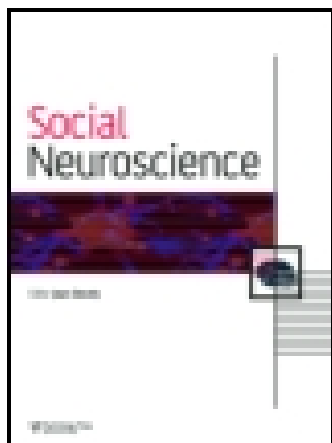


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Neural Correlates of Facial Motion Perception

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Abstract

Several neuroimaging studies have revealed that the superior temporal sulcus (STS) is highly implicated in the processing of facial motion (see Allison, Puce & McCarthy, 2000). A limitation of these investigations, however, is that many of them utilise unnatural stimuli (e.g., morphed videos) or those which contain many confounding spatial cues. As a result, the underlying mechanisms may not be fully engaged during such perception. The aim of the current study was to build upon the existing literature by implementing highly detailed and accurate models of facial movement (as described in Girges, Spencer & O'Brien, 2015). Accordingly, neurologically healthy participants viewed simultaneous sequences of rigid and nonrigid motion that was retargeted onto a standard CGI face model. Their task was to discriminate between different facial motion videos in a two-alternative forced choice paradigm. Presentations varied between upright and inverted orientations. In corroboration with previous data, the perception of natural facial motion strongly activated a portion of the posterior STS. The analysis also revealed engagement of the lingual gyrus, fusiform gyrus, precentral gyrus and cerebellum. These findings therefore suggest that the processing of dynamic facial information is supported by a network of visuo-motor substrates.

Key words

Face perception; facial motion; functional MRI; superior temporal sulcus

Introduction

The human visual system has developed highly specialised mechanisms which facilitate the detection and interpretation of facial motion (Allison, Puce & McCarthy, 2000). Puce, Allison, Bentin, Gore and McCarthy (1998) first described functional activity in the posterior superior temporal sulcus (pSTS) to perceived eye and mouth movements. Similarly, Lloyd-Fox and colleagues found a greater haemodynamic response in the STS complex when 5-month-old infants viewed video clips of female actors moving specific face parts (Lloyd-Fox, Blasi, Everdell, Elwell & Johnson, 2009). Natural video sequences of facial motion also significantly activated the pSTS, even when stimulus motion was controlled for (Schultz & Pilz, 2009). More recent studies have reported parallel results. Polosecki *et al.*, (2013) found only the STS to show specific sensitivity to videos of actors vocalising and generating expressions. Increasing the frame rate and correct frame order of facial motion also evoked a greater BOLD response in the STS, indicating its involvement in accessing the fluidity and meaning of facial movements (Schultz, Brockhaus, Bühlhoff & Pilz, 2013). Chewing gestures or fearful expressions further yielded a consistent lateralisation in the right pSTS relative to phase-scrambled stimuli (De Winter *et al.*, 2015). These findings suggest that the processing of variant and changeable facial aspects occurs primarily within the STS.

While informative, many of the abovementioned investigations have implemented abstract or unnatural depictions of facial movement (e.g., implied motion images or morphed videos from static images). These representations, however, may not fully engage the underlying mechanisms (Schultz & Pilz, 2009). In a previous paper, we addressed this issue by exploiting recent developments in marker-less technology in order to generate accurate and realistic models of facial movement (Girges, Spencer & O'Brien, 2015). Simultaneous sequences of rigid and nonrigid motion were recorded from human actors and applied to a standard CGI face. The purpose of this was to limit interferences from residual spatial (non-motion) cues which may confound perception.

With reference to this stimulus set, the aim of the present research was to examine the neural processing of facial motion. By doing so, we can validate its use in studies of human face perception and build upon any

existing literature which has utilised ecologically invalid presentations. Accordingly, neurotypical observers took part in a facial motion discrimination task whereby judgements were based solely on differences in motion patterns. The stimuli were also presented in an inverted orientation to form a baseline condition. This experimental paradigm affects face recognition by disrupting configural processing and early structural encoding (Girges, Wright, Spencer & O'Brien, 2014).

Methods

Participants

Ethical approval was acquired from Brunel University. Eight adults (2 males, 6 females, age: $M = 24.75$, $SD = 3.92$, $Range = 21 - 32$ years old) with normal or corrected-to-normal vision participated in the current study. None of the sample reported any history of neurological or psychological disorders. Participants were given a description of the study and written informed consent was obtained. They were debriefed after the experiment was terminated.

Stimuli

Dynamic face stimuli were taken from a video database developed by Girges, Spencer and O'Brien (2015). The movement of 15 non-professional human actors, as they recited a range of poems, was captured and retargeted onto a standard avatar. Final animations exhibited both rigid (head rotations and translations) and nonrigid (expressional changes) motion patterns, as well as natural speech and eye-gaze movements. Individual differences in facial form were limited by all animations sharing the same appearance. To form the baseline condition, each stimulus was inverted by rotating the original video file along an 180° axis (see Girges, Spencer & O'Brien (2015) for full details concerning the stimuli method).

