved with fixation; the first task was counterbalanced between subjects and across runs within subjects.

#### fMRI data acquisition and analysis methods

Subjects were scanned in the Siemens 1.5 T scanner at the MGH NMR center in Charlestown, MA, using a head coil. Standard echoplanar imaging procedures were used (TR = 2 s, TE = 30 ms, flip angle 90°). Twenty 5 mm thick axial slices covered the whole brain, excluding the cerebellum.

MRI data were analyzed using SPM 99 (http://www.fil.ion. ucl.ac.uk/spm/spm99.html) and in-house software. Each subject's data was motion corrected and then normalized onto a common brain space (the MNI template). Data were then smoothed using a Gaussian filter (Full Width Half Maximum = 8 mm), and high-pass filtered during analysis. Every experiment used a blocked design, and was modeled using a boxcar regressor.

Individual subjects' ROIs were defined anatomically. Based on sulcal and gyral landmarks, spheres of 3 mm radius were centered on the anatomical location in each subject's brain most closely corresponding to the peaks of lesion overlap derived from the previous lesion study (Heberlein et al., 2004). A very small radius was chosen to maximize anatomical specificity.

Within the ROI, the average Percent Signal Change (PSC) relative to fixation baseline (PSC = 100 \* raw BOLD magnitude for (condition – fixation) / raw BOLD magnitude for fixation) was calculated for each condition (averaging across all voxels in the ROI, all TRs in the block, and all blocks of the same condition). This calculation yielded a single grand average PSC value per ROI for each condition. These values were then entered into repeated measures statistical tests. Because the definition of the ROIs was independent from the data used in the repeated measures statistics, Type I errors were drastically reduced.

<sup>&</sup>lt;sup>2</sup> The prior lesion study had used these four words, with an additional option of 'neutral', in a forced-choice task. These are four of the 6 Ekman (Ekman and Friesen, 1971) "basic emotions"; the other two, disgust and surprise, are not well conveyed by body movement and so were not used.

<sup>&</sup>lt;sup>3</sup> Note that each of these four words represents one end of a continuum loosely based on four of the "big five" personality traits (McCrae and Costa, 1987), specifically Reliability, Extraversion, Warmth/Agreeableness, and Novelty Seeking. While the words we chose may not exactly capture these dimensions, they nevertheless were reliably interpreted as stable traits by subjects. Because our goal was independent of the validity of these constructs, it was important to us only that the trait words we chose were recognizable exemplars of qualities generally agreed upon to be more stable over time than the basic emotion words we used. We used four, and not five, to match the number of emotion words.

# **ARTICLE IN PRESS**

A.S. Heberlein, R.R. Saxe / NeuroImage xx (2005) xxx-xxx



Fig. 1. (a) Group analysis of areas more active during emotion than during personality judgments, random-effects analysis, n = 7, P < 0.001, uncorrected (shown are both a relevant slice from SPM and a projection onto a 3D template brain). Compare with panel (b), from Heberlein et al. (2004), the lesion overlap of subjects who were more abnormal on emotion than on personality judgments.

In order to further characterize the role of each region in the attribution of mental states, we divided the bold response into three time periods: cue (first 2 TRs), movie (next 3 TRs), and response (final 2 TRs). The mean PSCs from each period were then entered into a separate repeated measures ANOVA for each region.

## Results

# Behavioral data

A comparison of mean reaction times from the two tasks showed that personality judgments took significantly longer than emotion judgments (emotion: 1.67 s; personality: 2.06 s; paired 2-tailed *t* test, P < 0.01).

# Group analyses

Group analyses comparing whole-brain activation during emotion judgment trials and personality judgment trials showed a significantly greater activation in a small region of the right postcentral gyrus (MNI peak [63 -30 39]) for emotion trials as compared to personality trials (Fig. 1a).<sup>4</sup> Notably, this region of activation corresponded with the region of maximal lesion overlap among subjects in the previous lesion study who showed greater impairment on the emotion task than on the personality judgment task (Fig. 1b).

In comparisons of personality trials with emotion trials, both a large region encompassing left frontal operculum/premotor regions  $[-54\ 18\ 12]$  and a region around the posterior superior temporal sulcus (pSTS,  $[-63\ -51\ 6]$ ) were more active (Fig. 2a). Similarly, these regions of activation corresponded with the region of maximal lesion overlap among subjects in the previous lesion study who showed greater impairment on the personality task than on the emotion judgment task (Fig. 2b).

