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Brain activity for peripheral biological motion in the posterior superior temporal gyrus and the fusiform gyrus: Dependence on visual hemifield and view orientation

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ABSTRACT

Biological motion, the movement of the human body presented by a small number of point lights, activates among other regions lining the posterior superior temporal sulcus (pSTS) and gyrus (pSTG) and of the fusiform gyrus. In previous studies with foveal stimuli the activity in the pSTS/pSTG was often confined to the right hemisphere and bilateral in fusiform gyrus. We presented biological motion stimuli in peripheral vision and measured the BOLD responses with functional MRI to test whether the right dominance in pSTS/pSTG also occurred with peripheral stimuli. We found activation exclusively in the right pSTG for both visual hemifields. In the fusiform gyrus activation was found in both hemispheres and for peripheral stimuli strongest for contralateral stimulation. However, in both fusiform gyri leftward-facing stimuli activated different subfields than rightward-facing stimuli, indicating a clustering of the selectivity for the orientation of the human body form. No such clustering was observed in the pSTG. The results indicate for the fusiform gyrus an organization with respect to the view orientation of the stimulus.

Introduction

The human visual system is equipped with mechanisms sensitive to activities performed by other individuals. For example, humans can easily recognize actions, such as walking, from moving point lights attached to the major joints of an otherwise invisible body (Johansson, 1973). The recognition of such point-light walkers is known as biological motion perception. Many brain imaging studies investigated the neuronal networks underlying biological motion perception. Among others, they identified regions in the posterior bank of the human superior temporal sulcus (pSTS) (Beauchamp et al., 2003; Bonda et al., 1996; Grèzes et al., 2001; Grossman and Blake, 2001, 2002, 2004; Grossman et al., 2005; Michels et al., 2005; Pelphrey et al., 2003; Peuskens et al., 2005; Puce et al., 1998; Santi et al., 2003; Saygin et al., 2004; Thompson et al., 2005) and gyrus (pSTG) (Grèzes et al., 1998; Howard et al., 1996; Santi et al., 2003; Servos et al., 2002; Vaina et al., 2001) and the fusiform gyrus (Beauchamp et al., 2003; Bonda et al., 1996; Grossman and Blake, 2002, 2004; Michels et al., 2005; Peelen and Downing, 2005; Pelphrey et al., 2005; Ptito et al., 2003; Santi et al., 2003; Vaina et al., 2001). Most of these studies reported stronger activation in the right pSTS/pSTG than in the left pSTS/pSTG (Beauchamp et al., 2003; Bonda et al., 1996; Grèzes et al., 1998, 2001; Grossman and Blake, 2001; Grossman et al., 2000, 2005; Pelphrey et al., 2003; Peuskens et al., 2005; Puce et al., 1998; Santi et al., 2003; Wheaton et al., 2004). A possible explanation for this asymmetric activation pattern is a functional lateralization. However, previous imaging studies have used only parafoveal stimuli. Therefore, it is unknown how well the right hemisphere dominance holds up for peripheral stimuli.

The perception of biological motion differs somewhat between foveal and peripheral viewing. Detection of biological motion in random dot noise is more difficult in the periphery than in the parafovea (Ikeda et al., 2005), presumably because of differences in visual grouping processes that are required to join the individual light points into a coherent body structure. Indeed, peripheral discrimination of point-light walkers is good if stimuli are not embedded in noise (Thompson et al., 2007). We have recently observed an asymmetry of the recognition ability of biological motion in the visual periphery in which a walker facing away from fixation is better recognized than a walker facing towards fixation (de Lussanet et al., 2008). This behavioral observation could be traced back to asymmetrical BOLD activation by the walker stimulus in areas of the mirror-neuron system (which also responds to biological motion; Santi et al., 2003; Tai et al., 2004).

Here we use the BOLD activations in posterior temporal cortex to investigate the organization of pSTS/pSTG for peripheral biological motion stimulation. The processing of central and peripheral visual

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stimuli is organized retinotopically in lower and mid-level visual areas (Engel et al., 1997; Huk et al., 2002; Sereno et al., 1995) and the strongest activations occur usually in the hemisphere contralateral to the stimulus. Higher visual areas, such as pSTS/pSTG, are thought to lack such retinotopy. In monkeys, cells in STPa (presumably homologous to human pSTS) possess large receptive fields that extend to the ipsilateral visual field without any retinotopic organization (Bruce et al., 1981). Cells in STPa respond to peripherally presented biological motion (Oram and Perrett, 1994). Electrophysiological studies in STPa furthermore showed that biological motion sensitive cells often show a preference for a particular orientation (i.e. facing direction) of the walker stimulus, or for a combination of orientation and motion direction of the walker (e.g. facing right and walking forward) (Jellema et al., 2004; Oram and Perrett, 1994, 1996). Other neurons in STPa respond to static views of bodies or faces (Perrett et al., 1991, 1994). Since biological motion perception may be achieved by the analysis of templates (Lange and Lappe, 2006; Lange et al., 2006) or snapshots (Giese, 2004) of human body configuration it is interesting to investigate any functional specialization within pSTS/pSTG for different orientations of the walker. In the monkey, cells recorded during presentation of walking stimuli did not seem to cluster by their function. Cells with different sensitivities (form, motion, and location) were found within a range of <1 mm (Jellema et al., 2004). However, the STS region contains a functional organization for objects of different visual categories (Logothetis et al., 1999; Pinsk et al., 2005; Tsao et al., 2003). For instance, Pinsk et al. (2005) reported distinct face and body-selective regions in the posterior and anterior STS.

