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Neural responses to rigidly moving faces displaying shifts in social attention investigated with fMRI and MEG☆

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ABSTRACT

A widely adopted neural model of face perception (Haxby, Hoffman, & Gobbini, 2000) proposes that the posterior superior temporal sulcus (STS) represents the changeable features of a face, while the face-responsive fusiform gyrus (FFA) encodes invariant aspects of facial structure. 'Changeable features' of a face can include rigid and non-rigid movements. The current study investigated neural responses to rigid, moving faces displaying shifts in social attention. Both functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG) were used to investigate neural responses elicited when participants viewed video clips in which actors made a rigid shift of attention, signalled congruently from both the eyes and head. These responses were compared to those elicited by viewing static faces displaying stationary social attention information or a scrambled video displaying directional motion. Both the fMRI and MEG analyses demonstrated heightened responses along the STS to turning heads compared to static faces or scrambled movement conditions. The FFA responded to both turning heads and static faces, showing only a slight increase in response to the dynamic stimuli. These results establish the applicability of the Haxby model to the perception of rigid face motions expressing changes in social attention direction. Furthermore, the MEG beamforming analyses found an STS response in an upper frequency band (30–80 Hz) which peaked in the right anterior region. These findings, derived from two complementary neuroimaging techniques, clarify the contribution of the STS during the encoding of rigid facial action patterns of social attention, emphasising the role of anterior sulcal regions alongside previously observed posterior areas.

1. Introduction

In functional magnetic resonance imaging (fMRI) studies, face-responsive activations are frequently seen in the posterior superior temporal sulcus (STS), the fusiform gyrus (the Fusiform Face Area or FFA) and posterior sections of the lateral occipital lobes (the Occipital Face Area or OFA; Andrews & Ewbank, 2004; Hoffman & Haxby, 2000; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Bentin, Gore, & McCarthy, 1998). These regions have been proposed as a core neural system for face perception by Haxby, Hoffman, and Gobbini (2000), who describe a fully integrated system in which the OFA, FFA and STS respond to the presentation of a face but with a division of labour between the FFA and posterior STS.

The dissociation of function between these ventral (FFA) and dorsal (STS) face-responsive regions has been demonstrated in various ways; for example by the finding that selective attention to the identity of a face increases activation in the FFA, whereas attention to the static gaze direction in the same stimulus produces a preferential activation of the posterior STS (Hoffman & Haxby, 2000). Based on such evidence, Haxby et al. (2000) proposed that invariant aspects of facial structure, used for purposes such as face recognition, are encoded in the face-responsive fusiform region, while changeable aspects of a face (e.g. the eyes and mouth), needed for social communicative functions, are represented in the posterior STS. As Haxby et al. note, this division between aspects of face perception signalled primarily from changeable and non-changeable cues parallels a distinction commonly made in cognitive models of face perception (Bruce & Young, 1986).

The perception and interpretation of changeable facial aspects is integral to social communication. In particular, perceiving another individual's gaze direction provides information about what is

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important to them in the surrounding environment, from which one can extrapolate to their thoughts, motivations and intentions within the current circumstances (Baron-Cohen, 1995, for a recent review see; Frischen, Bayliss, & Tipper, 2007). Gobbini and Haxby (2007) incorporated these processes into a revision of their neural model of face perception, suggesting that the involvement of the posterior STS extends beyond a basic visual analysis of the face to extract the intentional information conveyed by these changeable features.

In everyday interaction, the changeable aspects of a face form a continuous display of dynamic social signals. These facial movements can be either rigid or non-rigid. Both types of motion convey salient social information. Rigid head motions provide insight in the direction of attention of an individual and provide a different view of the face (Pike, Kemp, Towell, & Phillips, 1997), while non-rigid motions of internal face features provide visual information relating to speech, expression and eye movement (O'Toole, Roark, & Abdi, 2002). Gaze direction, or *social attention*, can be determined from both non-rigid internal eye motions and rigid head motions (Langton, 2000; Langton, Honeyman, & Tessler, 2004; Perrett, Hietanen, Oram, & Benson, 1992). Previous studies examining the neural basis of the perception of social attention have focused on internal eye-gaze direction, either in a static face (Engell & Haxby, 2007; Hoffman & Haxby, 2000; Materna, Dicke, & Thier, 2008; Taylor, George, & Ducorps, 2001; Wicker, Michel, Henaff, & Decety, 1998) or through a non-rigid motion of the eyes (Conty, N'Diaye, Tijus, & George, 2007; Pelphrey, Singerman, Allison, & McCarthy, 2003; Pelphrey, Viola, & McCarthy, 2004).

Head orientation also represents an important cue of social attention direction. Information about head orientation and eye direction are integrated in the perception of gaze (Langton, 2000; Langton et al., 2004; Perrett et al., 1992). Single cell studies in the macaque STS have indicated that individual cells respond to a conjunction of information from the eyes, head and body when computing the direction of social attention (Perrett et al., 1992). Furthermore, research with human participants has shown that when directional information from eye-gaze direction and head orientation is in conflict recognition of social attention is slowed (Langton, 2000; Langton et al., 2004) and the fMRI-indexed STS response may be reduced (George, Driver, & Dolan, 2001). However, with rigid head motion, these head and eye cues are inherently congruous and thus potentially elicit an increased STS response.

The first experiment of the current study was therefore designed to investigate the applicability of the Haxby model of face perception (Haxby et al., 2000) to faces that move rigidly to convey a congruent head-eye shift in social attention. FMRI was used to identify the spatial profile of the haemodynamic response to dynamic shifts in social attention conveyed by rigid face movements when contrasted with static social attention stimuli and non-social directional motion. By carrying out a concurrent functional localiser scan, designed to activate the core system of Haxby et al.'s face perception model, the activations identified in the main experimental contrasts could be defined both in terms of their anatomical location and their functional role within current conceptions of face perception (Gobbini & Haxby, 2007; Haxby et al., 2000). Furthermore, a functional region of interest (fROI) analysis allowed for an examination of the main experimental contrasts within functionally defined regions of visual cortex (for discussion see; Saxe, Brett, & Kanwisher, 2006).

Having established the spatial profile of the haemodynamic response to rigidly moving social attention stimuli, the second experiment was designed to increase understanding of these activations by employing a direct measure of neural activity, magnetoencephalography (MEG). Recent advances in MEG beamforming source localisation potentially deliver spatial results of a similar resolution to fMRI (Hillebrand, Singh, Holliday, Furlong, & Barnes, 2005; Singh, 2006) and have successfully been used to investigate cognitive function (Bayless, Gaetz, Cheyne, & Taylor, 2006; Cornelissen, 2009; Itier, Herdman, George, Cheyne, & Taylor, 2006; Pammer et al., 2004; Pammer, Hansen, Holliday, & Cornelissen, 2006; Singh, Barnes, Hillebrand, Forde, & Williams, 2002; Singh, Barnes, & Hillebrand, 2003). However, this body of research remains in its youth, therefore the above-described fMRI experiment provided a spatial structure around which to frame source localisations identified through MEG beamforming before gaining further insight from the multidimensional MEG signal.

Due to its excellent temporal resolution, MEG can be used to investigate both the time course and frequency content of neural responses. MEG has been employed to examine the time course of neural responses to faces (Itier et al., 2006; Liu, Harris, & Kanwisher, 2002; Sato, Kochiyama, Uono, & Yoshikawa, 2008; Taylor et al., 2001), but as of yet little is known about the frequencies of neural oscillation which contribute to the neural system underlying face perception. Coherent object perception has been associated with an increase in oscillatory power in frequencies above 30 Hz in EEG studies (Rodriguez, 1999; Tallon-Baudry & Bertrand, 1999) and a decrease in oscillatory power in frequencies below 30 Hz in both EEG and MEG studies (Lachaux, 2005; Maratos, Anderson, Hillebrand, Singh, & Barnes, 2007). Decreased oscillatory power in frequencies below 30 Hz has also been observed with MEG when participants viewed point-light displays of biological motion (Singh et al., 2002). On this basis, MEG beamforming was carried out in two distinct frequency bands, a lower band (4–30 Hz) and an upper band (30–80 Hz), so as to examine the spatial distribution of neural oscillations within these frequency ranges during the perception of dynamic social attention stimuli.

In both the fMRI and MEG experiments, neural responses to dynamic face stimuli which conveyed social attention through a rigid and congruous head and eye shift (Turning Heads) were investigated. These activations were compared to those elicited by a static averted face displaying stationary social attention information (Static Heads) and also to a moving scramble video, conveying a directional shift but in a non-social domain (Moving Scrambles). The Turning Heads stimuli included turns that communicated both a shift towards the participant as if to engage in mutual gaze (Mutual Head Turns) and a shift away from the participant to averted gaze (Averted Head Turns). Traditionally defined face-responsive regions were identified by contrasting fMRI activations to static face and place stimuli (Andrews & Ewbank, 2004; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Kanwisher et al., 1997). These face-responsive regions were identified with a separate localiser scan for two reasons. In the fMRI whole-brain analysis the brain activations elicited by the main experimental conditions could be ascribed a functional label relating to current models of face perception (Gobbini & Haxby, 2007; Haxby et al., 2000). Additionally, analyses could be restricted to these face-responsive regions using a fROI approach which benefits from increased statistical power and allows for an examination of the main experimental effects within functionally defined brain regions.

In the fMRI experiment, Turning Heads were contrasted with Moving Scrambles to identify regions that were responsive to faces which display social attention information, while controlling for the neural response to directional movement. Activations were anticipated in the STS, FFA and OFA of the Haxby model (Haxby et al., 2000), and would therefore be thought to represent a response to the basic perceptual analysis of a face which may be augmented by the social attention conveyed by the dynamic face stimulus (Gobbini & Haxby, 2007). By then contrasting Turning Heads with Static Heads, the neural activations were narrowed to those that appear to dynamic social attention over and above static social attention. In this contrast, activations were again anticipated in the STS to both the dynamic and intentional components of the Turning Heads stimuli, while any residual FFA and OFA activation might be ascribed to the increase in facial structural information available from the changing face angle (O'Toole et al., 2002; Schultz & Pilz, 2009). Contrasts between Mutual and Averted Head Turns were expected to reveal differential activations in the STS.