#### ROI results

The average central voxel of the anatomically defined right somatosensory/supramarginal gyrus ROI (RSS/SMG) was [60 –21 21]. In the RSS/SMG ROI, as predicted by the lesion results, the overall BOLD response was higher when subjects were judging the emotion of the walker (percent signal change (PSC): 0.25) than when subjects were judging personality (PSC: 0.14, P < 0.01, paired-samples *t* test). The effect of condition in the RSS/SMG was confirmed by a repeated-measures ANOVA (F(1,7) = 21.7, P < 0.005) and did not interact with time period (F(2,14) = 0.65, n.s.; Fig. 3).

The average central voxel of the left frontal operculum (LFO) ROI was [-54 24 6]. In the LFO ROI, as predicted by the lesion results, the overall BOLD response was higher when subjects were judging the personality of the walker (PSC: 0.45) than when subjects were judging emotion (PSC: 0.20, P < 0.005, paired-samples t test). A repeated-measures ANOVA further revealed both a main effect of condition (Personality > Emotion, F(1,7) = 32.8, P < 0.001) and an interaction with time period (F(2,14) = 6.04, P < 0.02). Inspection of the means revealed that the difference between personality and emotion conditions in the LFO was greater during the movie and response phases of the block than during the cue (Fig. 4).

The profile of response in the RSS/SMG was significantly different from the response in the LFO (interaction of region by condition, F(1,7) = 87.1, P < 0.001, repeated measures ANOVA).

#### Follow-up experiments

These data confirmed the results of the lesion study: making emotion judgments engaged right postcentral/supramarginal regions more than making personality trait judgments, and making personality trait judgments engaged left frontal opercular/premotor areas more than making emotion judgments. However, the left prefrontal opercular area which was more active for personality judgments is also one which has been shown to be more active with increasing difficulty of verbal tasks (Smith and Jonides, 1997; Jonides et al., 1998; Poldrack et al., 1999; Chein and Fiez, 2001) and semantic ambiguity (e.g.,

<sup>&</sup>lt;sup>4</sup> We are reporting only voxel-wise significant (P < 0.001) activations in regions about which we had hypotheses. Given the small number of subjects, and our focus on the region-of-interest analyses, we do not attempt to draw conclusions about any other significant activations.

# **ARTICLE IN PRESS**

A.S. Heberlein, R.R. Saxe / NeuroImage xx (2005) xxx-xxx



Fig. 2. (a) Group analysis of areas more active during personality than during emotion judgments, random-effects analysis, n = 7, P < 0.001, uncorrected (shown are both a relevant slice from SPM and a projection onto a 3D template brain). Compare with panel (b), from Heberlein et al. (2004), the lesion overlap of subjects who were more abnormal on personality than on emotion judgments.

Thompson-Schill et al., 1997; Kan and Thompson-Schill, 2004; Rodd et al., 2005). The mean frequency of use of the emotion words was 58.75; the mean frequency of use of the personality trait words was 19.25 (Francis and Kucera, 1967). To control for the possibility that the lower frequency of the personality words per se led to greater LFO activation during this task (and, possibly, to the lesion overlap results in the previous study), we designed two follow-up experiments using altered versions of the task. Both of these follow-up experiments differed from the initial task in two ways: they used long lists of emotion and trait words which were matched for overall mean frequency of usage. and they reduced the memory component of the task. Both followed the same overall structure of the initial task, in that a cue was presented, followed by the stimulus, and then by a probe word. In neither follow-up task were subjects trained on the candidate probe words, and because of this, they were always presented with the whole probe word (see below for lists of probe words used).



Fig. 3. Time course of activation in RSS/SMG ROI, comparing emotion vs. personality rating conditions (Experiment 1, n = 7). Yellow bar corresponds to cue presentation, blue to stimulus presentation, and green to probe word presentation and answering. *Y* axis is percent signal change. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### Subjects

Eight healthy right-handed subjects (4 women), none of whom had participated in the initial experiment, participated in both follow-up experiments, with order of tasks counterbalanced between subjects.

#### Stimuli

The 12 movies from Experiment 1 were also used in Experiments 2 and 3.