In contrast to STPa, cells in the inferotemporal cortex (ITC) of the monkey, a possible homologue of the human fusiform gyrus, are anatomically clustered by their function for stimuli of the same object category (Tanaka, 1996; Wang et al., 1998). Wang et al. (1998) recorded responses of ITC cells to different facing directions of profile and front views of faces. The critical features for the activation of single cells were first determined in unit recordings with electrodes. In subsequent optical imaging, Wang et al. (1998) looked for the representation of the critical features and showed that the critical features activated different patchy regions, covering the site of the electrode penetration at which the critical feature had been determined. Because signals in optical imaging reflect average neuronal activities in the examined regions, the optical imaging result indicates a regional clustering of cells in the ITC by their feature selectivity. Some functional clustering is also seen in human fusiform gyrus. For instance, pictures of entire human bodies activate a different region of the fusiform gyrus than images of faces (Peelen and Downing, 2005; Peelen et al., 2006). With respect to template- or snapshot-based models of biological motion perception it is interesting to study responses to body actions with different facing directions in the fusiform gyrus, since the fusiform gyrus may provide shape information about body orientation for the analysis of body motion (Lange and Lappe, 2006).

In the present study we ask whether there are functional subregions in the fusiform gyrus that are specific for the facing direction of biological motion. Furthermore, we test earlier findings that the right STS is activated more strongly than the left STS with peripheral biological motion. Third, we investigate the differences in the activation in the fusiform gyrus for ipsilateral and contralateral peripheral stimulation.

Material and methods

Subjects

Twelve right-handed, neurological healthy males (mean age 29.4±5 years) participated in the study. Two of them wore non-magnetic goggles to correct for short-sightedness. The study was approved by the Ethics Committee of the Heinrich-Heine-University Düsseldorf and all subjects gave written informed consent. Apart from the three participating authors (LM, MdL, and RK), they were not informed about the purpose of the study. Three of the participants were unfamiliar with point-light biological motion.

One participant broke-off the experiment due to a claustrophobic reaction. One of the participants had to be excluded due to technical problems with stimulus presentation, and one had to be excluded because his data did not show significant activation patterns in the STS and fusiform gyrus. Thus, the data of nine participants are presented in this study.

Stimuli and setup

Nine computer-animated point-light stimuli were recorded from nine human walkers (MotionStar Wireless™, Ascension Technology Corp.). These stimuli depicted walking in place either while facing to the left (Fig. 1A) or to the right (Fig. 1B). The stimuli were presented as white dots on a dark background in a frame-by-frame video animation. Four light-points were presented for each stimulus frame. They were located on random positions between the main joints of the arms and legs (Beintema and Lappe, 2002). A single frame was presented for 50 ms. In the subsequent frame, the light-points were presented on different random locations on the arms and legs. Each stimulus started from a randomly selected phase of the step cycle and was displayed for 780 ms, which corresponded to one step.

The stimulus induces a clear percept of a walking human (Beintema and Lappe, 2002) allowing the discrimination of facing direction, walking direction and body coherence (Beintema et al. 2006) but differs from the often-used point-light walker of Johansson in that the light points are not continuously fixed to the joints but rather trace the walker's limbs over time. Three reasons prompted us to use this stimulus over the traditional Johansson walker. First, previous investigations had shown that this stimulus is more effective in driving FG activity than Johansson-type biological motion (Michels et al. 2005), presumably since it encourages the use of form information. Second, the stimulus easily allows the adjustment of the difficulty of the detection task by varying the number of points that are shown (Beintema et al. 2006). Since we wanted subjects to stay attentive over the course of the experiment we wanted to use a stimulus that requires some effort to see. With four points per frame, subjects were able to discriminate the stimulus from a scrambled control well above chance level but below a mean performance of 90%. With the classical point-light walker, and for a stimulus with 8 points per frame for that matter, performance was nearly perfect such that the task became very easy which may result in inattentiveness over such a long experimental session. Third, we decided to limit the experiment to one stimulus type to keep the total duration of each session within a reasonable time limit (1 h), and thus, to prevent tiredness of the subjects.

In one third of the trials the stimulus was a scrambled control that contained the same low-level visual cues but did not depict a human walker. In the scrambled stimuli the pairs of joints of the walkers were randomly shuffled in space, thereby destroying the spatial structure of the body but retaining the height, width, symmetry and rhythm of body motion. Each pair of joints (wrists, shoulders, elbows, wrists, ankles, knees) received the same positional offset. The light points were randomly placed, frame-by-frame, along the (invisible) lines connecting the respective scrambled joints positions.

The stimuli were projected on a screen located inside the tube of the scanner and viewed through a tilted mirror (40 cm effective viewing distance). To compensate for the degradation of retinal acuity with eccentricity the peripheral stimuli were scaled in size (Rodieck, 1998). Central walkers were 4° tall (light-point size 0.10°) and peripheral ones were 7.7° tall (light-point size 0.74°). Three red dots were continuously present, and marked the centers of the possible the stimulus locations. These locations were at visual eccentricities −20°