In the MEG experiment, the Turning Heads (incorporating both Mutual and Averted Head Turns), Static Heads and Moving Scrambles conditions, each comprising identical stimuli to those used in the fMRI experiment, were again examined. MEG beamforming source localisations were used to both spatially identify neural responses and examine the frequency of neural oscillations contributing to these responses. It was anticipated that frequencies below and above 30 Hz (the lower band, 4–30 Hz, and upper band, 30–80 Hz, respectively) would contribute differentially to the perception of dynamic, rigid social attention.

2. Experiment 1—an fMRI investigation of neural responses to moving faces displaying shifts in social attention

2.1. Experiment 1—methods

2.1.1. Participants

Seventeen healthy volunteers (seven males, ten females, mean age = 24.94, s.d. = 4.16) participated in the fMRI experiment. The participants were right handed and had normal or corrected-to-normal vision. All gave informed consent to participate in the study. Ethical approval for this study was obtained from York Neuroimaging Centre (YNiC) and York University Department of Psychology.

2.2. Localiser scan

The localiser scan was carried out prior to the main experimental scan. It was designed to activate face-responsive regions so that activations identified by the main experimental contrasts in the whole-brain analyses could be functional labelled with relation to Haxby's (2000) neural model of face perception (for discussion see; Friston, Rotshtein, Geng, Sterzer, & Henson, 2006). An fROI analysis was performed to examine the main experimental effects in functionally defined face-responsive regions.

2.2.1. Materials

The stimuli comprised gray-scale photographs of four object categories: human faces of varying identity, pose and expression; inanimate objects; clothed human bodies (without heads); scenes and phase-scrambled images. Images of faces were collected from the PICS database (http://www.pics.psych.stir.ac.uk/) and were not familiar to any of the participants. Photographs of inanimate objects and places were obtained from various sources including commercial clipart collections (CorelDraw, Microsoft). Images of human bodies were obtained from a stimulus set used by Downing et al. (2006). To create the phase-scrambled images, a Fourier transform was performed on a set of pseudo-randomly selected stimulus images. The phase spectrum was randomly scrambled whilst the frequency spectrum was maintained, then an inverse transform was performed to create a phase-scrambled image with the same spatial frequency content as the original image. Stimuli were presented using the 'Presentation' software package (Neurobehavioural Systems Inc.).

2.2.2. Design and procedure

A counterbalanced block design was used in the localiser scan. Each scan included four blocks of each of the five stimulus types: faces varying in identity; pose and expression; places; bodies; objects and phase-scrambled images. Each 9-s stimulus block contained 10 images, with each image being presented for 700 ms followed by a 200 ms blank screen. Blocks were separated by 9-s periods of fixation during which a white-cross appeared on a grey screen, of the same average luminance as the stimulus images.

A small red dot appeared in one or two images per block (∼14% of trials). The participant's task was to make a button-press response as quickly as possible to the appearance of the red dot. These trials were included to ensure that the participant remained attentive to the stimuli throughout the localiser scan.

2.3. Main experimental scan

The main experimental scan followed the functional localiser scan. It was designed to identify brain regions which show an increased response to facial action patterns of social attention by contrasting activations to Turning Heads stimuli with those to Static Heads and Moving Scrambles. Stimulus contrasts could also be carried out between Mutual and Averted head turns.

2.3.1. Materials

The stimulus materials for the main experiment consisted of video clips of four actors (two male, two female, mean age = 25.25, s.d. = 2.63). Video clips were acquired with a digital video recorder against a common background and under common lighting conditions, at a distance of approximately 1.5 m. The actors displayed a neutral facial expression. Actors sat in the centre of circle surrounded by posts that measured 30° intervals. Fixation points were made on the posts at eye height.

Four *Turning Heads* video recordings were made for each model, two (one for each side of the head) from an initial 30° averted position to the central camera (0°) and two from the same starting position to a further averted location at 60° (Fig. 1A). Through-out shifts, actors tried to keep their eye-gaze direction congruent with their

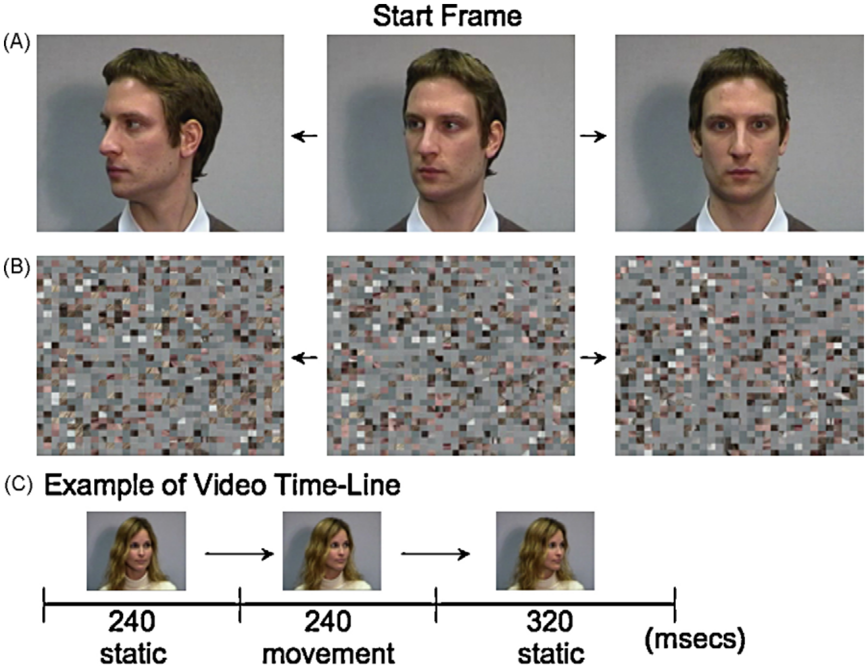

Fig. 1. Main experimental stimuli. (A) Example frames from the Turning Heads videos. The movement begins from the frame shown in the central pane, 'Start Frame', and ends with either the frame shown in the left- or right-hand pane. (B) Equivalent example frames from the Moving Scrambles videos. (C) The time-course of the moving video clips. N.B. The Static Heads video displays only the 'Start Frame', represented in (A), for the entire stimulus presentation.

head orientation and used the marked posts to guide their movement. Using Adobe Premiere, the temporal parameters of each of these clips were made equivalent (for more detail see the Design and procedure section). To control for facial, movement and lighting asymmetries in the different head orientation movements each video clip was mirror reversed, creating four more video clips for each actor. In total thirty-two *Turning Heads* video clips were made.

The video clips for the *Static Heads* comparison condition were created by taking one frame, from each actors' set of videos, that showed the head oriented at 30° to the left. This frame was presented for 800 ms. Equivalent clips were made with heads oriented at 30° to the right. Again, these clips were mirror reversed. In total, sixteen static video clips were made.

For the *Moving Scrambles* comparison condition, sixteen video clips were selected from the experimental video clips, eight showing leftward shifts and eight showing rightward shifts. Using Matlab (Mathworks), a 32 × 32 grid was applied to each of 20 video frames (Fig. 1B). The grid squares were scrambled in exactly the same way for each frame such that, once the frames were reconstructed into the 800 ms video clip, the video exhibited leftward or rightward motion within the same time parameters as the original video clip.

2.3.2. Design and procedure

The experiment was implemented as a counterbalanced block design such that there were four different conditions each associated with 8 blocks of stimuli. The four conditions were Mutual Head Turns, Averted Head Turns, Static Heads and Moving Scrambles. These are described below:

Mutual Head Turns: Video clips in which an actor appeared to turn towards the participant to simulate direct gaze. Half of the turns originated from 30° to the left (with respect to the participant) and the other half from 30° to the right.
Averted Head Turns: Video clips in which an actor appeared to turn away from the participant. Half of the head turns started from 30° to the left and turn to 60° to the left and the other half started from 30° to the right and turn to 60° to the right.
Static Heads: Video clips displayed a static head that remained oriented 30° from the participant (half left, half right) for the duration of stimulus presentation.
Moving Scrambles: Scrambled video clips of the head turns in which no face was perceptible but that retained a sense of directional motion, half towards the left and half towards the right.

The video clips conveying motion (Mutual Head Turns, Averted Head Turns and Moving Scrambles) all displayed the same timing parameters, each was 800 ms in total duration, starting with 240 ms of static, followed by a movement commencing at 240 ms and continuing steadily over 240–480 ms, then the stimulus became static again for the final 320 ms of the video (Fig. 1C). Therefore, the Static Heads condition only differentiated from the the two Head Turns conditions at 240 ms, as from 0 to 240 ms all three conditions displayed a static head that remained stationary at 30° from the participant.

The stimuli were displayed in blocks of 12 s. Each stimulus block contained 8 video clips, with each 800 ms video clip separated by a 700 ms blank screen. Each stimulus condition was repeated 8 times in a counter balanced block design. Blocks were separated by periods of fixation when a grey screen appeared for 12 s. Therefore, each block, including both the passive and active periods, was a total of 24 s in length. There were 32 stimulus blocks. The total duration of the experiment was 12 min 48 s.

A small red dot appeared on one or two videos in most blocks. As in the localiser scan, the participant's task was to make a button-press response as quickly as possible to the appearance of the red dot. These trials were included to ensure that the participant remained attentive to the stimuli throughout the experiment.

2.3.3. MRI data acquisition

fMRI measurements were performed on a 3.0 Tesla scanner (General Electric HD Excite), using an eight-channel eight-element phased-array birdcage coil (General Electric) tuned to 127.4 MHz. Foam padding was used around the participant's head to minimise movements. Participants wore earplugs to protect their ears from the noise of the scanner.