Functional MRI Task and Design

Conditions were configured in MATLAB and presented using an LCD display with a resolution of 1024 x 768 and 60Hz refresh rate. The experiment comprised 40 interleaved blocks of either upright or inverted facial motion. Within each block, two successive videos (separated by a 1-second interstimulus interval) were displayed. Using

a two-alternative forced-choice procedure, participants were required to judge whether the videos were identical to each other. Responses were made via a button press (left = identical, right = different) and response timeout was set to 5 seconds. Each video was presented for 8 seconds and the task took approximately 16 minutes to complete. See Figure 1.

Image Acquisition and Analysis

Images were acquired on a 3.0 Tesla Siemens Magnetom Trio scanner with a 32 channel array head coil. Functional MRI was performed using a standard gradient echoplanar imaging (EPI) sequence (TR 3000ms, TE 30ms, flip angle 90°, 3mm slice thickness, 64 x 64 matrix, 160 contiguous axial slices, bandwidth 1396 Hz/pixel). Functional scanning runs comprised up to 320 volumes lasting 16 minutes. Anatomical T1-weighted MPRAGE 3D MRI sequence images were also acquired during the scanning session (TR 1830ms, TE 4.43ms, flip angle 11°, 160 axial slices, 1mm isotropic voxels, 256 x 256 matrix, bandwidth = 130 Hz/pixel). Visual stimuli were projected onto a screen (via a Sanyo LCD projector, PLC-XP1000L, native resolution = 1024 x 768) in the bore of the magnet and viewed through an angled mirror above the head coil. All stimuli were shown within a window measuring 420 x 420 pixels on the screen. At the effective total viewing distance (from projection screen to the coil mirror to the participants' eyes) of approximately 82cm, this corresponded to 12.0° x 12.0°.

The data were pre-processed and analysed by using Statistical Parametric Mapping (SPM8, Wellcome Institute of Cognitive Neuroscience, London, UK) in MATLAB. For individual data sets, the images were corrected for head movement by realigning each EPI volume to match the volume in the first scan. The resulting images were then normalised to stereotaxic MNI coordinates using trilinear interpolation. As a final pre-processing step, the normalised images were smoothed using a Gaussian filter with a full-width at half maximum parameter set to 8mm.

The analysis was based on a regular whole-brain SPM approach. Statistics were performed separately at each voxel and modelled using a box-car function convolved with a canonical hemodynamic response function. Contrasts were defined to compare the neural difference between upright and inverted facial motion by

subtracting one beta from the other. Group averages of these first-level analyses are reported below. A random-effects (RFX) analysis was also conducted across the group based on individual statistical parameter maps to allow for population inference. Regions of interest (ROI) were limited to the occipital and temporal lobes (conducted via the WFU PickAtlas toolbox in SPM8).

Results

Group Average

When discriminating between different videos of facial motion, the upright > inverted contrast revealed significant activations in the bilateral pSTS, extending into the middle temporal cortex (Figure 1). Activity was also observed in the bilateral lingual gyrus (LG), right fusiform gyrus (FG), left cerebellum and a region of the right precentral gyrus known to contain the dorsal premotor cortex (dPMC; Table 1). The reverse contrast (inverted > upright) is presented in Table 1.

Figure 1 about here

Table 1 about here

RFX Analysis

Greater neural activity for observing upright versus inverted facial motion was seen in the bilateral STS. Activity extended to the middle temporal cortex, but only on the left hemisphere. Regions within the left calcarine sulcus, FG and precuneus also appeared responsive to upright facial motion (Table 1). These results support those reported in the group average analysis.

Discussion

Discriminating upright videos of facial motion evoked the greatest activity in the STS compared to discriminations with inverted types. Specifically, a large cluster was observed in the right posterior limb (pSTS). These findings corroborate previous studies which report the STS to be the region most strongly associated with the analysis of variant facial aspects (Puce *et al.*, 1998; Lloyd fox *et al.*, 2009; Schultz & Pilz 2009; Polosecki *et al.*, 2013;

Schultz *et al.*, 2013). For example, Pelphrey, Morris, Michelich, Allison & McCarthy (2005) found that the mid-posterior and right pSTS were sensitive to mouth and eye movements respectively. Similarly, there is evidence that the event-related N170 response to averted eye-gaze and mouth opening movements reflects the engagement of the STS (Rossi, Parada, Kolchinsky & Puce, 2014).

The perception of facial motion evoked a response in part of the medial visual occipital cortex known as the lingual gyrus. Those who have examined the neural correlates of dynamic emotion recognition have reported similar activities occurring within portions of this substrate (Trautmann-Lengsfeld, Domínguez-Borrás, Escera, Herrmann & Fehr, 2013). By contrast, studies which implement computer-generated displays of nonrigid motion suggest that the lingual gyrus may only process categorical information. Indeed, Sarkheil, Goebel, Schneider and Mathiak (2013) observed a greater engagement of the lingual gyrus when participants were instructed to indicate the gender of a face compared to emotional ratings. However, it is possible that discrepant data is related to the subtype of motion viewed. For example, nonrigid motion appears to facilitate gender discriminations specifically because such facial aspects are functionally related to speech and expression which differ significantly between the sexes (Hill & Johnston, 2001). Nonetheless, the neural encoding of facial motion seems to be supported by early visual mechanisms.