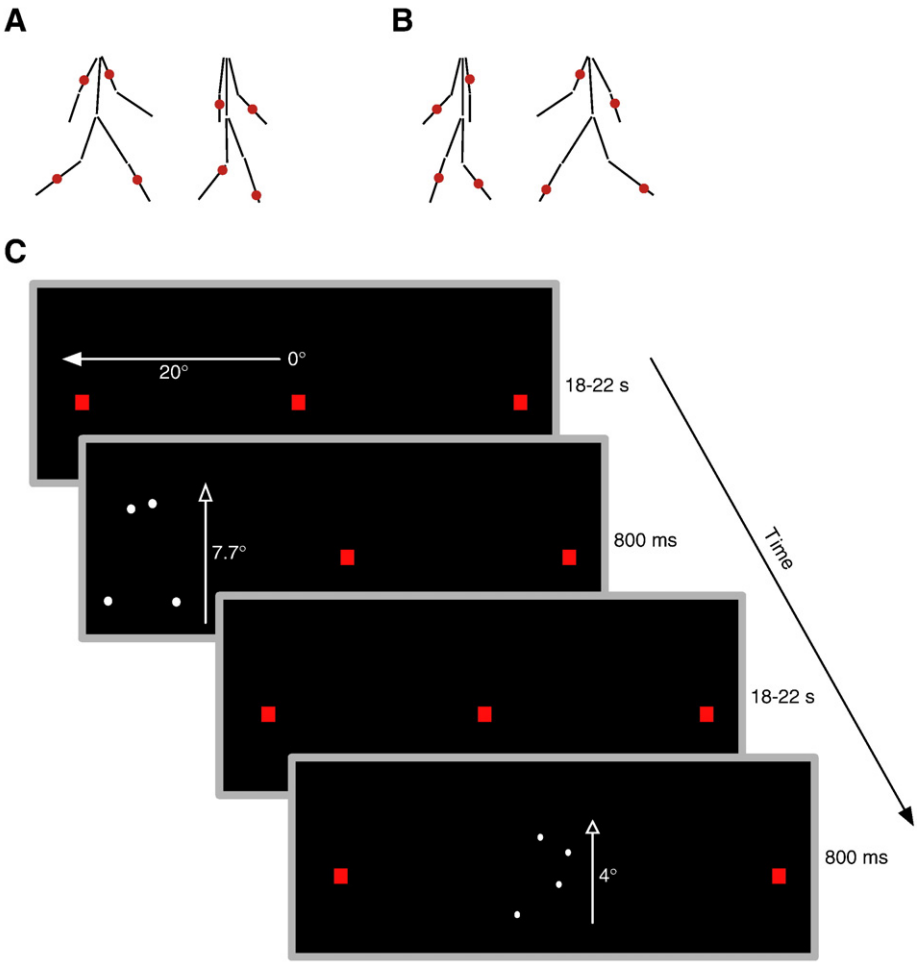

Fig. 1. (A) (B) Two consecutive frames of a point-light walker. The stimulus was either rightward-facing (A) or leftward-facing (B). Stimuli were presented as white dots on a dark background in a frame-by-frame video animation. Four light-points were presented for each stimulus frame. They were located on random positions between the main joints of the arms and legs. Black lines (not visible during stimulus presentation) indicate all possible dot positions. (C) The experimental design during scanning. Biological motion stimuli were presented either in the left visual hemifield (i.e. at −20°), at the center of the screen, or in the right visual hemifield (i.e. at +20°). Each experimental condition was separated by an interstimulus interval period lasting for 18–22 s. The place markers (red dots) were shown at possible stimulus locations and disappeared for the time of stimulus presentation. The peripheral stimuli were scaled to correct for the lower spatial resolution in the visual periphery.

(i.e. to the left), 0°, and +20° (i.e. to the right; Fig. 1C). Participants fixated the central red dot throughout a functional run of the scanning session. Stimuli depicted walkers facing to the left or to the right, or a scrambled control, and were centered at one of the three locations. This resulted in nine active conditions (six biological motion conditions, three scrambled control conditions). Each condition was presented nine times in each functional run. We recorded three functional runs resulting in 27 trials per condition. The order of the 81 trials within a functional run was randomized.

Procedure and experimental design

The fMRI experiment was a slow event-related design. Each subject participated in three consecutive fMRI scans and had a final high-resolution MRI scan. Throughout the scanning, subjects fixated a red dot in the center of the screen (Fig. 1C). After the stimulus was shown at one of the three possible locations, it vanished and subjects indicated the stimulus facing direction by button press with the right index and middle finger. By this the participant was to report the facing direction, even in the cases where he was unsure (e.g. in the case of a scrambled stimulus). Each trial lasted 18 to 22 s (the interstimulus interval was thus 17.2–21.2 s). Before the scanning, the subjects were explained the task. Directly before the experiment, participants performed a practice session outside the scanner tube.

To check fixation control, for two of the participants who had never seen biological motion before, the eye movements were recorded at 500 Hz (Cambridge Research System, Rochester). At the beginning of each session, this system was calibrated on the basis of a fixation dot at a centrally (0°) presented dot. In offline analysis we determined trials in which a saccade occurred during the stimulus presentation.

Data acquisition

The responses of the subjects, the presented conditions, the recorded eye movements, the timing of the stimulus presentation and of the functional scanning slices were all recorded by a PC, using in house-programmed software. The presented condition and the time of stimulus presentation were coded directly in the presented stimulus as small white squares, outside the field seen by the participant. These white squares were recorded using photodiodes connected to the PC. The scanning was carried out on a Siemens Magnetom Vision 1.5 T MRI scanner (Erlangen, Germany) using standard echo-planar imaging (EPI) with a standard radio-frequency head coil for signal transmission and reception. Thirty consecutive oblique axial slices encompassing the whole brain (interslice gap 0.1 mm) were acquired oriented parallel to the plane of the anterior–posterior commissure. To collect the functional MR images, the following EPI sequence-parameters were used: TR (time of repetition): 4.09 s, TE (time of echoplanar): 66 ms, flip

angle 90°, FOV (field of vision): 192 mm, voxel size: 3×3×4.4 mm^3. The T1-weighted anatomical scan was recorded with a resolution of 1×1×1 mm^3.