Before scanning an automatic shim was performed to maximise magnetic field homogeneity. fMRI data were acquired using a gradient single-shot echo planar imaging (EPI) sequence with the following acquisition parameters; thirty-eight contiguous slices, repetition time (TR) 3000 ms, echo time (TE) 25.6 ms, flip angle 90°, field of view (FOV) 288 mm, matrix 128 × 128, slice-thickness 3 mm, oriented approximately parallel to the anterior–posterior commissure line but optimised for coverage of the occipitotemporal cortex.

To facilitate localisation and coregistration of functional data to the structural image, a T1-weighted in-plane anatomical image was acquired using a fluid attenuated inversion recovery (FLAIR) sequence with the parameters; TR 2375 ms, TE 13.8 ms and inversion time (TI) 1050 ms. In-plane anatomical images for each individual had the same prescription as the fMRI acquisitions.

Three structural scans were acquired. A sagittal isotropic 3D fast spoiled gradient recall echo (3D FSPGR) structural T1 weighted scan was acquired for each participant with the following parameters; TR 8.03 ms, TE 3.07 ms, flip angle 20°, FOV 290 mm, matrix 256 × 256 and slice thickness 1 mm. A sagittal isotropic fast recovery fast spin echo (FRFSE-XL) structural T2 weighted scan was acquired with the following parameters; TR 8940 ms, TE 203 (effective), flip angle 90°, FOV 290 mm, matrix 256 × 256 and slice thickness 1 mm. An axial high definition isotropic fast spin echo (FSE T2) structural T2 weighted scan was acquired with the scanning parameters of; TR 5240 ms, TE 99.26 ms, flip angle 90°, FOV 260 mm, matrix 512 × 512 and slice thickness 6 mm.

The FLAIR images were skull-stripped using a brain extraction tool (BET, Smith, 2002) to remove non-brain tissue from the image. The skull-stripped volume was then used as an intermediary level in a FLIRT multi-stage registration process (Jenkinson & Smith, 2001) from the partial brain EPI to the full-brain, high-resolution structural T1 image.

2.3.4. fMRI analysis

Functional MRI data were analysed using FEAT (FMRIB, Oxford, UK; http://www.fmrib.ox.ac.uk/fsl). Before statistical analysis, the data were preprocessed using MCFLIRT motion correction, spatial smoothing (Gaussian, FWHM 8 mm) and a temporal high pass filtering (cutoff, 0.01 Hz).

First-level general linear model (FILM) analysis with time series prewhitening (Woolrich, Ripley, Brady, & Smith, 2001) was used for each individual EPI sequence, providing contrasts for group effects analysed at the higher level. For each individual, GLM results were calculated and transformed into standard MNI (Montreal Neurological Institute) space (Jenkinson & Smith, 2001). Second-level analyses, across all 17 participants, were carried out using FLAME Bayesian mixed-effects analysis (Beckmann, Jenkinson, & Smith, 2003) to generate z-statistic images based on the contrast between conditions. The z-statistic images were thresholded with clusters determined by $z > 2.3$ and a cluster significance threshold of $p < .05$ (Forman et al., 1995).

Functionally defined regions of interest (ROI) were determined in the localiser scan by identifying voxels in each individual's temporal cortex where the contrast between face and place conditions indicated a greater response to faces (see Andrews & Ewbank, 2004). In both the localiser and the main experimental scan, the time series of the filtered MR data at each voxel was converted from units of image intensity to percentage signal change by subtracting and then normalising the mean response of each scan ($[x - \text{mean}]/\text{mean}x100$). All voxels from the ROI defined in the localizer scan were averaged to give a single time series in each ROI for each subject. The onset of the response from individual stimulus blocks was then normalised by subtracting every time point by the response at the onset of the stimulus block. The resulting data were then averaged to obtain the mean time course for each stimulus condition on a scan. The peak response was calculated as an average of the response at 9 and 12 s (localiser) and 12 and 15 s (main experiment) after the onset of a block. The peak responses from the face-selective regions in each subject were entered into a repeated-measures ANOVA to determine whether stimulus condition had a significant effect on response. Post-hoc analysis was performed using paired t-tests to reveal significant differences between pairs of conditions.

2.4. Experiment 1—results

2.4.1. Behavioural results

In an attempt to ensure attentional demands where equated across task conditions, participants were required to respond to the occurrence of a red dot appearing on one or two stimulus presentations per block. This task was used in both the localiser and the main social attention experiment scans.

Reaction time to press to the presence of the dot did not differ significantly across task conditions in the localiser scan, $F(5, 80) = 1.80$, $p > .05$, or the main social attention experiment, $F(1.58, 25.23) = 1.89$, $p > .05$. With regard to the behavioural data from the main experiment, Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(5) = 23.40$, $p < .05$), so degrees of freedom were corrected using the Greenhouse–Geisser estimates. It could thus be assumed that, in both the localiser scan and the main experiment, attentional demands were equivalent across task conditions and therefore would not account for differences in the haemodynamic responses to different categories of stimuli.

2.4.2. Localiser scan

Face-selective regions were characterised as those that responded more strongly to face stimuli than to place stimuli (Andrews & Ewbank, 2004; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Kanwisher, McDermott, & Chun, 1997) and were identified across participants in bilateral posterior STS, the fusiform gyrus (corresponding to the FFA; Kanwisher et al., 1997) and in the posterior regions on the lateral surface of the occipital lobe (corre-

Table 1
Average size and coordinates of the face-selective regions across subjects in fMRI

Brain region	x	y	z	Max. z-value	Volume (mm^3)
Left fusiform face area	−40	−57	−22	5.45	932
Right fusiform face area	44	−56	−23	5.51	1664
Left occipital face area	−45	−79	−9	5.21	1354
Right occipital face area	46	−75	−5	5.74	2179
Right posterior superior temporal sulcus	50	−62	3	5.11	1749

sponding to the OFA; Andrews & Ewbank, 2004; Haxby et al., 2000; Hoffman & Haxby, 2000). These regions were defined as functional ROI (Table 1).

The mean time course of response to different stimulus conditions in these ROI is shown in Fig. 2. An ANOVA revealed a main effect of stimulus condition in the FFA ($F(4, 60) = 61.60, p < .001$), OFA ($F(4, 60) = 73.23$, $p < .001$), and STS ($F(4, 52) = 49.24$, $p >$ .001), which was due to a larger response to faces compared to the other stimulus conditions. Each ROI was defined separately for each individual and further analyses were performed on the peak responses in these regions. There was no difference in the pattern of response between the right and left hemispheres. Accordingly, subsequent analyses were based on a pooled analysis in which ROIs from the right and left hemispheres were combined.

In order to compare the overlap in regions that show significant activation for face > place and each of the main experimental contrasts, the face > place z-statistic image was overlaid separately on each main experimental contrast z-statistic map on a standardised MNI brain (see Figs. 3 and 4). These figures are discussed in further detail in the following section.

2.4.3. Main experiment

For the initial stimulus contrast analyses, four blocks of stimuli were randomly selected from both the Averted and Mutual Head Turns conditions. These were grouped together to create a *Turning Heads* condition equivalent in number of contributory stimulus blocks to both the Moving Scrambles and the Static Heads conditions. The initial stimulus contrast was performed to identify responses to faces displaying social attention cues, by identifying voxels that demonstrated a greater response to Turning Heads stimuli than to Moving Scrambles stimuli. This contrast revealed voxel clusters in the bilateral posterior STS which extended along almost the entire length of sulcus in the right hemisphere. Activations were also found in the right fusiform gyrus, the right posterior section of the lateral occipital lobe, and the bilateral temporo-parietal junction (TPJ) and precuneus (Table 2). Overlaying the spatial map generated by this contrast alongside that generated by the face > place localiser contrast, revealed substantial overlap in functionally defined face-selective regions, including the bilateral posterior STS, the right FFA and OFA (Fig. 3).

To identify regions showing an increased response to moving faces expressing a change in social attention as compared to the response to static social attention information conveyed by a stationary image, the activations elicited by the Turning Heads stimuli were contrasted with those elicited by the Static Heads stimuli. Increased responses to Turning Heads stimuli were found bilaterally in the posterior STS, the occipito-temporal junction (corresponding to visual motion area V5/MT; Tootell, Hadjikani, Mendola, Marrett, & Dale, 1998), cuneus and precentral gyrus (Table 3). A small, weak response was also apparent in the right fusiform gyrus. Again, this activation map was overlaid on the map generated by the face > place localiser contrast to identify regions of overlap in functionally defined face-selective regions. Overlap was evident in both the left and right STS, extending back towards more posterior sections of the lateral occipital lobe and in a small region of the right FFA (Fig. 4). It is important to note both the similar recruitment of the posterior STS and the differential involvement of the FFA when contrasting Turning Heads with Moving Scrambles (Fig. 3) as compared to contrasting Turning Heads with Static Heads (Fig. 4).

Potential differences in neural responses to turning head stimuli that convey divergent social attentional signals were investigated by contrasting Mutual Head Turns and Averted Head Turns. In the whole-brain group analysis, there were no regions showing responses that were significantly greater to Mutual Head Turns than to Averted Head Turns, but Averted Head Turns elicited significantly more activation in primary visual areas than did Mutual Head Turns.

