



Plastic reorganization of neural systems for perception of others in the congenitally blind



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ABSTRACT

Recent evidence suggests that the function of the core system for face perception might extend beyond visual face-perception to a broader role in person perception. To critically test the broader role of core face-system in person perception, we examined the role of the core system during the perception of others in 7 congenitally blind individuals and 15 sighted subjects by measuring their neural responses using fMRI while they listened to voices and performed identity and emotion recognition tasks. We hypothesised that in people who have had no visual experience of faces, core face-system areas may assume a role in the perception of others via voices. Results showed that emotions conveyed by voices can be decoded in homologues of the core face system only in the blind. Moreover, there was a specific enhancement of response to verbal as compared to non-verbal stimuli in bilateral fusiform face areas and the right posterior superior temporal sulcus showing that the core system also assumes some language-related functions in the blind. These results indicate that, in individuals with no history of visual experience, areas of the core system for face perception may assume a role in aspects of voice perception that are relevant to social cognition and perception of others' emotions.

1. Introduction

There is extensive work on the neural systems for face and voice recognition (Gobbini and Haxby, 2007; Haxby et al., 2000; Tsao et al., 2008; Yovel and Belin, 2013). Voices, as compared to non-vocal sounds, activate Temporal Voice Areas (Belin et al., 2004; Pernet et al., 2015), which include the middle and anterior superior temporal sulcus (maSTS), the superior temporal gyrus (STG), as well as the insula and the prefrontal cortex (Ethofer et al., 2012; Leaver and Rauschecker, 2010; Moerel et al., 2012; Remedios et al., 2009; Romanski et al., 2005). The distributed system for face perception in humans (Fairhall and Ishai, 2007; Gobbini and Haxby, 2007; Haxby et al., 2000, 2002; Haxby and Gobbini, 2011; Ishai et al., 2005) includes visual areas involved in the perception of invariant visual attributes diagnostic of identity and of changeable aspects diagnostic of facial expression and direction of attention (the 'core system'), and some additional areas that play a role in extracting information, such as person knowledge, associated with faces ('the extended system').

The two networks for voice and face processing are largely distinct with anatomical overlap confined to the posterior STS/STG regions (Watson et al., 2014a, 2014b). The interdependence between these networks is uncertain. The function of the core system areas for face perception, however, appears to extend beyond face-processing to a more general and abstract role in social cognition and perception of others (Gobbini et al., 2011). For example, viewing point-light displays depicting biological motion or geometric shapes depicting social interactions, neither of which depicts biological form, activates both the face selective region of the lateral fusiform gyrus (the 'fusiform face area', FFA) and posterior superior temporal sulcal (pSTS) areas of the core system (Bonda et al., 1996; Castelli et al., 2000; Gobbini et al., 2007; Grossman and Blake, 2002; Schultz et al., 2003).

Examining cortical activation in individuals who have not had visual experience provides insight into the principles that guide cortical organization in terms of both preservation of regional function in the absence of visual input and the nature of plastic changes. Studies of the congenitally blind have demonstrated the striking preservation of organization

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that had been thought to be shaped by visual experience (He et al., 2013; Holig et al., 2014b; Mahon et al., 2009; Peelen et al., 2013; Pietrini et al., 2004; Ricciardi et al., 2014; Wang et al., 2015), as well as the extensive capacity of the visual system to take over new functions (Amedi et al., 2003, 2004; Buchel et al., 1998a; Buchel et al., 1998b; Cohen et al., 1999; Collignon et al., 2007, 2011; for a review, see Noppeney, 2007; Raz et al., 2005; Sadato et al., 1996). Bedny et al. (2011) showed that reorganization of function in the visual cortices of the congenitally blind includes language processing in the occipital lobe extending into the left posterior fusiform gyrus. Holig et al. (2014b) found an area in the anterior ventral temporal cortex that shows a priming effect for voice identity in the congenitally blind, near an area that shows face-selectivity and view-invariant representation of face identity in the sighted (Guntupalli et al., 2017), suggesting a role of this area in the supramodal representation of person identity.

Here, we ask whether the visual cortices in the ‘core system’ retain their preference for information relevant to social interaction in the congenitally blind. In theoretical terms, ascertaining that the organization of the core system for perception of others is preserved in the absence of visual experience with faces would provide evidence for the general hypothesis that the principles underlying the development of the functional organization of this system are better captured by more abstract concepts involving social perception than by visual perception of a particular stimulus class, i.e. faces.

In the present study blind and sighted participants processed the identity and emotional content of voices speaking word phrases or producing non-linguistic sounds. By manipulating the social content of the stimuli (full phrases versus vocalisations, variation in emotional content), rather than the presence or absence of conspecific information (human versus non-human sounds), we were able to present identity and emotional content across all stimuli while simultaneously manipulating the richness of person information contained in the stimuli.

We employed a combination of univariate and multivariate information-based measures to determine where emotion and identity are represented in the brains of the blind as compared to the brains of the sighted.