#### Task

#### Probe words for both Experiments 2 and 3

The probe words used for both experiments were as follows: Emotion words: afraid, angry, blissful, cheerful, delighted, enraged, exultant, fearful, frightened, glum, happy, infuriated, irate, livid, lugubrious, melancholy, mournful, sad, scared, sorrowful, terrified (mean frequency of word use, 18.42; Francis



Fig. 4. Time course of activation in LFO ROI, comparing emotion vs. personality rating conditions (Experiment 1, n = 7). Yellow bar corresponds to cue presentation, blue to stimulus presentation, and green to probe word presentation and answering. *Y* axis is percent signal change. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and Kucera, 1967). Personality words: adventurous, amiable, anxious, bashful, bold, brave, cocky, confident, cowardly, coy, deceitful, extraverted, friendly, loyal, neurotic, outgoing, proud, shy, trustworthy, unreliable, vivacious (mean frequency of word use, 13.38).

Note that word use frequencies were not available for two emotion words which are apparently used so infrequently as to exclude them from the Brown Corpus: lugubrious and sorrowful. This implies, however, that were their word use frequencies available, the mean frequency of emotion word use would be even lower than 18.42, thus making it even less likely that we would replicate the findings from Experiment 1 in the follow-up experiments if the LFO activation difference was based on word frequency differences.

Because word use frequencies tended to be skewed, we also compared log mean frequencies. These were 1.92 and 1.92 for emotion and personality trait words, respectively.

# Experiment 2

In the first follow-up experiment, the cue consisted of the probe word itself, and the words "emotion" and "personality" were not part of the trial at any point. Subjects saw a probe word (e.g., delighted), followed by the stimulus, and then by the same probe word. As in Experiment 1, subjects rated the fit of the probe word to the stimulus they had just seen. This task controlled for both word frequency differences and the memory demands of rehearsal (because subjects were not trained on the 21 possible probe words for each condition, they could not have been rehearsing the lists of possible probes while viewing the stimuli), two potential task demands that could have led to the LFO activation in the initial experiment. However, it was similar to the initial task in that subjects were aware of the specific probe word (or short set of probe words) on which they were evaluating the stimulus while they were watching the stimulus. Thus, activation differences during stimulus viewing and/or rating would presumably be due to differences in the state of attributing specific personality traits, as compared to the state of attributing specific emotions.

# Experiment 3

In the second follow-up experiment, the cue consisted of the word "emotion" or "character" (which was changed from personality, because "character" has the same number of syllables as "emotion"). Thus, while subjects were watching the stimulus, they knew what type of judgment they would make, but did not know what specific probe word they would be judging. Then, as in the initial experiment, they saw a stimulus followed by a probe word from the appropriate list, and responded by rating the fit of the word to the stimulus they had just seen. Like Experiment 2, this task controlled for both word frequency differences and the memory demands of rehearsal. However, it differed from Experiment 2 and the initial task in that subjects did not know the specific probe word (or short set of probe words) on which they were evaluating the stimulus. Thus, activation differences during stimulus viewing would presumably be due to differences in the state of attributing personality traits in general, as compared to the state of attributing emotions in general.

Image acquisition and analysis parameters were the same for both follow-up experiments as they were for Experiment 1. Again, regions of interest were drawn on each subject's brain corresponding to peak lesion overlap from the previous lesion study.

### **Results, follow-up experiments**

#### Behavioral data

Averaged across these two experiments, mean response times for the two types of judgments were comparable (Emotion: 1.51 s; Personality: 1.56 s; paired 2-tailed t test, P > 0.4).

## Group analyses

#### Experiment 2

The 'Personality' > 'Emotion' contrast yielded a peak activation in a region of LFO comparable to that observed in Experiment 1 [ $-45\ 30\ -15$ ]. There were no voxel-wise significant activations in any of the regions about which we had prior hypotheses for the 'Emotion' > 'Personality' contrast.

#### Experiment 3

There were no voxel-wise significant activations in any of the regions about which we had prior hypotheses for either contrast in this experiment.

# ROI results

The average center voxel of the anatomically defined left frontal operculum ROI (LFO) was [-51 21 9]. The average central voxel of the right somatosensory/supramarginal gyrus ROI (RSS/SMG) was [63 -15 21].

