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THE CONTRIBUTION OF THE FUSIFORM GYRUS AND SUPERIOR TEMPORAL SULCUS IN PROCESSING FACIAL ATTRACTIVENESS: NEUROPSYCHOLOGICAL AND NEUROIMAGING EVIDENCE

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Abstract—Current cognitive models suggest that the processing of dynamic facial attributes, including social signals such as gaze direction and facial expression, involves the superior temporal sulcus, whereas the processing of invariant facial structure such as the individuals' identity involves the fusiform face area. Where facial attractiveness, a social signal that may emerge from invariant facial structure, is processed within this dual-route model of face perception is uncertain. Here, we present two studies. First, we investigated the explicit judgments of facial attractiveness and attractiveness-motivated behavior in patients with acquired prosopagnosia, a deficit in familiar face recognition usually associated with damage to medial occipitotemporal cortex. We found that both abilities were impaired in these patients, with some weak residual ability for attractiveness judgments found only in those patients with unilateral right occipitotemporal or bilateral anterior temporal lesions. Importantly, deficits in attractiveness perception correlated with the severity of the face recognition deficit. Second, we performed a functional magnetic resonance imaging study in healthy subjects that included an implicit and explicit processing of facial attractiveness. We found increased neural activity when explicitly judging facial attractiveness within a number of cortical regions including the fusiform face area, but not the superior temporal sulcus, indicating a potential contribution of the fusiform face area to this judgment. Thus, converging neuropsychological and neuroimaging evidence points to a critical role of the inferior occipitotemporal cortex in the processing of facial attractiveness.

Key words: esthetic, attraction, face perception, fusiform, prosopagnosia, temporal.

Faces are a rich class of visual stimuli that provide a variety of information about an individual, such as their identity, gender, age and race. Faces also convey information relevant for social interactions such as an individual's emotional state or direction of eye-gaze. An understanding of the neural mechanisms involved in processing these different aspects of faces is the focus of extensive research (Haxby et al., 2000).

Neuropsychological (e.g. Bowers et al., 1985; de Gelder et al., 2000) and, more recently, neuroimaging (e.g. Kanwisher et al., 1997; Ishai et al., 1999; Hoffman and Haxby, 2000) findings suggest that selective brain regions within the occipito-temporal cortex make distinct contributions to the complex process of face perception. The superior temporal sulcus (STS), a region located in the lateral occipitotemporal cortex, is suggested to process dynamic facial properties (Puce et al., 1998; Hoffman and Haxby, 2000): that is, structural elements that can change from moment to moment, such as the direction of gaze and emotional expressions, both of which play important roles in social interactions (Allison et al., 2000). On the other hand, the fusiform face area (FFA), a region located in the medial occipitotemporal cortex, is preferentially involved in processing temporally-invariant facial structure: that is, elements that remain constant over such dynamic variations, which provide the chief cues to properties such as identity and gender (Sergent et al., 1992; Kanwisher et al., 1997; George et al., 1999; Hoffman and Haxby, 2000).

Less explored than identity, expression and gaze direction is another facial property: attractiveness. Perceptions of facial attractiveness can influence many judgments we make about others, including their desirability and personality (Dion et al., 1972), likelihood of mating success (Thornhill et al., 1995; Pashos and Niemitz, 2003), earning potential (Frieze et al., 1991), and competency in school and work (Dipboye et al., 1975). Given the contribution of facial attractiveness to these social judgments, some have postulated that facial attractiveness may be another property processed by the STS (Winston et al., 2007). Indeed, according to Winston et al. (2007), the role of the STS in facial attractiveness judgments may be consistent with the "intention–detection" of the observer, that is the process of assessing the attractiveness of a conspecific as the social evaluation of another's intentions toward ourselves. However, one might also argue that, unlike the social signals of

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Abbreviations: AMG, amygdala; EPI, echoplanar imaging; FFA, fusiform face area; fMRI, functional magnetic resonance imaging; ISI, inter-stimulus-interval; MRI, magnetic resonance imaging; OFC, orbitofrontal cortex; OFA, occipital face area; ROI, region of interest; STS, superior temporal sulcus.

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Table 1. Subjects' demographic and lesion data

Subject	Site of lesion	Gender	Age (years)	BFRT	WRMT(F)	WRMT(W)	d′
001	Unknown	Male	25	39	30	45	−0.61
005	Unilateral (right) medial occipotemporal	Male	63	35	33	42	0.67
008	Bilateral anterior temporal	Female	37	25	13	45	0.68
009	Unilateral (right) medial occipotemporal	Male	50	43	33	43	0.88
010	Bilateral occipitotemporal	Male	42	37	24	48	−0.22
011	Bilateral occipitotemporal	Male	52	32	33	45	−0.18
014	Unilateral (left) lateral occipotemporal	Male	29	34	33	47	0.9
015	Bilateral anterior temporal	Male	24	45	27	45	0.88