Image processing and data analysis

Standard pre-processing was performed, including motion correction, slice time scan correction, and linear trend removal, as implemented in the BrainVoyagerQX 1.6 software package (Brain Innovation B.V., Maastricht, the Netherlands). For each subject, the 3-D images were transformed into Talairach space. Anatomical locations of the position of activation were estimated with the reference to the standard stereotaxic atlas (Talairach and Tournoux, 1988) and a brain atlas (Mai et al., 2005). Positive Talairach locations (x, y, z) are defined in mm to the right, anterior, and superior with respect to the anterior commissure. For co-registration, the functional slice time-course images were realigned with the talairached anatomical images by applying an alignment algorithm. Then for each functional run a volume time-course file of the BOLD signal was created. For the whole-brain analysis, we applied a spatial smoothing in 3-D (kernel: 8 mm FWHM) and temporal smoothing (3 cycles per run) after the co-registration step. For the single-subject analysis only temporal smoothing was applied (3 cycles per run). The BOLD signal within the last 6 s before stimulus presentation served as baseline data.

Statistical and region of interest analysis

The general linear model was based on a Gaussian hemodynamic response function. The Talairach transformed contrast images were entered into a group-level random effect analysis (Holmes and Friston, 1998) to generalize the activation to the population level. Only clusters that were over 50 mm^3 in size and $p<0.001$ were reported if not stated otherwise. p-values were corrected for multiple comparisons by applying the false discovery rate (FDR) method (Benjamini and

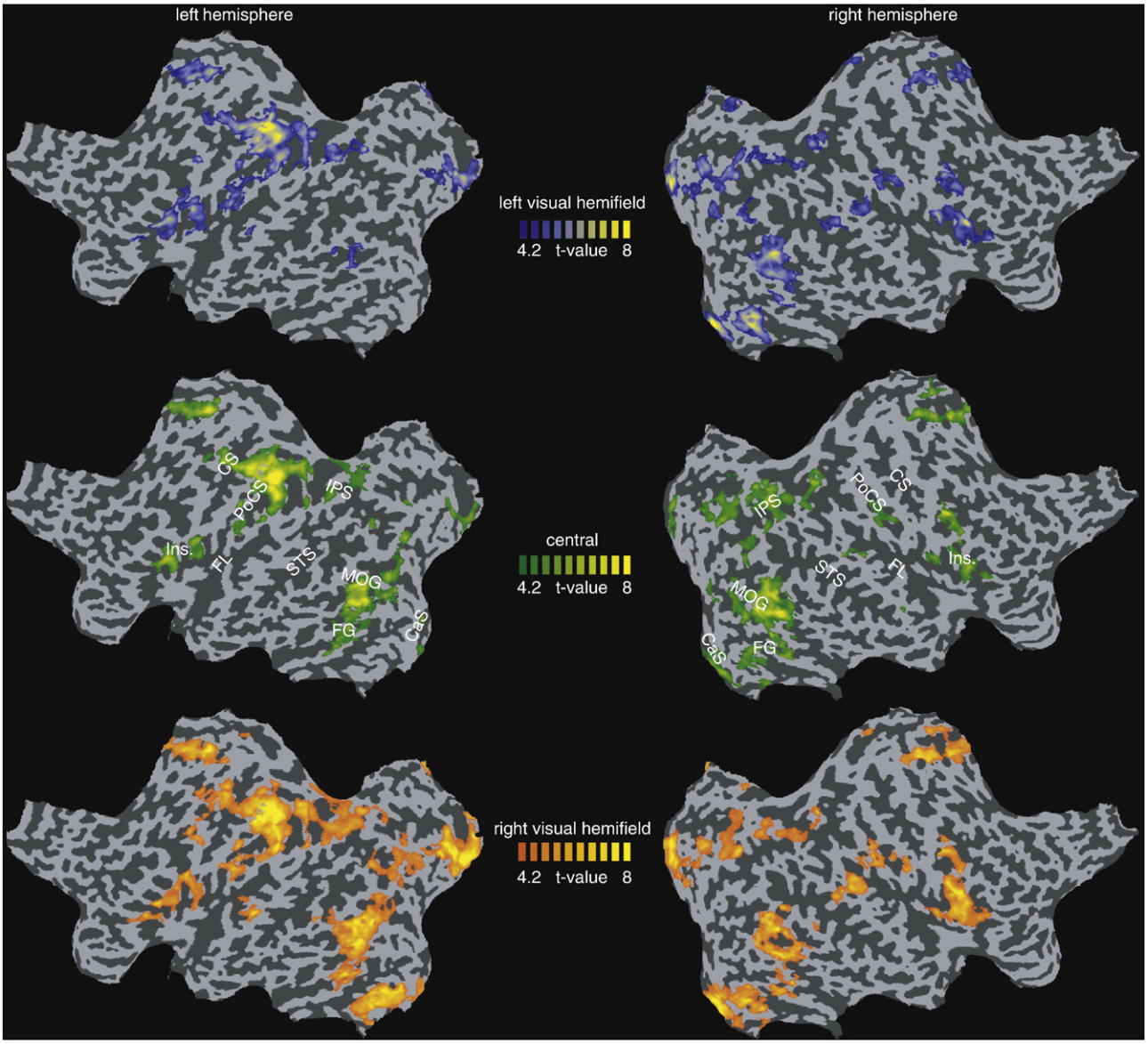

Fig. 2. Group activation map (random effect analysis; $p<0.0001$, corrected for multiple comparisons) for biological motion presented in the left visual hemifield (blue), central (green), and in the right visual hemifield (orange) versus baseline on a flattened Talairach-normalized brain of one subject. The BOLD signal within the last 6 s before stimulus presentation served as baseline data. Dark and light grey regions represent sulci and gyri respectively. CS, central sulcus; CaS, calcarine sulcus; FG, fusiform gyrus; FL, fissura lateralis; Ins., Insula; IPS, intraparietal sulcus; MTG, middle temporal gyrus; STS, superior temporal sulcus; and PoCS, postcentral sulcus. Activation for peripheral biological motion conditions is stronger in the contralateral hemisphere but is also present in the ipsilateral hemisphere for stimuli in the right visual field. In all conditions pSTG activation occurred only in the right hemisphere.