To further investigate any differences between conditions in the main experiment, a fROI analysis was conducted (Fig. 5). An ANOVA of the data in the main experimental session showed a significant main effect of condition in the FFA ($F(3, 48) =$ 38.53, $p < .001$). Post-hoc tests revealed that response in the FFA to the Moving Scrambles condition was significantly lower than to the Mutual Head Turns ($t(16) = 9.5$, $p < .001$), Averted Head Turns ($t(16) = 6.8$, $p < 0.001$), and Static Heads conditions

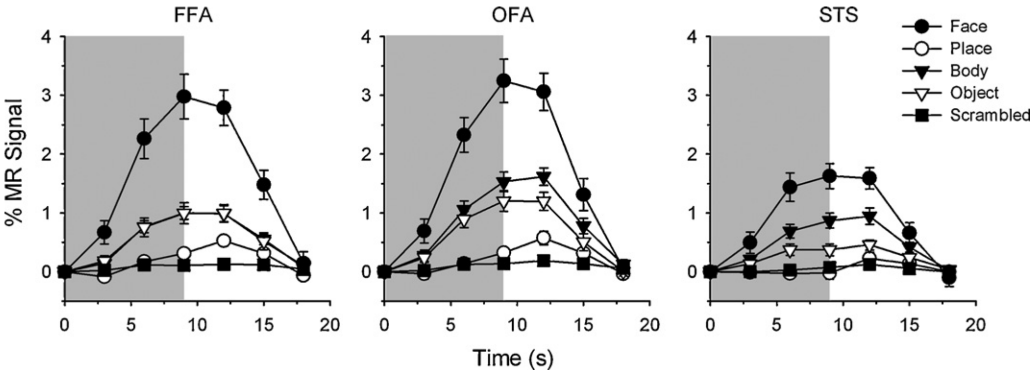

Fig. 2. Time-courses of response to each category of stimulus in the different face-selective regions (FFA: fusiform face area, OFA: occipital face area, STS: superior temporal sulcus). The shaded area represents the duration of each stimulus block and error bars represent S.E.

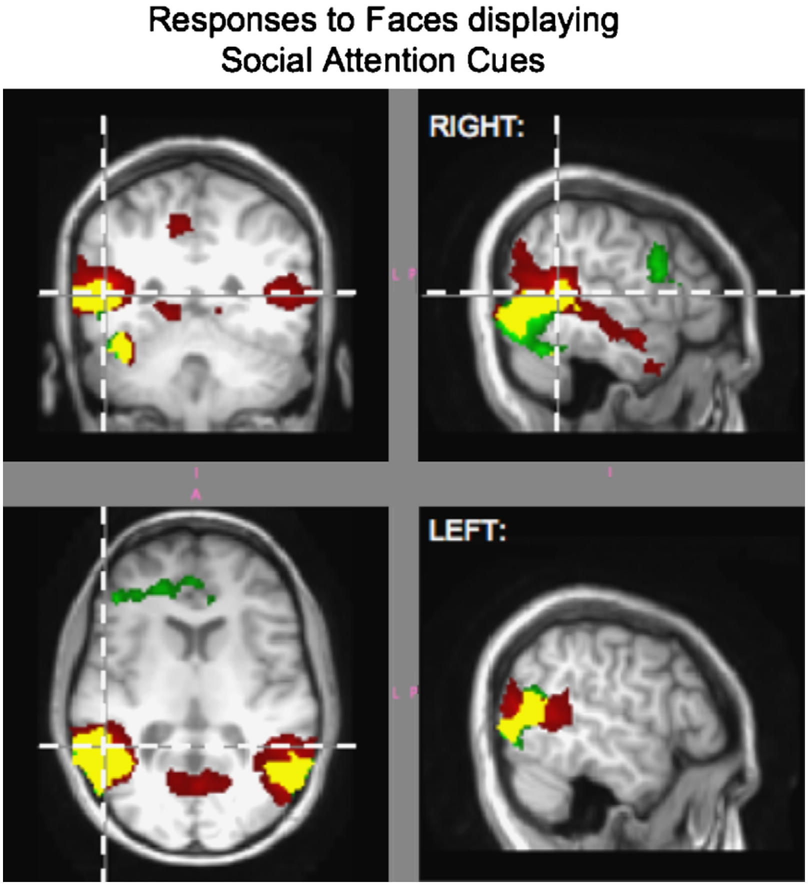

Fig. 3. Group *z*-statistic images of the fMRI activations elicited by the contrast of Turning Heads > Moving Scrambled (red) overlaid on the localiser contrast of face > place (green). Overlapping regions are shown in yellow. The cross-hairs in three of the tiles show the spatial relation between these three slices and are focused on the right posterior STS, while the lower right image displays the equivalent location in the left hemisphere. Note the activation by Turning Heads of the right and left face-responsive posterior STS, shown in yellow, and the extended activation along the right STS in response to Turning Heads, shown in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 2
Brain regions with stronger response to Turning Heads than to Moving Scrambles in fMRI ($p < .05$, cluster corrected, $N = 17$)

Brain region	*x*	*y*	*z*	Max. *z*-value	Volume (mm^3)
Right posterior superior temporal sulcus	50	−48	12	5.68	21,424
Left posterior superior temporal sulcus	−56	−54	4	4.68	8,456
Right temporo-parietal junction	58	−62	14	4.62	6,528
Left temporo-parietal junction	−54	−70	6	5.31	6,768
Right fusiform gyrus	42	−56	−28	4.73	3,280
Right posterior lateral occipital lobe	48	−76	−14	4.82	3,969
Right middle superior temporal sulcus	52	−2	−22	3.74	3,024
Right anterior superior temporal sulcus	50	6	−3	2.96	1,968
Right precuncus	8	−54	46	3.76	3,096
Left precuncus	−8	−54	46	3.76	1,824

Table 3
Brain regions with stronger response to Turning Heads than to Static Heads in fMRI ($p < .05$, cluster corrected, $N = 17$)

Brain region	*x*	*y*	*z*	Max. *z*-value	Volume (mm^3)
Right occipito-temporal junction	46	−68	2	5.62	14,824
Left occipito-temporal junction	−52	−80	−2	4.56	8,392
Right posterior superior temporal sulcus	58	−44	6	4.66	8,456
Left posterior superior temporal sulcus	−58	−54	8	3.85	6,680
Right fusiform gyrus	42	−64	−18	2.81	688
Right cuneus	18	−96	2	3.62	3,000
Left cuneus	−22	−90	2	4.13	2,296
Right precentral gyrus	58	2	36	3.60	6,600
Left precentral gyrus	−40	−6	58	3.48	3,808

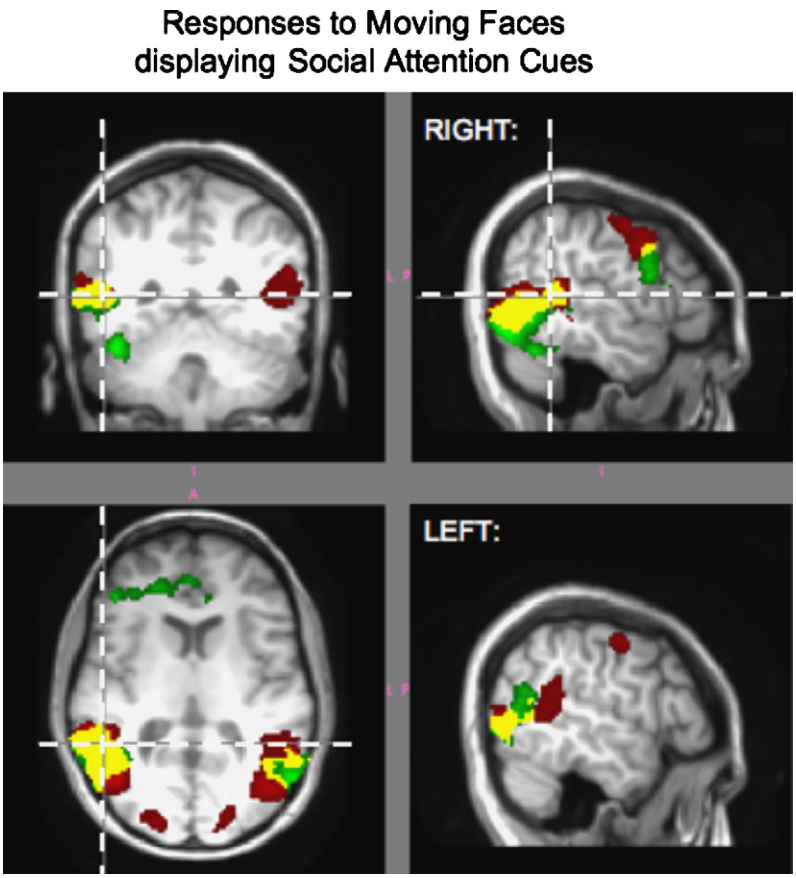

Fig. 4. Group z-statistic images of the fMRI activations elicited by the contrast of Turning Heads > Static Heads (red) overlaid on the localiser contrast of face > place (green). Overlapping activations are coloured yellow. *Note* the activation by Turning Heads of the right and left face-responsive posterior STS, in yellow, and the decreased involvement of the FFA in comparison to that found in the Turning Heads vs. Moving Scrambles contrast (Fig. 3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

($t(16) = 4.8$, $p < .001$, see Fig. 5). Response to the Mutual Head Turns condition was significantly higher than in both the Averted Head Turns ($t(16) = 3.7$, $p < .01$) and Static Heads ($t(16) = 3.9$, $p < .01$) conditions, but no difference was found between the Averted Head Turns and Static Heads conditions ($t(16) = 1.5$, $p = .1$).

There was also a main effect of condition in the OFA ($F(3, 48) = 29.22$, $p < .001$). A post-hoc analysis again indicated a significantly lower response to the Moving Scrambles condition than to the Mutual Head Turns ($t(16) = 7.3$, $p < .001$), Averted Head Turns($t(16) = 5.4$, $p < .001$), and Static Heads conditions ($t(16) = 4.0$, $p < .001$). Response to the Mutual Head Turns condition was significantly higher than in both the Averted Head Turns ($t(16) = 2.1$, $p < .05$) and Static Heads conditions ($t(16) = 4.9$, $p < .001$) and the Averted Head Turns condition was found to elicit a significantly greater response than the Static Heads condition ($t(16) = 3.2$, $p < .01$).