# Experiment 2

In the left frontal operculum region, as in the initial experiment, a repeated measures ANOVA revealed a significant main effect of condition ('Personality' > 'Emotion', F(1,7) = 13.0, P < 0.01), as well as a trend towards an interaction with time period (F(2,14) = 3.4, P = 0.064). Inspection of the means suggested that the difference between conditions was greater during the cue and the movie, than during the response period. It is therefore unlikely that differences in lexical frequency or word length alone were responsible for the original finding of greater LFO activity during Personality as compared to Emotion judgments.

The results in the RSS/SMG were mixed. A repeated measures ANOVA revealed a significant main effect of condition in the same direction as in the LFO ('Personality' > 'Emotion', F(1,7) = 13.0, P < 0.01), mediated by a strong interaction with time period (F(2,14) = 5.38, P < 0.02). Inspection of the means revealed that the response to 'Emotion' blocks was actually higher than the response to 'Personality' blocks, during both the cue and the movie, but this pattern reversed during the response.

## Experiment 3

In the second follow-up experiment, in which subjects did not know specific emotion or personality trait words while they were viewing the stimuli, there was no significant effect of condition in the LFO (F(1,7) = 0.64, n.s.) and no interaction with time period (F(2,14) = 0.42, n.s.). There were also no significant effects in the

# **ARTICLE IN PRESS**

RSS/SMG (main effect of condition: F(1,7) = 0.85, n.s.; interaction with time period: F(2,14) = 0.67, n.s.).

# Further analyses

Using the data from all three experiments, we further examined the responses of three other brain regions known to be associated with social cognition. Multiple studies (Fletcher et al., 1995; Goel et al., 1995; Brunet et al., 2000; Castelli et al., 2000; Gallagher and Frith, 2003; Gallagher et al., 2000) have found greater activation in the temporoparietal junctions and in medial prefrontal regions when subjects were making social/ mental attributions. We defined three ROIs based on the peak activations described by Gallagher et al. (2000), all of which were more active both when subjects interpreted stories requiring mental state attributions (as compared to stories not requiring such attributions) and when they interpreted cartoons requiring mental state attributions (as compared to control cartoons). Coordinates of these three peaks were as follows: left temporoparietal junction (TPJ): [-54, -66, 22]; right TPJ: [60, -46, 22]; mPFC: [-10, 48, 12]. We centered spheres of 6 mm radius on each of these peaks for each of our subjects. (A slightly larger ROI was used for this analysis than for the above ROI analyses because of the anatomical imprecision inherent in using a group average peak to define an ROI on an individual brain.) Using data from both groups of subjects, and all three experiments, we compared activation in these three regions during emotion judgments as compared to personality judgments. As in the above analyses, we compared mean percent signal change (PSC) across the whole block (cue, movie, response).

Neither the left nor the right TPJ distinguished between attributing emotion and attributing personality (PSC, left: Emotion = 0.26, Personality = 0.25, P > 0.5 paired-samples *t* test; Right: Emotion = 0.41, Personality = 0.39, P > 0.5 paired-samples *t* test). However, the mPFC responded significantly more when subjects attributed personality than when they attributed emotion to the same point-light walkers (Emotion



Fig. 5. Time course of activation in mPFC ROI, comparing emotion vs. personality rating conditions (mean of Experiments 1, 2, 3; n = 15). Yellow bar corresponds to cue presentation, blue to stimulus presentation, and green to probe word presentation and answering. *Y* axis is percent signal change. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

PSC = -0.17, Personality PSC = -0.10, P < 0.05 pairedsamples *t* test). Although the overall percent signal change was negative (i.e., lower than the signal measured during passive fixation) in both conditions, inspection of the means revealed that the BOLD response to attribution of Personality was greater than fixation during the response period (Fig. 5). An activation in the mPFC region was evident in a random-effects analysis as well. This same pattern in the mPFC was visible at trend level in the data just from Experiment 1 (Emotion PSC: -0.19, Personality PSC: -0.13, P = 0.13 paired-samples *t* test); interestingly, the ITPJ comparison was also significant in Experiment 1 alone (Emotion PSC = 0.33, Personality PSC = 0.38, P < 0.05 paired-samples *t* test).