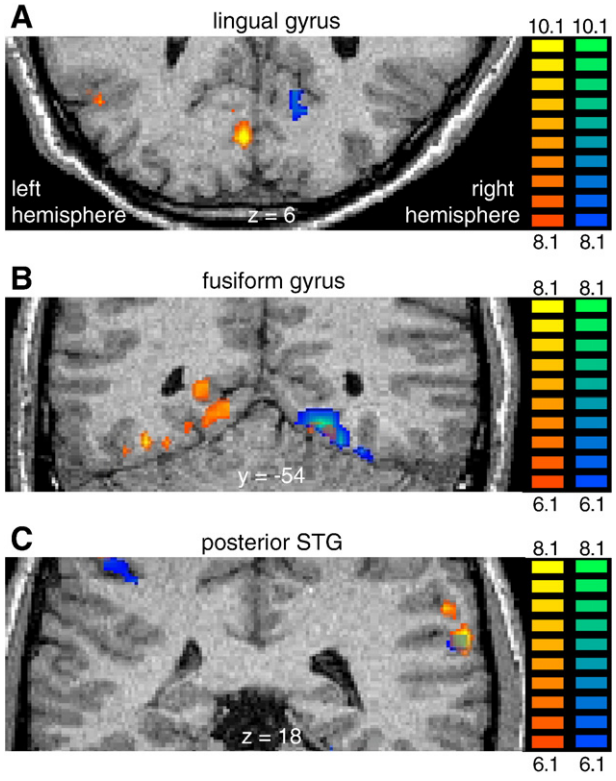

Fig. 3. Group activity (all $p<0.001$) evoked by peripheral biological motion versus the pretrial baseline (the BOLD signal within the last 6 s before stimulus presentation) in three visual regions. Condition-specific t-values for the peripheral biological motion conditions (A–C) are indicated by the different color bars. In blue colors: activation is shown for stimuli presented in the left visual hemifield and in orange colors: activation is shown for stimuli presented in the right visual hemifield.

Hochberg, 1995; Genovese et al., 2002). For the group analysis, we first contrasted the biological motion conditions at −20°, 0°, and at +20° against baseline and against scrambled controls. Next, we compared each of the biological motion conditions to the specific scrambled control conditions, e.g. −20° versus scrambled controls at −20°. Finally, we contrasted the stimuli with different facing directions for each of the biological motion condition versus baseline.

For the single-subject analysis, we performed a peak activation analysis in the pSTS/STG and in fusiform gyrus. Here, we used the same contrasts as for the group analysis (except of the contrast biological motion versus scrambled controls). We used a minimum cluster size of 10 mm^3 and reported peak activation at $p<0.05$ (corrected for multiple comparisons) if not stated otherwise. The size of the two regions of interest was defined by anatomical criteria. For example, the occipito-temporal sulcus was used as the lateral and the collateral sulcus was used as the medial border. For the posterior border, we selected the anterior tip of the parieto-occipital sulcus, and for the anterior border the anterior end of the occipito-temporal sulcus was selected. This procedure was assessed for each of the subjects' brain. For statistical comparisons outside BrainVoyager we used two-tailed paired t-tests.

Results

Behavioral results

The eye movement recordings revealed that for the two participants, who had never seen biological motion before, there were very few saccades in the order of less than 1% of fixations. The analysis of the behavioral responses of all subjects in the facing discrimination task showed a perceptual asymmetry that has been previously reported in a different paper: Walkers facing away from the point of fixation were better recognized than walkers facing towards the point of fixation. This perceptual asymmetry correlated with significant BOLD signal changes in primary somatosensory cortex (BA 2) and inferior frontal gyrus (BA 44), but not in fusiform gyrus or pSTG, the targets of the present analysis (de Lussanet et al., 2008).

FMRI results

Fig. 2 shows maps of BOLD group activation against baseline for stimulation in the left, central, and right visual fields. The figure confirms that visual areas such as V1, V2, and MT were activated, as well as known biological motion-related areas such as pSTG, fusiform gyrus, Insula (Pelphrey et al., 2005; Saygin et al., 2004), premotor cortex (Saygin et al., 2004), and superior parietal lobe (Bonda et al., 1996; Buccino et al., 2001). Peripheral stimulation yielded stronger activation in the contralateral than in the ipsilateral hemisphere in occipital, ventral-temporal and parietal areas. This pattern of activation confirms that the participants generally fixated well, which is in agreement with the eye-movement recordings in two participants.

For all three stimulus locations, significant pSTG activation occurred only in the right hemisphere. Fig. 3 shows the activation by peripheral stimulation in sections through early visual cortex, fusiform gyrus, and pSTG. For early visual areas and fusiform gyrus, stimulation in the left visual field (blue) activated the right hemisphere, and stimulation in the right visual field (yellow) activated the left hemisphere. In pSTG, peripheral stimuli in either visual field activated the same area in the right hemisphere (peak Talairach coordinates: $x=58$, $y=-36$, $z=18$ for stimulation in the left visual field and $x=59$, $y=-37$, $z=18$ for stimulation in the right visual field). The same area was also activated for central stimulation ($x=63$, $y=-37$, $z=16$) and for the contrast of biological motion against scrambled control stimuli (Fig. 4).