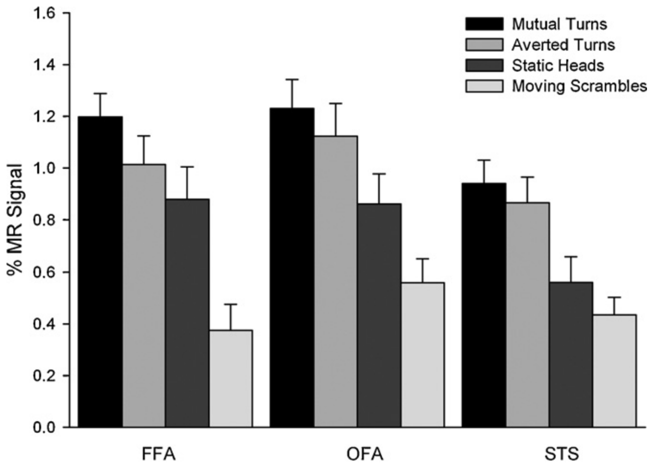

Fig. 5. Bar graph representing the peak MR response to each stimulus category within face-selective areas across all subjects. Error bars represent ±S.E.

A significant effect of condition was also found in the STS ($F(3, 42) = 32.96$, $p < .001$). Post-hoc tests revealed that response in the STS to the Moving Scrambles condition was significantly lower than to the Mutual Head Turns ($t(14) = 6.0$, $p < .001$) and the Averted Head Turns conditions ($t(14) = 5.9$, $p < .001$), but not lower than the Static Heads condition ($t(14) = 2.1$, $p < .05$). Response to both the Mutual Head Turns and Averted Head Turns conditions was higher than to the Static Heads conditions ($t(14) = 6.6$, $p < .001$; $t(14) = 8$, $p < .001$), but no significant difference was found between the Mutual Head Turns and Averted Head Turns conditions ($t(14) = 1.7$, $p < .11$).

2.5. Experiment 1—discussion

The fMRI investigation of the haemodynamic response to rigidly moving faces displaying social attention cues demonstrated an involvement of the face-responsive bilateral posterior STS in the encoding of an eye and head turn displaying a shift in attention. These activations occurred both when contrasting Turning Heads to Moving Scrambles, demonstrating the involvement of these areas in the perception of faces displaying social attention, and also when comparing Turning Heads to Static Heads, suggesting that these regions are recruited by dynamic shifts of social attention in preference to static gaze direction. The right fusiform gyrus activation was substantially greater when contrasting Turning Heads with Moving Scrambles than when contrasting Turning Heads with Static Heads, demonstrating the involvement of this region in the perception of both static and dynamic faces, with a preferential engagement of a small region of right fusiform gyrus by dynamic faces over static faces.

By combining the main fMRI experiment with a functional localiser technique, it was possible to label activations identified in the whole brain analyses not only anatomically but also functionally as face-selective areas (Friston, Rotshtein, Geng, Sterzer, & Henson, 2006). The posterior activations within the STS could be defined as the superior areas within the Haxby et al. face perception model (Gobbini & Haxby, 2007; Haxby et al., 2000; Hoffman & Haxby, 2000) proposed to be involved in encoding changeable aspects of a face and moment-to-moment facial dynamics (Allison, Puce & McCarthy, 2000), while the ventral fusiform activation occurred within the FFA, which is thought to represent relatively invariant components of facial structure. The current findings demonstrate a heightened activation of the posterior STS to dynamic, rigid social attention stimuli. This activation may represent both the biological motion of the face (Allison et al., 2000) and the social intention implicit in this motion (Gobbini & Haxby, 2007; Pelphrey et al., 2003, 2004). The current results also show the involvement of the FFA in the basic perceptual analysis of a face (Turning Heads) compared to a non-face (Moving Scrambles), and revealed a response within a small region of the FFA to the increased facial structural information available across the changing face viewpoints in the dynamic face stimuli (Turning Heads) compared to the single viewpoint of the static face stimuli (Static Heads; O'Toole et al., 2002; Schultz & Pilz, 2009).

The concurrent functional localiser scan also afforded the opportunity to conduct an fROI analysis in which the main experimental effects could be examined exclusively within face-selective regions, thereby increasing statistical power. The results elicited by these analyses were compatible with the above-described whole-brain analyses. In the STS region, there was a greater response to Turning Heads (both Mutual and Averted Head Turns) than to Static Faces and Moving Scrambles (Fig. 5). The FFA and OFA also showed a significant difference in responding to Turning Heads (including both Mutual and Averted Head Turns in the OFA but only the Mutual Head Turns in the FFA) as compared to Static Faces and Moving Scrambles, however this difference in response was smaller than for the STS. Interestingly, there was a significantly greater response in the FFA and OFA to Mutual than to Averted Head Turns. No difference in responding to these stimuli was identified in the STS. This result adds to a complex literature regarding the neural basis of the perception of gaze direction. Previous studies have reported increased responding in the fusiform gyrus to direct gaze (George et al., 2001; Pageler et al., 2003). In one case this activation was modulated by head orientation (Pageler et al., 2003) with the strongest response to direct gaze in combination with a forward face, whereas the other study found no effect of head orientation identifying an equally strong response to direct gaze independent of the forward or deviated head orientation (George et al., 2001). Given the evidence that the FFA is involved in the perception of facial structure (Hoffman & Haxby, 2000), it seems most likely that the current finding of an increased response in the FFA to Mutual Head Turns over Averted Head Turns represents the increase in facial structural information available in a forward as compared to an deviated face (Pageler et al., 2003).

Contrary to predictions no differential response to mutual and averted stimuli was observed in the posterior STS. Different studies have suggested increased responses in the STS when gaze turns towards the observer (Conty et al., 2007; Pelphrey et al., 2004), when gaze diverts from the observer (Engell & Haxby, 2007; Hoffman & Haxby, 2000; Sato et al., 2008) or equal responses to both gaze motions (Wicker et al., 1998). Across these studies, neither the level of motion nor the intentionality expressed by the gaze stimuli was controlled. Differential quantities of motion suggested by the various stimulus sets, from dynamic videos (Pelphrey et al., 2004), through more stilted, apparent motion sequences (Conty et al., 2007), to static stimuli are likely to have influenced posterior STS responses (Engell & Haxby, 2007; Hoffman & Haxby, 2000; Sato et al., 2008). Furthermore, the posterior STS has been implicated as an 'intention detector' across a wide variety of task situations, from those with fairly explicit intentionality conveyed in a familiar social setting, e.g., a person pausing to browse a bookcase (Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004), to more abstract intentional representations, such as relations between geometric shapes appearing to interact in a meaningful manner (Castelli, Happe, Frith, & Frith, 2000; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007). Although the current study attempted to increase differential STS responding by using a congruous and rigid head-eye turn as a signal of social attention, there was no explicit manipulation of the intentional context. In this study and those mentioned above, implicit differences in the intention communicated may alter according to the experimental context. This may have contributed to the variation in STS responses to different gaze directions reported across the current literature.

In the whole-brain analysis, an extended activation of the right STS was identified by contrasting Turning Heads with Moving Scrambles, but not by contrasting Turning Heads with Static Heads. This right STS region was not found to be responsive to faces alone; it is not apparent in the faces versus places contrast of the functional localiser scan. The face stimuli in the localiser scan were not manipulated in terms of social attention, however in the main experiment the social attentional nature of the face stimuli was emphasized both in the static averted head and eyes of the Static Heads stimuli and during the dynamic, rigid head-eye shift of the Turning Heads stimuli. Therefore, the response of the extended STS may represent an involvement of this region in the perception of social attention whether conveyed by a static or dynamic face stimulus.

Notably, the spatial profile of fMRI activations produced by the Turning Heads versus Moving Scrambles contrast showed a striking similarity to those of a recent study examining neural responses to the presentation of Heider–Simmel animations (Gobbini et al., 2007). These animations display geometric figures which appear to socially interact with implicit intentions and goals. Viewing these stimuli elicited a haemodynamic response bilaterally along the extent of the STS towards the anterior STS, in the fusiform gyrus and the precuneus, in correspondence with the activations found in the present fMRI investigation. Therefore, these brain regions may be similarly implicated by both scenarios in the representation of the intentions deduced from socially meaningful dynamic stimuli.

3. Experiment 2—an MEG investigation of neural responses to moving faces displaying shifts in social attention

The second experiment was designed using MEG to augment understanding of the cortical regions involved in the perception of moving faces signaling a rigid change in social attention direction. The above-reported fMRI results provided a spatial framework for MEG source localisations identified with an MEG beamforming technique (Hillebrand et al., 2005; Singh, 2006). In the current study, MEG beamforming was used to gain insight into the spatial distribution of neural oscillations within two distinct frequency ranges, a lower range (4–30 Hz) and an upper range (30–80 Hz), during the perception of a dynamic, rigid social attention shift. The temporal window for MEG analyses was narrowed to focus on this critical motion period (240–480 ms). Neural responses to rigidly moving faces displaying a change in social attention (Turning Heads) were again compared to those elicited by static faces (Static Heads) and scrambled videos displaying directional motion (Moving Scrambles). An identical stimulus set was used as that in the above fMRI-experiment.

3.1. Experiment 2—methods

3.1.1. Participants

Twenty students participated in the experiment. The data from three of these participants were not analysed due to movement during the scanning session or contamination by electromagnetic noise. In total, the data from 17 participants (ten male, seven female, mean age = 25.47, s.d. = 4.56) were analysed. All participants were right handed and had normal or corrected-to-normal vision. All gave informed consent to participate in the study. Ethical approval for this study was obtained from YNiC and York University Department of Psychology.

3.1.2. Materials

The stimulus materials were the same video clips as used in the fMRI experiment reported above (see also Fig. 1).