#### Discussion

A recent lesion overlap study (Heberlein et al., 2004) found that judgments about emotional states and personality traits rely on at least partially nonoverlapping neural circuits. Our initial experiment, Experiment 1, clearly supported this dissociation. The most important evidence comes from our tightly constrained, lesionoverlap-based ROI analyses, which were very unlikely to yield false positive results. In each subject, we used sulcal and gyral landmarks to define anatomical regions of interest, corresponding to the regions of maximal overlap from the lesion study. As predicted, the left frontal operculum ROI-where damage selectively impaired attribution of personality traits-was more active while normal subjects made personality trait judgments, and the right somatosensory/supramarginal ROI-where damage selectively impaired attribution of emotion-was more active while subjects made emotion judgments. This result provides a striking example of convergent evidence from two different methodologies. Though many textbooks or reviews of cognitive neuroscience (e.g., Frackowiak et al., 1997; Heilman and Valenstein, 2003; D'Esposito and Devinsky, 2004; Farah, 2004) discuss a need for the use of converging methods to compensate for the weaknesses of both lesion and functional imaging techniques, it is still fairly uncommon to find such evidence (Fellows et al., 2005). The correspondence between the activation patterns observed in each task comparison and the lesion overlap patterns seen in the relevant task-impairment images is remarkable (Figs. 1 and 2). Furthermore, our use of subject-specific ROIs based on lesion overlaps from subjects impaired on the same task is, to our knowledge, a novel combination of these methods, and our findings from these ROI analyses reinforce the observed correspondence between the group activation analyses and the lesion overlap analyses.

In both the lesion study and the current Experiment 1, the most consistent result was the association between left frontal operculum and the attribution of personality traits. However, both of these studies suffered from a possible confound with verbal difficulty: the personality trait words were both longer and lower frequency than the emotion words, and reaction times in the personality trait judgment trials were longer. The first follow-up study (Experiment 2) in the current series eliminated this confound. LFO activation during personality trait judgments, relative to emotion judgments, was as robust as in the initial experiment, even though in this second experiment the personality and emotion words were matched in frequency and length, and yielded identical reaction times. Thus, it appears that some component of making judgments about a moving person's enduring traits recruits LFO cortices more strongly than making judgments about that person's emotional states. However, it should be noted that the other follow-up experiment found no such difference.

The question remains open why personality trait attribution recruits regions of left inferior frontal gyrus more than emotion attribution. As described above, previous studies associate this region with verbal processing and semantic ambiguity, but not with a domain-specific function in social cognition. Experiment 2 eliminates the possibility that this activation reflected simple verbal difficulty. However, it may be that relative to knowledge about (others') emotions, knowledge about personality traits is encoded in verbal representations, and so disproportionately depends on verbal semantic processing.

That personality trait attribution requires greater recruitment of 'person-related' cognition than emotional state attribution is supported by our finding of greater mPFC activation in personality trait judgments, as compared to emotion judgments. Activation in medial PFC regions has been observed in functional imaging studies of mental state attribution, as well as in other studies of person-related cognition. Neuroimaging investigations of 'theory of mind' capacity have frequently suggested that medial prefrontal cortices are recruited during the attribution of beliefs to others (for review, see Gallagher and Frith, 2003), while studies of self-referencing have associated this region with monitoring one's own internal states (Gusnard et al., 2001). Furthermore, at least two studies have associated enhanced mPFC response with semantic processing of information about personality traits (Kelley et al., 2002; Mitchell et al., 2002).

Results relating emotion attribution to the RSS/SMG region were less consistent in the current data. In Experiment 1, both whole-brain random-effects analyses and individual subject anatomical ROI analyses confirmed the predicted enhancement of RSS/SMG activation during emotion attribution. The association between emotion recognition and the RSS/SMG has also been reported previously: the right somatosensory cortices have been implicated in judgments of facial emotions (Adolphs et al., 2000; Winston et al., 2003) and emotional prosody (Adolphs et al., 2002). These authors interpret these results in terms of a simulation model of emotion recognition. Right somatosensory cortices may be involved in representing the bodily feelings associated with one's own emotions; the same feelings are then recapitulated when inferring another's emotional state from his/her bodily expression. Note that a similar technique might be less applicable to the attribution of personality traits, which are not straightforwardly associated with bodily sensations.

However, both of our follow-up experiments (designed to rule out a confound in the LFO, and not predicted to affect the response of RSS/SMG) failed to replicate this association. At least three different factors may have contributed to this failure. First, emotion attribution may be relatively automatic, leaving room for only subtle enhancements of the response of the neural circuit, based on task instructions or attention. This is consistent with the observation that both the personality task and the emotion task activated the RSS/SMG in Experiment 1.

