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Research report

Face perception in pure alexia: Complementary contributions of the left fusiform gyrus to facial identity and facial speech processing

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ABSTRACT

Recent concepts of cerebral visual processing predict from overlapping patterns of face and word activation in cortex that left fusiform lesions will not only cause pure alexia but also lead to mild impairments of face processing.

Our goal was to determine if alexic subjects had deficits in facial identity processing similar to those seen after right fusiform lesions, or complementary deficits affecting different aspects of face processing.

We studied four alexic patients whose lesions involved the left fusiform gyrus and one prosopagnosic subject with a right fusiform lesion, on standard tests of face perception and recognition. We evaluated their ability first to process faces in linear contour images, and second to detect, discriminate, identify and integrate facial speech patterns into perception.

We found that all five patients were impaired in face matching across viewpoint, but the alexic subjects performed worse with line-drawn faces, while the prosopagnosic subject did not. Alexic subjects could detect facial speech patterns but had trouble identifying them and did not integrate facial speech patterns with speech sounds, whereas identification and integration was intact in the prosopagnosic subject.

We conclude that, in addition to their role in reading, the left-sided regions damaged in alexic subjects participate in the perception of facial identity but in a non-redundant fashion, focusing on the information in linear contours at higher spatial frequencies. In addition they have a dominant role in processing facial speech patterns, another visual aspect of language processing.

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Among the most highly expert forms of visual processing performed by humans are face recognition and visual word reading. Functional imaging shows that both of these involve extensive networks in both hemispheres (Barton et al., 2010; Haxby, Hoffman, & Gobbini, 2000), but with the critical difference that faces evoke larger and greater activation in the right hemisphere (Kanwisher, McDermott, & Chun, 1997) and words in the left hemisphere (Cohen et al., 2002). However, within the activated regions in either hemisphere there remains significant spatial overlap between voxels activated by words and those activated by faces (Nestor, Behrmann, & Plaut, 2013). This is a challenge to modular accounts that propose cerebral regions dedicated to processing a single type of stimulus. Rather, the recent 'many-to-many' hypothesis (Behrmann & Plaut, 2013) argues, first, that object processing involves networks of regions instead of a single region, and second, that the individual regions of this network participate in processing multiple object types, so that any apparent specificity for a particular object is only partial. Hence, object specificity is not reflected by activity within one single region, but emerges from a distinct pattern of network activation (Reinke, Fernandes, Schwindt, O'Craven, & Grady, 2008).

The fusiform cortex likely plays an important role in networks of expert visual processing (Weiner et al., 2016). The fusiform face area in the right hemisphere is highly activated by faces (Kanwisher et al., 1997), and damage to this region is evident in subjects with an apperceptive form of prosopagnosia (Barton, Press, Keenan, & O'Connor, 2002), the inability to recognize familiar faces. The visual word form area in the left hemisphere is active during perception of written text (McCandliss, Cohen, & Dehaene, 2003) and a lesion here can lead to pure alexia, an acquired impairment of reading efficiency (Leff, Spitsyna, Plant, & Wise, 2006). The lateralization of lesions in prosopagnosia and pure alexia echoes that of functional activation, with prosopagnosia occurring primarily after right-sided or bilateral lesions (Barton, 2008; Davies-Thompson, Pancaroglu, & Barton, 2014) and pure alexia almost always following left-sided lesions (Kleinschmidt et al., 2006). This complementary pattern of lateralization for words and faces is not accidental but may have evolved through competition between words and faces for high-level perceptual resources in these cortical regions (Behrmann & Plaut, 2013; Dehaene et al., 2010; Dundas, Plaut, & Behrmann, 2013).

A key prediction of the 'many-to-many' hypothesis is that selectivity in prosopagnosia and pure alexia is relative, so that prosopagnosic subjects will show subtle deficits in visual word processing and alexic subjects will show subtle deficits in face processing (Behrmann & Plaut, 2013). However, it is not clear whether the types of visual word processing deficits in prosopagnosic subjects are similar or complementary to those seen in alexia, and likewise for the face processing deficits in alexia. In support of similar deficits, a study of four alexic and three prosopagnosic subjects found that the prosopagnosic subjects had mild word recognition deficits while pure alexic subjects had mild face recognition deficits (Behrmann & Plaut, 2014). However, other studies of visual word processing in prosopagnosia have not found impaired reading ability in those with lesions limited to the right hemisphere (Hills, Pancaroglu, Duchaine, & Barton, 2015; Susilo, Wright, Tree, & Duchaine, 2015). Interestingly, some have reported impaired perception of handwriting or font style in acquired prosopagnosia (Barton et al., 2010; Campbell, Landis, & Regard, 1986; Hills et al., 2015; Rentschler, Treutwein, & Landis, 1994), indicating possible hemispheric differences in the type of text processing, with the left involved in identifying word content and the right in processing style (Hills et al., 2015). On the other hand, most subjects with developmental prosopagnosia have intact perception of both words and style in text (Rubino, Corrow, Duchaine, & Barton, 2016; Starrfelt, Klargaard, Petersen, & Gerlach, 2016).

It is equally important for the many-to-many hypothesis to investigate similar questions about the presence and nature of face processing deficits in pure alexia. Some studies have reported findings of reduced efficiency of face identification or perception similar to but less severe than that seen in prosopagnosia (Behrmann et al., 2014; Roberts et al., 2015). What type of complementary face processing deficits might occur with left hemisphere damage is not clear, but following prior suggestions (Plaut et al., 2011) we considered two possibilities. First, it has been proposed that the left hemispheric lateralization of visual word processing is due to constraints relating to optimizing connectivity to non-visual language processing in the left hemisphere (Plaut & Behrmann, 2011). If so, one might speculate that aspects of face processing that are more relevant to language processing may also follow this optimizing principle, and be lateralized to the left hemisphere. Highly relevant to this are older reports of impaired lip-reading in one alexic but not in one prosopagnosic subject (Campbell et al., 1986, 1990). As these are single cases it would be critical to replicate these findings in more subjects, given their importance to the current hypothesis. Second, visual word and face stimuli differ significantly in their properties. Faces are three-dimensional structures with complex surfaces and textures, while words are high-contrast line elements that emphasize the higher spatial frequencies. If these differences are reflected in specialized processing capabilities of the left and right fusiform gyri, then processing of facial stimuli that similarly emphasize high spatial frequencies at high contrast may be vulnerable to left fusiform damage. This parallels general proposals about differential hemispheric sensitivities for high and low spatial frequencies (Robertson & Ivry, 2000) and some evidence that orthographic and other perceptual deficits following lesions of the left fusiform gyrus reflect the loss of high-spatial frequency information (Roberts et al., 2013). Indeed, Ossowski and Behrmann (2015) even suggest that the left hemispheric bias for high spatial frequencies in general might emerge as a consequence of the acquisition of orthographic competence.

In this study we examined four alexic subjects with left fusiform lesions and one prosopagnosic subject with a right fusiform lesion. First, we asked if the alexic subjects showed impairments in the perception and recognition of facial identity analogous to the key deficit in prosopagnosia. Second, we investigated whether the alexic subjects showed complementary face perception deficits that could reflect hypothesized left hemispheric contributions to face processing, and whether these differed from the subject with prosopagnosia. This had two components. In one, we studied whether alexic subjects were impaired in the discrimination of facial identity