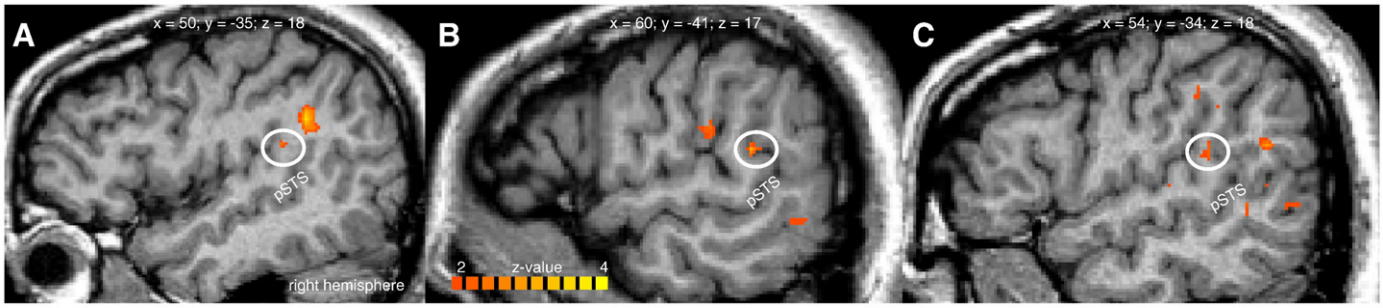

Fig. 4. Statistical activation maps for the contrast biological motion versus scrambled controls ($t>2$, $p<0.05$, random effect analysis). Results are shown for biological motion stimuli presented in the left visual hemifield (A), for centrally presented stimuli (B), and for stimuli presented in the right visual hemifield (C). The Talairach coordinates are reported on the top of each subfigure. For the three biological motion conditions activation was stronger in the right pSTG close to the fissura lateralis.

Analysis of facing direction

We next analyzed BOLD responses to the two facing directions (leftward, rightward) for the peripherally presented stimuli. In the pSTG there was no systematic difference in either the group or the single subject analysis. For the fusiform gyrus, Fig. 5 shows group activity against baseline for leftward-facing (blue) and rightward-facing (yellow) walkers in each hemifield. The left side of Fig. 5 shows activations from stimuli in the right hemifield; the right side shows activations from stimuli in the left hemifield. The coronal sections (Fig. 5A) show distinct activation clusters for the different facing directions. In the left fusiform gyrus, activation for leftward-facing stimuli was more lateral ($x=-36, y=-56, z=-18$) than for rightward-facing stimuli ($x=-30$, $y=-55$, $z=-18$). In the right fusiform gyrus, activation for rightward-facing stimuli was more lateral ($x=29, y=-40, z=-19$) than for leftward-facing stimuli ($x=23$, $y=-44$, $z=-17$). The extent of the activation clusters is shown in Fig. 5B on an inflated brain.

These results were corroborated by the single-subject analysis. Fig. 6 shows activity against baseline for leftward-facing (blue) and rightward-facing (yellow) walkers in each hemifield for the nine subjects. Table 1 lists the locations of the peak activations in the fusiform gyrus for each subject. Paired *t*-tests revealed a significant