Second, all previous studies that have reported an association between the RSS/SMG and emotion recognition, including the current Experiment 1, have limited the emotion probes to basic emotions-happy, sad, angry, afraid-that have well-defined and relatively universal physical expressions. According to the simulation model, the role of the RSS/SMG is in covertly modeling the observed emotion in the subject's own motor and sensory systems. The emotion words used in the follow-up studies–e.g., delighted, melancholy, glum–may not be associated with as well-defined physical expressions.

Third, the anatomical location of the RSS/SMG was less clear than that of the LFO. The region of maximal overlap defined by the previous lesion study fell at the junction of the postcentral and supramarginal gyri, in a region which differed markedly between individuals. Thus, variance between individuals in the anatomical region that we selected for the region of interest may have conspired to wash out any small remaining differences in enhancement of activation during emotion attribution.

All in all, the fMRI results reported here suggest a significant differential recruitment of nonoverlapping neural circuits during judgments of emotions and personality traits from simple biological motion stimuli. The left frontal opercular region and the right somatosensory/supramarginal gyrus region appear to be recruited differentially by emotion and personality attribution tasks, given the same body movement cues. However, differences in how the task is presented affect whether this difference in recruitment is observed. In particular, both functional patterns were apparent when subjects knew the actual or possible probe word that they would be required to judge (lesion study, initial experiment, and Experiment 2), but not when they knew only the general category of the judgment ('emotion' vs. 'personality' or 'character'; Experiment 3). A possible interpretation of this difference is that the category words were less meaningful to subjects than the actual probe words: if the words "personality" or "character", and "emotion", mean little to subjects as categories, but the probe words (as categorized by psychologists) do differ meaningfully along these dimensions, then we should expect differences only when subjects are thinking of the probe words. Further studies manipulating subjects' expectations and prior knowledge of the categories of social judgment types may help address these differences.

#### Acknowledgments

We are grateful to Ralph Adolphs, Martha Farah, Joshua Greene, Yuhong Jiang, Nasheed Jamal, Kyungmouk Steve Lee, Lindsey Powell, and especially to Nancy Kanwisher, for help and advice on multiple fronts during the completion of this work. The research reported here was supported by grant NIMH 66696 to Nancy Kanwisher. ASH is supported by NIH T32-NS07413 at the Children's Hospital of Philadelphia.

### References

- Adolphs, R., 2002. Behav. Cogn. Neurosci. Rev. 1 (1), 21-61.
- Adolphs, R., Damasio, H., Tranel, D., Cooper, G., Damasio, A.R., 2000. J. Neurosci. 20 (7), 2683–2690.
- Adolphs, R., Damasio, H., Tranel, D., 2002. Emotion 2, 23-51.
- Allison, T., Puce, A., McCarthy, G., 2000. Trends Cogn. Sci. 4 (7), 267–278.
- Ambady, N., Rosenthal, R., 1992. Psychol. Bull. 111 (2), 256–274. Bonda, E., Petrides, M., Ostry, D., Evans, A., 1996. J. Neurosci. 16 (11),
- 3737-3744. Brunet, E., Sarfati, Y., Hardy-Bayle, M.C., Decety, J., 2000. NeuroImage 11
- (2), 157–166.
- Castelli, F., Happé, F., Frith, U., Frith, C., 2000. NeuroImage 12, 314–325. Chein, J.M., Fiez, J.A., 2001. Cereb. Cortex 11 (11), 1003–1014.