3.1.3. Design and procedure

An event-related design was used with four main stimulus categories: Mutual Head Turns; Averted Head Turns; Static Heads; and Moving Scrambles. Stimulus events were coded such that a fifth condition, the Turning Heads condition, was created by randomly selecting half the trials from across the Mutual Head Turns and Averted Head Turns conditions. These conditions are described above in both the *Materials* and *Design and procedure* of the fMRI experiment.

During the experiment, each trial started with a 500 ms presentation of a fixation cross in the centre of the screen. This was followed by stimulus presentation. Each participant viewed all conditions. The temporal parameters of each condition were the same as described in the fMRI section.

On most trials, the stimulus presentation was followed by an inter-trial interval (ITI) of 1200 ms. However, one in nine trials was a response trial. During response trials a small capital letter B or R (font size 8) appeared immediately after stimulus presentation during the ITI. The letter was presented for 250 ms in the centre of the screen, at the location where the original fixation cross had appeared. The participant's task was to maintain fixation at this point so that if a letter appeared they could identify it and respond quickly and accurately with an appropriate button press. These trials were included to ensure that the participant remained attentive to the stimulus throughout the experiment. The trials that required a response were pseudo-randomly selected from across conditions.

After the response trial a redundant trial appeared. The redundant trials appeared superficially the same as the other trials, however redundant trials were always concatenated with the response trials. The stimuli for redundant trials were pseudo-randomly selected from the experimental video stimuli. These redundant trials were excluded from the final analysis of the data to prevent contamination of data by the motor response from the previous trial.

There were 144 trials associated with each condition. Seventy-two trials required a response each followed by a redundant trial which was subsequently removed from analyses. Trials were presented in a random order, with the exception that redundant trials always followed response trials.

All participants had a structural MRI scan on a different date. The acquisition parameters were identical to those described in the fMRI experiment.

3.1.4. MEG data acquisition

Before data acquisition, a 3D digitiser (Polhemus Isotrak) was used to digitise the shape of the participant's head in the MEG laboratory. Head coils were applied at five points as a marker from which to measure head position before and after scanning. Two participants moved more than a 0.75 cm exclusion criterion. These were two of the three participants from whom data was excluded from analysis.

MEG-data were collected using a 248-channel Magnes 3600 whole-head magnetometer MEG system (4D Neuroimaging). Data were recorded continuously at 678.17 Hz with a bandwidth of 200 Hz. Stimuli subtending a visual angle of approximately $8 \times 8^{\circ}$ were back-projected onto a screen at a viewing distance of 0.75 m in a dimly lit, magnetically shielded room. Trigger codes were recorded in the MEG-data at the onset of each visual stimulus and button response.

3.1.5. MEG data pre-processing

Before starting analysis, the data were examined on an epoch-by-epoch basis to identify artefacts relating to blinking, swallowing, eye movements, neck tension and electrical noise. Epochs contaminated by these artefacts were removed from subsequent analyses. One dataset was entirely contaminated by electrical noise thus was excluded from further analyses (the third excluded dataset). Across the remaining 17 datasets, on average 6.45% (s.d. = 4.61) of trials were rejected, leaving a mean of 134.72 (s.d. = 6.64) trials per condition. Aberrantly responsive MEG channels were also removed from analyses.

Prior to source-space analyses, the head surface extracted for each participant during digitisation was used to co-register (using a surface-based alignment procedure; Kozinska, Carducci, & Nowinski, 2001) the participant's MEG data with their structural MRI.

3.1.6. MEG analysis

Source localisation was carried out using a minimum variance beamforming technique (Barnes & Hillebrand, 2003; Barnes, Hillebrand, Fawcett, & Singh, 2004; Fawcett, Barnes, Hillebrand, & Singh, 2004; Hadjipapas, Hillebrand, Holliday, Singh, & Barnes, 2005; Huang, 2004; Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997; Vrba & Robinson, 2001). This type of beamformer has been used extensively in investigations of cognitive neuroscience (Bayless et al., 2006; Itier et al., 2006; Pammer et al., 2004, 2006; Singh et al., 2002, 2003; Taylor, Mills, Smith, & Pang, 2008). The beamformer constructs a spatial filter for each target point in a predefined grid volume of the brain. The spatial filter essentially focuses ('beam forms') a location of interest by emphasising the contribution from that target location to the recorded signal and attenuating signals from all other locations. The weights of the spatial filter are formed from a calculation of the covariance matrix of the sensor data and prior knowledge of the sensitivity of the sensors to a putative source at every grid point in turn (the leadfields). The data values in the covariance matrix are determined by a pre-specified time period of interest and the frequency range selected. The MEG data are projected through this spatial filter to give an estimate of electrical activity at the target grid point across the specified time period and frequency range for each epoch. An estimate of neural activity is made for each target location so that the brain can be scanned for sources without a priori assumptions about the total number of active sources. To account for differing levels of background activity in different brain regions, the projected source power is normalised as a function of depth by dividing by projected noise power, from an empty room, to give the neural activity index (NAI).

In the group analysis, a standard grid was defined in the MNI brain, which was then transformed to each individual's brain using the affine transformation delivered by FSL's FLIRT. This allowed direct comparison of the NAI across individuals for each grid point. Therefore, beamforming delivered a standardised NAI (sNAI) for each individual. *t*-Test contrasts between active (stimulus on) and passive (baseline) periods, were then carried out in the time-period and frequency range stipulated for the creation of the covariance matrix. The *t*-statistic was transformed to a *z*-score to normalise for degrees of freedom. A *z*-score was found for each individual at the same target grid point. Across participants a group *t*-score could then be calculated for that anatomical location. The statistical significance of this *t*-score was established by permuting the sign of the *z*-statistic across individuals to create a non-parametric distribution of the maximum statistics. A spatial image, or statistical non-parametric map (SnPM), of the brain could then be created. Locations of source activity corresponded to '*Maxima*', increases in power in comparison to baseline, and '*Minima*', decreases in power in comparison to baseline, in the SnPM. Changes in oscillatory power in both directions have been demonstrated during object perception and the perception of biological motion (Lachaux et al., 2005; Maratos et al., 2007; Rodriguez et al., 1999; Singh et al., 2002; Tallon-Baudry & Bertrand, 1999). Both are assumed to be equally meaningful indices of neural activity (Pfurtscheller & Lopes da Silva, 1999, see later discussion).

In the present study, beamforming was carried out on a 5 mm × 5 mm × 5 mm grid. Similarly to the fMRI experiment, the analyses focused primarily on the three main video conditions of Turning Heads, Static Heads and Moving Scrambles. Two band-pass filters were applied to the data prior to beamforming. The lower band encompassed responses within the theta, alpha and beta ranges (4–30 Hz), while the upper band (30–80 Hz) included frequencies traditionally viewed as within the gamma range (Chaumon, Schwartz, & Tallon-Baudry, 2008; Cheyne, Bells, Ferrari, Gaetz, & Bostan, 2008; Fries, Nikolic, & Singer, 2007; Lachaux, 2005; Tallon-Baudry & Bertrand, 1999). The active period was selected as the time window, 240–480 ms, corresponding to the period of motion in both the Turning Heads and Moving Scrambles videos. This active period was contrasted with a passive period of the same duration which was defined as the time window between −320 and −80 ms before stimulus onset. For each contrast the passive period was always selected as the fixation cross period prior to the presentation of a Static Heads stimulus. Given the randomized trial presentation, there could be no fixed-order 'carry-over' from responses to a previous stimulus event, nor could there be any anticipatory response to a particular class of stimulus, so this passive period was assumed to be a representative baseline against which all active periods could be compared. For each contrast, statistical significance levels were established using a permutation test with 10,000 permutations, considered sufficient for a powerful determination of critical thresholds (Nichols & Holmes, 2002).

3.2. Experiment 2—results

At 240 ms, motion began in both the Turning Heads and Moving Scrambles videos, while the Static Heads video remained stationary. Focusing an active beamforming window around the period of movement, 240–480 ms, revealed oscillations within the lower fre-

Table 4
MEG source localisations identified between 240 and 480 ms (corresponding to the period of movement for Turing Heads and Moving Scrambles) for each experimental condition for different frequency bands ($N = 17$)

		Brain region	*x*	*y*	*z*	Min. *t*-value
Lower band 4–30 Hz	Static Heads	Right inferior occipital gyrus	40	−86	−22	−8.41
		Right middle occipital gyrus	20	−90	14	−8.01
		Cuneus	0	−100	−6	−7.52
		Right fusiform gyrus	60	−60	−26	−6.97
		Left inferior occipital gyrus	−40	−90	−16	−6.50
	Turning Heads	Right cuneus	24	−70	14	−9.73
		Righit middle occipital gyrus	20	−100	14	−8.86
		Right fusiform gyrus	60	−56	−26	−8.85
		Right parahippocampal gyrus	30	−46	−6	−7.87
		Left inferior temporal gyrus	−66	−56	−12	−6.81
	Moving Scrambles	Right cuneus	4	−100	−2	−10.77
		Lingual gyrus	0	−100	−16	−10.17
		Right inferior occipital gyrus	34	−86	−22	−6.24
Upper band 30–80 Hz	Static Heads	Right posterior superior temporal gyrus	54	−46	18	−9.62
		Left posterior superior temporal sulcus	−36	−46	14	−9.57
		Left parahippocampal gyrus	−26	−40	−6	−9.45
		Left middle inferior temporal gyrus	−64	−30	−22	−9.08
		Right middle superior temporal gyrus	70	−20	−2	−8.83
	Turning Heads	Right anterior superior temporal sulcus	50	4	−42	−12.42
		Left parahippocampal gyrus	−36	−50	−6	−11.47
		Right anterior inferior temporal gyrus	44	−16	−42	−11.97
		Left anterior superior temporal sulcus	−40	24	−36	−11.14
		Right posterior superior temporal gyrus	44	−50	18	−7.89
	Moving Scrambles	Right middle superior temporal sulcus	60	−30	−2	−13.98
		Left middle superior temporal sulcus	−50	−10	−60	−10.74
		Right posterior superior temporal gyrus	64	−50	18	−10.04
		Left parahippocampal gyrus	−20	−36	−12	−9.94
		Right anterior superior temporal sulcus	50	10	−36	−8.49

Filters: Lower band 4–30 Hz and upper band 30–80 Hz.

quency range in the right ventral visual stream to both the Turning Heads and Static Heads stimuli (Table 4). To concentrate on maximally responsive regions within this frequency range the *p*-value was set to .01. Note that the permutation analyses were carried out separately for each comparison thus critical *t*-values may differ at the same level of significance (critical *t*-values at $p = .01$ for the comparisons shown in Fig. 6A are $t = -6.09$ for Static Heads, $t = -6.01$ for Turning Heads and $t = -6.20$ for Moving Scrambles). As shown in Fig. 6A, the identified power changes were spatially more extensive to Turning Heads stimuli than to Static Heads stimuli and included the area that was functionally defined as the FFA in the fMRI localiser scan. In contrast the Moving Scrambles condition only elicited source localisations in posterior occipital regions.