BFRT, Benton Face Recognition Test (x/54); WRMT (F), Warrington recognition memory test faces component (x/50); WRMT (W), Warrington recognition memory test word component (x/50); d′, discriminative power on famous face familiarity test (Barton et al., 2001).

gaze direction and expression, attractiveness is based more on temporally invariant rather than dynamic aspects of facial structure: in general, perceptions of physical beauty persist despite moment-to-moment fluctuations in facial expression or gaze. Indeed, while a pleasant expression can contribute to attractiveness, current research suggests that the most important factors in attractiveness are averageness, symmetry, and sexual dimorphism, facial properties that are stable over time (Rhodes, 2006). In this respect, attractiveness may be more similar in processing demands to the properties of identity and gender, and may therefore require the contribution of the FFA as well. The present study aims at testing this specific hypothesis.

In order to provide converging evidence for our hypothesis, we have performed two studies, which used a neuropsychological and a neuroimaging approach respectively. In the first study, we assessed whether patients with prosopagnosia, i.e. the inability to recognize the identity of familiar faces (Barton, 2003; Harris and Aguirre, 2007), retain the ability to process facial attractiveness. Acquired prosopagnosia usually results from bilateral or unilateral right medial occipitotemporal lesions, often involving the right fusiform gyrus (Meadows, 1974; Damasio et al., 1982; Bouvier and Engel, 2006). The extent of lateral occipitotemporal damage in these subjects is more variable, which may account for the observation that the perception of facial expression can be spared in these subjects (Bowers et al., 1985; de Gelder et al., 2000). If the perception of facial attractiveness is consistently impaired in this population, and even correlates with the severity of the impairment in facial identity processing, this would support the hypothesis that a medial occipitotemporal processing stream which includes the fusiform gyrus contributes to the perception of facial attractiveness, as well as the impairment in identity recognition.

Although lesion studies can provide important information on the role of certain cortical regions for a given cognitive function, the large size and variable nature of lesions across individuals make it difficult to confidently ascribe a particular function to a specific cortical region of interest (ROI). For this reason, we performed a second study in healthy individuals, in which we used functional magnetic resonance imaging (fMRI) to further examine the contribution of the STS and FFA during the processing of facial attractiveness. According to the critical role of the STS and FFA in processing emotional expressions (social interaction cues) (Puce et al., 1998; Hoffman and Haxby, 2000) and invariant facial attributes (i.e. identity and gender) (Sergent et al., 1992; Kanwisher et al., 1997; George et al., 1999; Hoffman and Haxby, 2000) respectively, we performed a ROI analysis to specifically examine the neural activity within these two regions while participants processed faces of varying degrees of attractiveness in both an implicit and explicit manner.

EXPERIMENTAL PROCEDURES

Neuropsychological study

Participants. We tested eight subjects with prosopagnosia and 19 healthy control subjects. All subjects had normal or corrected-to-normal vision and gave informed consent in a manner consistent with the principles of the Declaration of Helsinki. The study protocols were approved by the institutional review boards of the University of British Columbia and Vancouver General Hospital.

In Table 1 we report the prosopagnosic subjects' scores on the Warrington Recognition Memory Test (Warrington, 1984), the Benton Face Recognition Test (Benton and Van Allen, 1972), and the assessment of facial recognition on a famous face familiarity test (Barton et al., 2001). Representative magnetic resonance imaging (MRI) scans are shown in Fig. 1, and anatomic templates in Fig. 2. More detailed case information on most of these subjects can be found in previous reports using the same subject identification numbers (Barton et al., 2004a,b; Barton and Cherkasova, 2005).

Subject 001, a 25-year-old right-handed male, suffered from cardiopulmonary arrest and coma at 18 months (Kosslyn et al., 1995). A structural MRI did not reveal any lesion (Hadjikhani and de Gelder, 2002); however, he demonstrated severe deficits in perceiving facial configuration similar to prosopagnosic subjects with lesions of the FFA (Kosslyn et al., 1995). Regarding perception of expression, he scored 24/36 on the Revised Eyes Test (Baron-Cohen et al., 2001) (www.autismresearchcenter.com/tests), which is within the normal range (control mean=26.2, S.D.=3.6).

Subjects 010 and 011 have bilateral, primarily occipitotemporal, lesions. Subject 010 is a 42-year-old right-handed male who has bilateral posterior occipitotemporal lesions following an automobile accident 21 years earlier, resulting in a subdural hematoma with associated prosopagnosia and right hemianopia. On the faces portion of the DANVA-2 (diagnostic assessment of nonverbal accuracy, (www.dyssemia.com/danva), a test that requires subjects to indicate which of four emotions corresponds to an expression on a test face, he made 12 errors, which is better than 95% limits for chance (15 errors) but slightly above the normal range for his age (mean=4.8 errors, S.D.=2.6). Nevertheless, his