# 8

# **ARTICLE IN PRESS**

- Cutting, J.E., Kozlowski, L.T., 1977. Bull. Psychon. Soc. 9 (5), 353-356.
- D'Esposito, M., Devinsky, O. (Eds.), (2004). Neurology of Cognitive and Behavioral Disorders. Contemporary Neurology. Oxford Univ. Press, Oxford.
- Dittrich, W.H., Troscianko, T., Lea, S.E., Morgan, D., 1996. Perception 25 (6), 727–738.
- Ekman, P., Friesen, W.V., 1971. J. Pers. Soc. Psychol. 17, 124-129.
- Farah, M., 2004. Visual Agnosia. MIT Press, Cambridge, MA.
- Fellows, L.K., Heberlein, A.S., Morales, D.A., Shivde, G., Waller, S., Wu, D., 2005. J. Cogn. Neurosci. 17, 850–858.
- Fiske, S.T., 1993. Annu. Rev. Psychol. 44, 155-194.
- Fletcher, P., Happé, F., Frith, U., Baker, S., Dolan, R., Frackowiak, R., Frith, C., 1995. Cognition 57 (2), 109–128.
- Frackowiak, R., Friston, K.J., Frith, C., Dolan, R., Mazziotta, J. (Eds.), (1997). Human Brain Function. Academic Press, San Diego.
- Francis, S., Kucera, H., 1967. Computing Analysis of Present-day American English. Brown Univ. Press, Providence, RI.
- Gallagher, H.L., Frith, C.D., 2003. Trends Cogn. Sci. 7 (2), 77-83.
- Gallagher, H.L., Happé, F., Brunswick, N., Fletcher, P.C., Frith, U., Frith, C.D., 2000. Neuropsychologia 38 (1), 11–21.
- Gilbert, D.T., 1998. Ordinary personology. In: Gilbert, S.T.F.D.T., Lindzey, G. (Eds.), The Handbook of Social Psychology. McGraw Hill, New York, pp. 89–150.
- Goel, V., Grafman, J., Sadato, N., Hallett, M., 1995. NeuroReport 6 (13), 1741-1746.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., Blake, R., 2000. J. Cogn. Neurosci. 12 (5), 711–720.
- Gunns, R.E., Johnston, L., Hudson, S.M., 2002. J. Nonverbal Behav. 26 (3), 129–158.
- Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001. Proc. Natl. Acad. Sci. U. S. A. 98 (7), 4259–4264.
- Heberlein, A.S., Adolphs, R., Tranel, D., Damasio, H., 2004. J. Cogn. Neurosci. 16, 1143–1158.
- Heilman, K., Valenstein, E. (Eds.), (2003). Clinical Neuropsychology. Oxford Univ. Press, Oxford.

- Johansson, G., 1973. Percept. Psychophys. 14, 202-211.
- Jonides, J., Smith, E.E., Marshuetz, C., Koeppe, R.A., Reuter-Lorenz, P.A., 1998. Proc. Natl. Acad. Sci. U. S. A. 95 (14), 8410–8413.
- Kan, I.P., Thompson-Schill, S.L., 2004. Cogn. Affect. Behav. Neurosci. 4, 466–482.
- Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. J. Cogn. Neurosci. 14 (5), 785–794.
- Kozlowski, L.T., Cutting, J.E., 1977. Percept. Psychophys. 21 (6), 575-580.
- Loula, F., Prasad, S., Harber, K., Shiffrar, M., 2005. Recognizing people from their movement. J. Exp. Psychol. Hum. Percept. Perform. 31 (1), 210–220.
- Macrae, C.N., Bodenhausen, G.V., 2000. Annu. Rev. Psychol. 51, 93-120.
- Makeig, P., 2001. Sensitivity to Kinematic Specification of Emotion and Emotion-Related States. Department of Psychology, Canterbury University, New Zealand.
- McCrae, R.R., Costa Jr., P.T., 1987. J. Pers. Soc. Psychol. 52 (1), 81-90.
- Mitchell, J.P., Heatherton, T.F., Macrae, C.N., 2002. Proc. Natl. Acad. Sci. U. S. A. 99 (23), 15238–15243.
- Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. NeuroImage 10 (1), 15–35.
- Pollick, F.E., Paterson, H.M., Bruderlin, A., Sanford, A.J., 2001. Cognition 82, B51–B61.
- Rodd, J.M., Davis, M.H., Johnsrude, I.S., 2005. The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. Cereb. Cortex. 15, 1261–1269.
- Scherer, K.R., 1986. Psychol. Bull. 99, 143-165.
- Smith, E.E., Jonides, J., 1997. Cognit. Psychol. 33 (1), 5-42.
- Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., Farah, M.J., 1997. Proc. Natl. Acad. Sci. U. S. A. 94 (26), 14792–14797.
- Wallbott, H.G., 1998. Eur. J. Soc. Psychol. 28, 879-896.
- Wellman, H.M., Bartsch, K., 1988. Cognition 30 (3), 239-277.
- Wellman, H.M., Woolley, J.D., 1990. Cognition 35, 245-275.
- White, P.A., 1995. The Understanding of Causation and The Production of Action. Lawrence Erlbaum Associates, Hillsdale, NJ.
- Winston, J.S., O'Doherty, J., Dolan, R.J., 2003. NeuroImage 20 (1), 84-97.