There is also evidence to suggest that the lingual gyrus is influenced by the face-selective fusiform gyrus in a feedforward and re-entrant manner (McKay *et al.*, 2012). While this cannot be fully commented on in the current study, small significant activities in regions corresponding to the fusiform face area (FFA) did emerge from the analysis. Such engagement could actually reflect the processing of facial form rather than of the motion contained within in it. In support of this claim, Schultz *et al.*, (2013) reported that the FFA was sensitive to manipulations which distorted the frame rate but not frame order of dynamic facial stimuli. The authors explain such finding by suggesting that this ventral temporal region is receptive to the increase in static information available from moving faces, rather than to the motion *per se*.

The analysis of facial movement also involves regions outside of the cerebral cortex. Large active voxels were seen in the left cerebellum during the discrimination of upright facial motion. It is widely acknowledged that the cerebellum has a role in motor functions, but there is evidence of this extending to sensory processing as well (Baumann & Mattingley, 2014). Lesions to this region can cause impairments on tasks detecting visual motion signals in noise, suggesting that it interacts with the dorsal stream (Jokisch, Troje, Koch, Schwarz & Daum, 2005). To our current knowledge, no study investigating facial motion processing has found this response. However, previous investigations which implement point-light walker stimuli have reported cerebellar activity (Sokolov, Erb, Grodd & Pavlova, 2014). For example, lobules Crus I and VIIB of the left lateral cerebellum exhibited an increased BOLD response during body motion perception (Sokolov *et al.*, 2012). The authors further noted a bi-directional communication between the left lobule Crus 1 and right pSTS. Evidently, the STS acquires many multimodal associations which are not limited to cortico-cortical connections.

Conclusion

Viewing upright facial motion strongly engaged the STS, further highlighting its role in biological motion processing. Portions of the primary visual cortex, ventral temporal cortex and cerebellum were also responsive to upright facial motion. Such finding suggests that the function of the STS is supported by multiple visuo-motor inputs. These data are therefore consistent with previous studies and builds upon existing literature employing ecologically invalid stimuli (e.g., morphed videos). The animations implemented here were highly reminiscent of real life facial motion, giving rise to a much more accurate neural representation.

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Tables

Table 1. The coordinates of the foci of activation in MNI space, their T-values and the cluster size* are shown (k = 10 voxels).

Group Average Analysis												
Anatomy	Upright > Inverted ($p < .05$, FWE)					Inverted > Upright ($p < .05$, FWE)						
	BA	Coordinates			T-value	Size	BA	Coordinates			T-value	Size
		x	y	z				x	y	z		
R. STS	22	52	-36	8	7.61	858						
R. STS	48	68	-36	22	5.72							
R. STS	42	60	-36	20	5.57							
L. LG	17	-2	-72	-4	7.25	899						
R. LG	18	6	-86	-6	6.49							
L. Cerebellum	18	-8	-82	-14	6.08							
L. Middle temporal	37	-62	-56	10	6.36	402						
L. Middle temporal	21	-62	-48	8	6.18							
R. FG	37	42	-44	-24	5.65	38						
L. Cerebellum	37	-42	-54	-24	5.53	50						
L. Cerebellum	37	-40	-44	-26	5.07							
R. Precentral	6	56	4	42	5.20	57						
R. Middle occipital							18	36	-82	8	9.25	572
L. Middle occipital							18	-34	-90	6	6.35	182
RFX Analysis												
Anatomy	Upright > Inverted ($p < .05$, FWE)					Inverted > Upright ($p < .001$, uncorrected)						
	BA	Coordinates			T-value	Size	BA	Coordinates			T-value	Size
L. Calcarine sulcus	17	-6	-78	6	13.80	101						
L. Calcarine sulcus	17	-10	-86	0	11.88							
L. Middle temporal	20	-52	-14	-12	11.37	62						
L. Middle temporal	22	-60	-38	8	11.04	193						
L. Middle temporal	22	-56	-46	12	9.03							
L. Middle temporal	22	-68	-34	6	6.91							
R. STS	22	60	-34	14	8.96	47						
L. Calcarine sulcus	17	0	-70	16	7.53	31						
L. Precuneus	18	2	-78	18	7.42							
L. FG	37	-36	-38	-24	7.29	22						
L. Middle occipital							18	-28	-96	22	8.46	56
L. Middle occipital							18	-36	-86	20	7.60	
R. Middle occipital							18	32	-80	40	5.99	14
L. Middle occipital							18	44	-84	10	5.68	19

*Missing values in the size column indicate an activation peak that is part of the cluster listed immediately above.

Figure Captions

Fig 1. (A) Example experimental trial; (B) activity in the right pSTS; (C) right lingual gyrus; and (D) left middle temporal cortex (extending into the STS) for upright > inverted facial motion. The image on which activity is overlaid is the mean of the structural images from all participants.