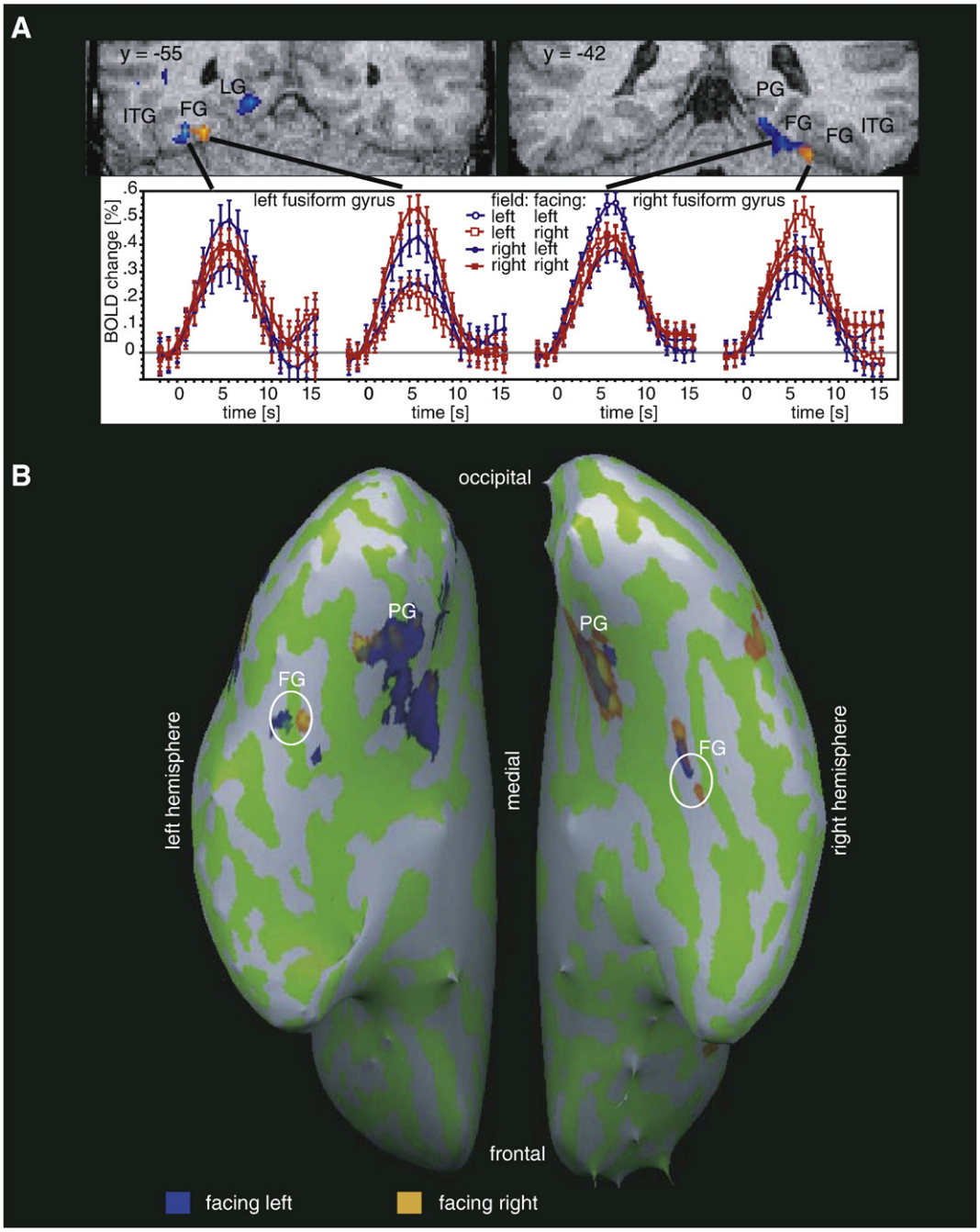

Fig. 5. Group-activity in the fusiform gyrus for contralaterally presented biological motion stimuli with different facing directions. In (A) the activation pattern ($p<0.0001$) is shown on a coronal slice. The peak activations for leftward-facing stimuli are shown in blue and for rightward-facing stimuli in orange. (B) Group-activity for the same contrasts on an inflated brain. The inflated brain was computed from the border of grey and white matter of the T1 scan of one of the subjects. White regions represent sulci, and green regions represent gyri. Activation clusters ($p<0.001$) for stimuli with different facing-directions were anatomically separated in both hemispheres. PG, parahippocampal gyrus; and FG, fusiform gyrus; ITG, inferior temporal gyrus; and LG, lingual gyrus.

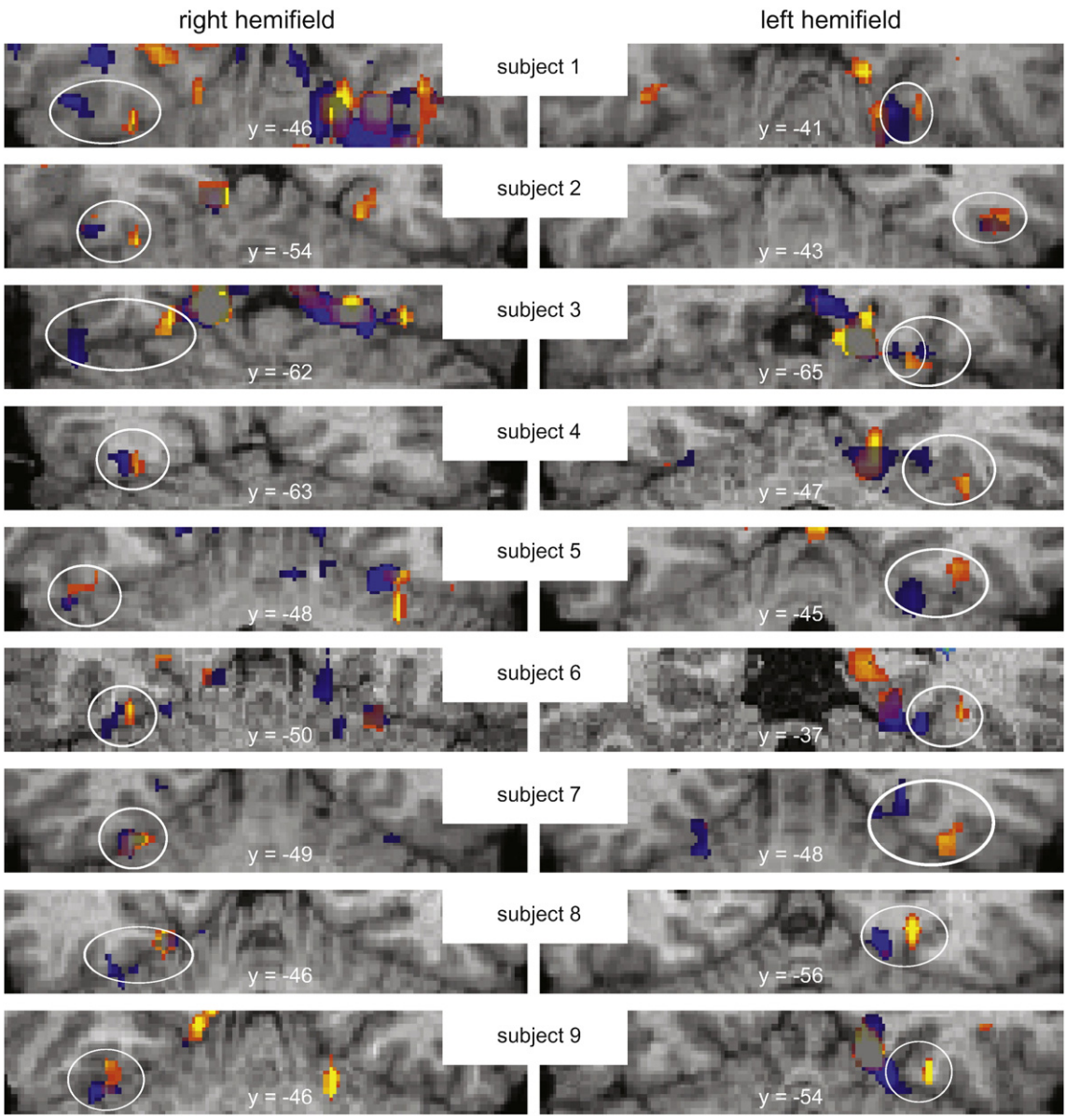

Fig. 6. Single-subject activity in the fusiform gyrus for contralaterally presented biological motion stimuli with different facing directions. For example, the panels in the left column show activity for stimuli presented in the right visual hemifield. The activation peaks (located within the white circles) for leftward-facing stimuli are shown in blue to green and activation peaks for rightward-facing stimuli are shown in orange. *t*-values are reported at $p<0.05$ corrected for multiple comparisons (for exceptions see Table 1).

difference in *x*-Talairach coordinates, confirming that clusters were different for the two facing directions.