In general the probability of significant activation was greater in the upper frequency range than in the lower range and therefore to show the maximally responsive regions within this upper band the *p*-value was set to .001 (critical *t*-values at $p = .001$ for the comparisons shown in Fig. 6B are $t = -7.74$ for Static Heads, $t = -6.94$ for Turning Heads and $t = -7.50$ for Moving Scrambles). Analyses revealed that the most salient activity, in all conditions, was apparent in decreases from baseline along the STS and surrounding gyri (Table 4, Fig. 6B). This appeared close to the right posterior STS in all conditions. The Turning Heads condition elicited a more powerful activation, which extended along the length of the right STS and peaked in the anterior region, in contrast to either of the other two conditions. A comparable STS activation was not found in the lower frequency range.

At the next stage of analyses, MEG responses to head turns with differing social interpretations were studied. No differential response was found to Mutual and Averted Head Turn conditions in either of the two frequency ranges previously stipulated. In the upper frequency range beamforming sources were identified along the extent of the STS to both the Mutual and Averted Head Turns. These showed a very similar spatial profile when compared with the responses elicited to the Turning Heads condition, again demonstrating the importance of the right anterior STS response during the perception of moving faces displaying social attention cues (in each condition, the peak MNI coordinate and statistical significance within the aSTS were as follows—Mutual Head Turns: MNI = 40, −6, −46, $t = -10.06$, $p < .001$; Averted Head Turns: MNI = 50, 0, −42, $t = -12.46$, $p < .001$).

3.3. *Experiment 2—discussion*

This study of MEG source activity to turning heads signalling a change in social attention revealed a bilateral response within the STS and surrounding gyri within an upper frequency range (30–80 Hz) during the time period involving movement in the dynamic conditions (240–480 ms). The posterior regions of the STS showed an equivalent change in oscillatory power to Turning Heads, Static Heads and Moving Scrambles. The source localisation of the power changes to Turning Heads stimuli, during the critical dynamic shift period, spread along the length of the right STS and peaked in the anterior region. There were no corresponding power change within the STS in the lower frequency range (4–30 Hz).

Oscillatory power changes in the lower frequency range from 240 to 480 ms localised to ventral visual areas in response to both Turning Heads and Static Heads conditions. The neural responses in these areas were more powerful and spatially extensive to the presentation of Turning Heads stimuli. Equivalent source localisations were not seen in the upper frequency band. Extrapolating from the fMRI functional localiser, this power change was shown to encompass the functionally defined face-responsive region of the fusiform gyrus. This result, again, demonstrated the involvement of the FFA in the basic perceptual analysis of a face (Haxby et al., 2000). This involvement appears heightened when increased

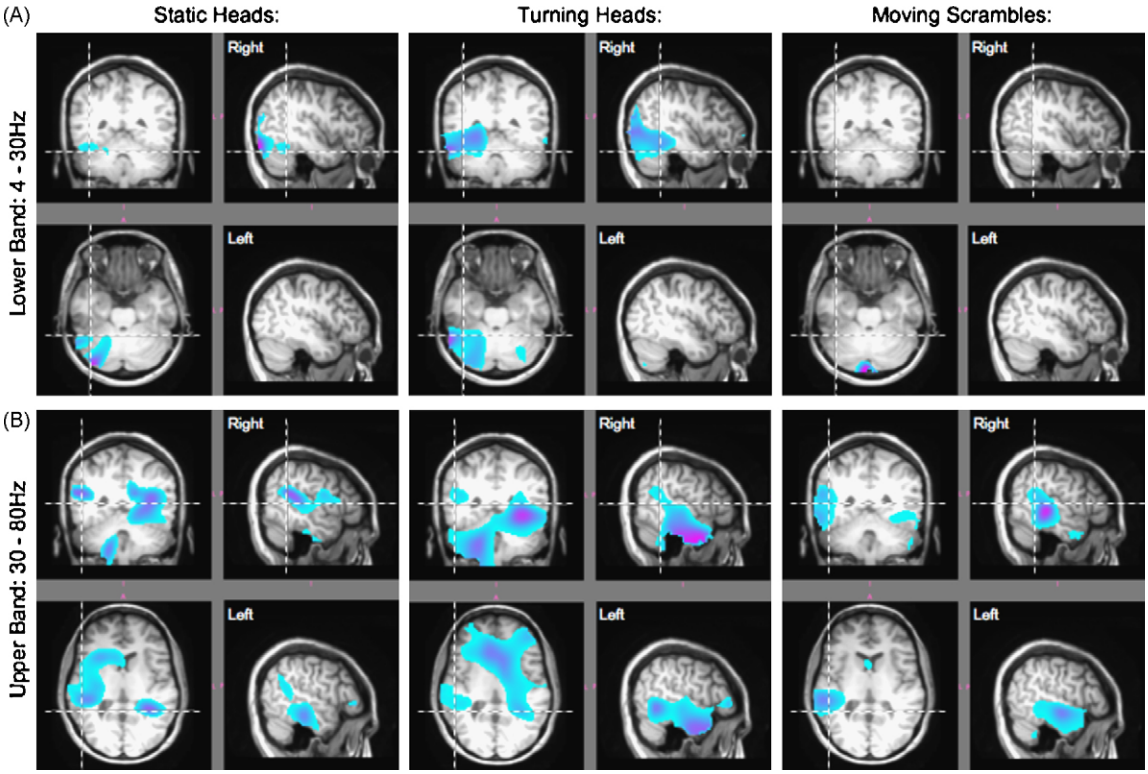

Fig. 6. Group MEG source localisations identified between 240 and 480 ms (corresponding to the period of movement for Turing Heads and Moving Scrambles) for each experimental condition for different frequency bands. (A) Lower band, 4–30 Hz. Cross hairs focused on right fusiform gyrus. *Note* the decreases in power within the core face-selective regions of the ventral visual stream to both Turning Heads and Static Heads. This response to Turning Heads encompasses the fMRI-defined FFA. (B) Upper band, 30–80 Hz. Cross hairs focused on right STS. Note that decreases in power occur in the right STS in response to all conditions. The response to Turning Heads, exclusively, extends along the length of the sulcus and peaks in the anterior region.

facial structural information is available across the changing face views of the dynamic stimuli (Schultz & Pilz, 2009).

Interestingly, spatially localised power changes in both lower and upper frequency bands represented decreases in oscillatory power compared to the baseline period. In contrast to this result, previous studies of coherent object perception have demonstrated increases in power above 30 Hz with EEG (Rodriguez, 1999; Tallon-Baudry & Bertrand, 1999) and decreases in power below 30 Hz with EEG and MEG (Lachaux et al., 2005; Maratos et al., 2007). Although well-documented, the functional significance and cortical origin of neural oscillations within certain frequency bands remains to be precisely determined. Decreases in oscillatory power are assumed to represent desynchronization of the underlying neural network (Pfurtscheller & Lopes da Silva, 1999). Based on information theory (Shannon, 1948, for discussion see; Yamagishi, Goda, Callan, Anderson, & Kawato, 2005), neural desynchrony may reflect an 'active' brain state in which neurons are operating independently to maximise the operational capacity of a brain region. The oscillatory power decreases described here, may therefore represent a mechanism for increased information processing occurring in both ventral and dorsal visual pathways during passive viewing of visual stimuli (see also, Kinsey et al., 2009).

The selective response of the right anterior STS to faces displaying dynamic social attentional shifts corresponds with previous neurophysiological studies emphasizing the involvement of the macaque anterior STS in the encoding of eye, head and body position signaling the direction of social attention (De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Perrett et al., 1985, 1992). Groups of these cells were found to be preferentially responsive to a particular looking direction, particularly if all directional cues were congruent (Perrett et al., 1992). Recently, this observation has been brought into the human domain with an fMRI-adaptation study. Calder et al. (2007) found separable coding of rightward and leftward gaze directions in the right anterior STS and suggested that this activation may represent the perceptual structure of the gaze, distinctly from the intention conveyed by the attentional direction of gaze. Akin to this, the neural activity localising to the right anterior STS in the current MEG study may represent the physical properties of the dynamic head-eye shifts.

3.4. General discussion

Both the fMRI and MEG analyses identified neural responses in the STS which showed greater activity to Turning Heads than to Static Heads and Moving Scrambles. These studies highlight the important contribution of the STS in the representation of rigid facial action patterns which display changes in the direction of social attention. Furthermore, the right fusiform gyrus was active to both Static and Turning Heads, but showed a slight increase in response to Turning Heads stimuli. These activations most likely represent the involvement of the right fusiform gyrus in the basic perceptual analysis of a face.