2. Materials and Methods

2.1. Participants

Seven blind (age: \bar{x} = 35.4, sd = 10.9; five female) and 15 sighted (age: \bar{x} = 32.2, sd = 13.5, ten female) participants partook in this study. Six blind subjects were so from birth, one lost sight at 16 months of age. Three had residual light detection in one or both eyes but none could perceive form or motion. All participants were right handed. Informed consent was given by all participants and all procedures approved by the University of Trento Human Research Ethics Committee.

2.2. Stimuli

Four professional actors (two female) depicted four emotional states (happiness, disgust, fear and neutral). Two different Stimulus-Types were presented. *Verbal* stimuli (word phrases) consisted of four phrases for each of the four emotions uttered by each of the four speakers (e.g. “Che schifo! (That’s disgusting!)”; “Che bello! (That’s wonderful!)”; “(Aah! Aiuto! (Aaah! Help!))”; “Sto leggendo (I’m reading)”). Phrases matched the emotional state both in terms of semantic content and intonation. *Vocalisations* were non-linguistic stimuli where emotion was conveyed solely through intonation. Each speaker portrayed each emotion once. Thus, we used 64 different stimuli with verbal phrases (4 phrases for 4 emotions by 4 speakers) and 16 different stimuli with nonverbal utterances (4 emotions by 4 speakers). Each phrase and vocalisation was recorded on an open-source audio-recording software (Audacity: <http://audacity.sourceforge.net>).

A preliminary study was conducted on 32 university students (who

were unaware of the aim of the study) to select the stimuli with accuracy of recognition higher than 70% for each emotion conveyed by phrases and vocalizations. For the 64 selected verbal phrases, the average accuracies were 82.1% for Happiness; 87.5% for Disgust; 73.2% for Fear; and 80.4% for Neutral. The 16 vocalisations were correctly rated as expressing Happiness 92.8%; Disgust 100%; Fear 71.4% and Neutral 100%.

Rather than artificially modulating the phrases and the vocalisations, auditory stimuli were left in their natural state. The same stimuli were used in both tasks (one-back repetition detection for identity and emotion) and both groups (blind and sighted). Therefore, all analyses emphasized contrasts that are orthogonal to the stimuli, namely the effects of Group and Task (see below). Consequently, stimuli varied in mean length both as a function of actor [1.48, 1.50, 1.05, 1.30 s; $F(3,60) = 5.4$, $p < 0.01$] and portrayed emotion [disgust: 1.36; happiness: 1.60; fear: 1.19 neutral: 1.18 s; $F(3,60) = 4.4$, $p < 0.01$]. Vocalisations (mean = 3.1 s) were longer than verbalisations (mean = 1.3 s) to facilitate recognition of the emotion conveyed by intonation, which was more difficult for vocalizations due to lack of semantic content.

2.3. Task

Immediately prior to the fMRI experiment, the participants were familiarized with the task. This practice session consisted of 16 trials with the same structure used during the fMRI experiment. Responses were recorded using an identical device to that in the scanner.

In separate fMRI runs, participants performed one-back repetition detection tasks based on either emotional content or identity. Because these tasks used the same stimuli, any effect of task is unrelated to stimulus variations (Hoffman and Haxby, 2000). At the beginning of each run the experimenter specified if participants had to recognize whether the stimulus presented conveyed the same emotion as the previous stimulus (independently of speaker identity or stimulus type), or was spoken by the same actor as the previous stimulus (independently of the emotion portrayed or stimulus type). Subjects pressed a button with the index finger for a “yes” response and with the middle finger for a “no” response. Trials consisted of the presentation of the auditory stimulus and a response period until 4.4 s after stimulus onset. Participants were told prior to the experiment that there were 4 different actors and 4 different emotions.

2.4. Procedure

Stimulus conditions followed a $4 \times 4 \times 2$ design (4 emotions, 4 speakers, 2 stimulus-types) and were presented in two different tasks. Four runs were acquired for each subject. Each run had 128 trials, consisting of 64 verbal phrases (all combinations of phrase, emotion, and speaker) and 64 vocalisations (each of 16 vocalisations – all combinations of emotions and speakers – was repeated four times). Each run also contained 16 4.4 s null events and was divided into four equal parts with 32 trials and 4 null events in each part. Stimuli were counterbalanced across runs so that the probability of a stimulus being preceded by each category of emotion or actor was equal. The order of runs with emotion and identity repetition tasks was counterbalanced across subjects. Within each run 10-second null events separated four blocks of stimuli. Each run began and ended with a 20 s baseline period.

2.5. MRI scanning

Stimuli were played through a SereneSound Audio System (Resonance Technology, Inc., California, USA.) at a level fixed across participants so as to be clearly audible above the scanner noise. Data collection was conducted at the Center for Mind/Brain Sciences (CIMeC), University of Trento on a Bruker BioSpin MedSpec 4T using a USA Instruments 8-channel phased-array head coil. One thousand two hundred and sixty volumes of 37 AC–PC aligned slices were acquired over 4 runs using an

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