Haxby et al. (2000) proposed a neural circuitry of face perception with a dissociation of function between the posterior STS and face-responsive fusiform region (the FFA). They provided evidence that the posterior STS is involved in the visual analysis of facial features which show a propensity to move, while the FFA encodes invariant facial aspects (Hoffman & Haxby, 2000). Our fMRI results demonstrate the applicability of this model to dynamic, rigid social attention situations. As hypothesised, the superior 'face' areas were found to be preferentially engaged by the perception of rigidly moving faces displaying shifts in social attention more than by the perception of non-social directional motion or the perception of static faces conveying stationary gaze direction information. This posterior STS activity may have been further augmented by an interpretation of the social intention underlying the head turn (Gobbini & Haxby, 2007; Hoffman & Haxby, 2000; Pelphrey et al., 2003, 2004). The FFA activation was considerably greater when contrasting Turning Heads with Moving Scrambles than when contrasting Turning Heads with Static Heads, indicating the involvement of this region in the perceptual analysis of both static and dynamic faces. The residual activation of a small region of the FFA to Turning Heads above Static Heads most likely represents a continual updating of facial structural information available across the changing face views of the rigid head turn (O'Toole et al., 2002; Schultz & Pilz, 2009). These results were corroborated by an fROI analysis which examined these main experimental effects in functionally defined face-responsive regions.

These spatial observations were substantially complemented by the MEG analyses. MEG is a direct measure of neural activity and therefore has excellent temporal resolution. This can be exploited to investigate either the time course or frequency content of neural responses. Here, MEG beamforming analyses were used to examine the frequencies of neural oscillation contributing to source activations. In the current study MEG beamforming identified a strong decrease in power along the length of the right STS in an upper frequency range during the critical motion period of a dynamic social attention shift. This oscillatory activity peaked in the right anterior region of the STS. In contrast, no corresponding STS response was seen in the lower frequency range during the same time-period. Instead decreases in power in these lower frequencies were observed in ventral visual regions, specifically in the functionally defined FFA in response to the Turning Heads stimuli. To the author's knowledge, this is the first report of source localisation of neural oscillations in lower and upper frequency ranges to distinct cortical regions described in a neural model of face perception (Haxby et al., 2000).

While the MEG analyses localised a strong right anterior STS response to Turning Heads stimuli, the fMRI result emphasized increased responding in the posterior STS. Altering the experimental design in accordance with each imaging technique may have influenced the anatomical distinction in the STS loci of activation. Within the block design of the fMRI experiment, the participant is aware of the social attentional signal displayed by all stimuli within that block after the first stimulus presentation. In comparison, within the randomised event-related MEG design, participants cannot anticipate the social attention signal conveyed by the upcoming stimulus until presentation, furthermore they cannot differentiate a dynamic social attention stimulus from a static until the point of motion. These differences may have created an emphasis on the social attentional component conveyed by a block of stimuli in the fMRI experiment, in contrast to an increased focus on the physical structure of each rigid head-eye shift in the MEG experiment. The anterior STS has recently been proposed to encode the perceptual structure of gaze (Calder et al., 2007), while the posterior STS is proposed to extract intentional information from changeable aspects of the face (Conty et al., 2007; Engell & Haxby, 2007; Gobbini & Haxby, 2007; Hoffman & Haxby, 2000; Pelphrey et al., 2004, 2003). Therefore, the different loci of STS activation found in the current fMRI and MEG experiments may be related to differences in the aspect of the rigid head-eye shift emphasised by each experimental design and therefore could reflect a potential segregation in function between the anterior and posterior STS. Accessing this distinction in social attention processing may be aided by an examination of gaze shifts with varying social or attentional saliency.

It may also be possible that the discrepancy in spatial emphases of the fMRI and MEG results represents underlying differences in the brain physiology measured by each neuroimaging technique. The magnetic fields detected outside the head in MEG are generated by the net current from thousands of post-synaptic potentials developing across pyramidal neurons in similarly oriented configuration (for more detail see; Singh, 2006). As such the neural activity estimated by the beamformer is thought to tap electrophysiological measures of local field potential (LFP), a weighted sum of the synchronized dentritic synaptic input into a neural volume, as opposed to the 'spike' data, assumed to represent the output of an area. The haemodynamic response, as indexed by fMRI, has been found to be better correlated with LFPs than with spiking activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001), implying that both fMRI and MEG are, to some extent, compatible in reflecting the input signals into a neural population. Therefore, the majority of the time it would be expected that fMRI and MEG identify equivalent regions of neural activation. However, in certain situations a small number of neurons may fire synchronously without generating significant metabolic demand. This would result in an MEG signal with no comparable fMRI response and has been previously reported during early stages of face perception (Furey et al., 2006). As regards the current results, it seems possible that the strong right anterior STS response measured by MEG may not have been associated with a significant increase in haemodynamic demand therefore it was not apparent in the fMRI results. This implies that the anatomical distinction in the STS loci of activation found between fMRI and MEG results may partially be accountable to differences in the brain physiology measured by each neuroimaging technique, rather than to the cognitive processes engaged by the slightly differing experimental designs (block vs event-related used for fMRI and MEG.

The current fMRI and MEG results could be explained in two main alternative ways. Firstly, the salience of the face was likely to increase during the motion period of the Turning Heads condition. Increased attention to the dynamic facial stimuli may have heightened the neural response in the STS and the fusiform gyrus, in keeping with previous observations of attentional modulation of face responses (Hoffman & Haxby, 2000; Furey, 2006; Wojciulik, Kanwisher, & Driver, 1998). Nevertheless, the behavioural reaction time measures indicated that no condition resulted in increased attentional capture, rendering the above speculation unlikely. Secondly, the dynamic head-turn stimuli comprised eight different views of the face as the head turned from the start to destination orientations. In contrast, the Static Heads stimuli comprised only one view of the face for the entire duration of presentation. Potentially, a population of neurons responsive to both these dynamic and static social attention stimuli may have adapted to the prolonged presentation of one face view in the Static Heads condition while remaining relatively responsive to the eight face views shown in the Turning Heads condition (see also; Fox, Iaria, & Barton, 2009; Schultz & Pilz, 2009). Neural adaptation is the decreased neural response that follows repeated presentation of identical images (Grill-Spector & Malach, 2001). This implies that the increased responses to Turning Heads stimuli over and above Static Heads stimuli may merely be a consequence of less adaptation to the Turning Heads stimuli than to the Static Heads stimuli. To rule-out this alternative explanation it would be necessary to create a control condition which included the same number of images as the Turning Heads stimuli but did not appear to convey face motion. However, the obvious ploy of scrambling the images in the Turning Heads stimuli would create a video in which the head appears to turn jumpily and unnaturally between the start and destination orientations of the original video. Recent studies examining responses to dynamic faces (Fox et al., 2009; Schultz & Pilz, 2009) have highlighted this issue and we echo their suggestion that this hypothesis requires further investigation in an independent study.

In both the fMRI and MEG experiments it was anticipated that there would be differences in STS responding to mutual and averted social attentional shifts, yet this was not observed in either. Instead, the fMRI fROI analysis identified differential responding in the FFA and OFA to Mutual and Averted Head Turns. As discussed above, this most likely relates to the increased structural information available from a forward as compared to a deviated face (Pageler et al., 2003) or perhaps a deeper encoding of a more socially salient face signalling an engagement of direct gaze (George et al., 2001). Although the stimuli were designed to maximise the potential STS response to social attention information by using a congruent head-eye turn, there was no explicit social context of the motion nor were there task instructions that encouraged an analysis of the socially meaningful nature of these dynamic shifts. Gaze is an exceptionally flexible social signal which is highly dependent on context, for example a shared look with a loved one may signal intimacy and warmth, whereas with a foe is more likely to warn of threat, alternatively a lack of eye-contact might suggest disinterest, rejection or avoidance or may just indicate that something eye-catching is in the surroundings (Emery, 2000). Given this ambiguity of the meaning, creating a social context for the mutual and averted shifts may be necessary to elicit a reliable difference in the STS to the intentionality of the stimulus.

fMRI-informed beamforming combines the advantages of fMRI, as a neuroimaging technique which offers high spatial resolution and has been widely employed to measure brain processes underlying psychological phenomena (for a discussion see Henson, 2005, but also, Coltheart, 2006), with MEG beamforming which offers exciting insights into the multidimensional structure of the neural signal but remains relatively new, particularly within the cognitive domain (see earlier discussion). This method affords the opportunity to represent when, where and in what frequency range neural activity occurs, providing a more thorough description of the neural basis of cognitive processes. In relation to the current findings, the functional significance of neural oscillations within certain frequency bands requires further delineation. It would be interesting to use fMRI-informed beamforming to examine whether other aspects of face perception, e.g. facial recognition, speech perception or emotion recognition, are associated with decreases in power in upper frequency ranges within dorsal face-responsive regions and in lower frequency ranges within ventral regions. By altering the cognitive load of such tasks one might be able to determine whether decreases in power are related to increased information processing (see also, Kinsey et al., 2009).

To conclude, as hypothesised, the fMRI and MEG analyses demonstrated an increased response along the STS to turning heads compared to the static faces or scrambled movement conditions. As predicted, both analyses also showed an involvement of the face-responsive fusiform gyrus in the perception of static and dynamic face stimuli and revealed a slight increase in response to the dynamic stimuli. These results are compatible with an influential neural model of face perception (Haxby et al., 2000), and further establish its applicability to the perception of rigidly moving faces displaying changes in social attention direction. In addition to this, MEG beamforming found that, during the time-period encompassing the rigid head-eye shift of the Turning Heads stimuli (240–480 ms), the ventral face response involved a change in oscillatory power in a lower frequency band (4–30 Hz), while the STS response involved a change in oscillatory activity within the upper frequency band (30–80 Hz) which was most prominent in the right hemisphere in anterior areas. This experiment, employing two complementary neuroimaging techniques, clarified the important contribution of the STS during the encoding of rigid facial action patterns of social attention, emphasising the role of anterior sulcal regions alongside the previously observed posterior areas and further encouraging an investigation of a potential segregation of function along the STS.

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