Discussion

The present investigation yielded two main results. First, peripheral biological motion stimuli from both visual hemifields activated, beside other areas, the right pSTG. Second, in the fusiform gyrus, but not pSTG, BOLD activation for walkers with different facing directions was anatomically separated in each contralateral hemisphere. The first finding is consistent with many previous studies that showed stronger right-hemispheric pSTS/pSTG activations to parafoveal biological motion stimuli (Beauchamp et al., 2003; Bonda et al., 1996; Grèzes et al., 1998, 2001; Grossman and Blake, 2001; Grossman et al., 2000, 2005; Pelphrey et al., 2003; Peuskens et al., 2005; Puce et al., 1998; Santi et al., 2003; Wheaton et al., 2004). Our study, for the first time, shows that this right hemispheric preference also exists for peripheral stimulation in either visual hemifield.

In the fusiform gyrus, walkers with different facing directions were represented in different sub-fields. This is consistent with a known clustering of selectivity for other objects (Gauthier et al., 2000; Kanwisher et al., 1997; Peelen and Downing, 2005). Our results indicate selectivity for different body configurations in the fusiform gyrus. This selectivity might be useful for biological motion recognition. Lange and Lappe (2006) and Lange et al. (2006) developed a two-stage hierarchical template-matching model of biological motion perception. The first stage performs an analysis of the shape of the human body for the estimation of the posture of the walker. The second stage performs an analysis of the dynamic evolution of the posture over time. The first stage requires template cells (snapshot neurons) that are sensitive to the different postures of the gait cycle of a leftward- or a rightward-facing walker. The activity of these template cells is used to calculate the percent correct level in a left-right discrimination task. Lange and Lappe (2006) suggested that the extrastriate body area (EBA) or the fusiform gyrus were candidate areas to contain such template neurons since the neural activity

Table 1
Talairach coordinates and *t*-values of the activation peaks in the fusiform gyrus for contralaterally presented biological motion stimuli with facing directions (left and right)

Right hemisphere								
Facing direction	Left	Right	Left	Right	Left	Right	Left	Right
Talairach coordinates (mm)								
Subject	*x*		*y*		*Z*		*t*-max	*t*-max
1	24	27	−44	−39	−20	−19	6.3	3.2*
2	42	41	−43	−46	−14	−14	4.6	5.3
3	27	30	−62	−65	−15	−17	4.5*	5.5
4	27	36	−49	−45	−16	−20	4.4	5.2
5	27	41	−44	−53	−18	−17	5.3	3.2*
6	29	36	−37	−38	−19	−15	4.3	3.3
7	24	35	−48	−48	−10	−20	5.1	4.7
8	20	26	−55	−55	−13	−11	4.9	5.7
9	20	27	−54	−54	−19	−18	7.4	4.8
Paired *t*-test	$p=.002$		$p=.586$		$p=.589$			
Left hemisphere								
Facing direction	Right	Left	Right	Left	Right	Left	Right	Left
Talairach coordinates (mm)								
Subject	*x*		*y*		*z*		*t*-max	*t*-max
1	−32	−47	−45	−47	−21	−18	3.1	3.5
2	−30	−40	−55	−52	−21	−14	4.6	4.7
3	−25	−44	−66	−65	−15	−20	5.8	4
4	−28	−30	−65	−64	−11	−13	7.2	6.6
5	−41	−45	−44	−49	−20	−22	3.9*	3.5*
6	−32	−38	−52	−50	−20	−24	4.5	3.9
7	−29	−30	−50	−49	−21	−22	5.2	5.1
8	−25	−34	−46	−46	−22	−19	5.4	5.2
9	−35	−38	−46	−46	−23	−21	3.7	5.2
Paired *t*-test	$p=.005$		$p=.891$		$p=.933$			

t-values are reported at a *p*-level of $p<0.05$ corrected for multiple comparisons ($^*p<0.01$ uncorrected). The upper part of the table lists the activation peaks for stimuli in the right visual hemifield. The lower part of the table lists the activation peaks for stimuli in the left hemisphere. In both the left and in the right visual hemifields the difference for the activation peaks was significant but only for the *x*-Talairach coordinate.

predicted from the model was comparable to the physiological responses of EBA and fusiform gyrus to biological motion. Our finding of sub-fields for leftward- and rightward-facing walkers in fusiform gyrus is consistent with this prediction.

Since biological motion is known to activate the EBA (Downing et al., 2001; Michels et al., 2005), we also looked for activity in an anatomically-defined EBA region (Michels et al., 2005). Biological motion indeed activated the EBA in all participants. The peripheral biological motion consistently activated the contralateral EBA. Different activations for the two walking directions appeared in some subjects but the clustering was not consistent across subjects.

In a previous work we have shown that the perception of peripheral biological motion stimuli depends on their orientation: Walkers facing away from the point of fixation are better recognized than walkers facing towards the point of fixation (de Lussanet et al., 2008). For example, in the right visual hemifield, rightward-facing walkers are well recognized whereas leftward-facing walkers are poorly recognized and look like scrambled controls. This leads to the question whether the different sub-fields in fusiform gyrus in fact represent recognized biological motion versus not recognized biological motion rather than left versus right-facing walkers. We believe this is not true for the following reason. In the earlier analysis, a direct contrast between recognized away-facing walkers and not recognized toward facing walkers showed significant activation differences only in primary somatosensory cortex (BA 2) and inferior frontal gyrus (BA 44) (de Lussanet et al., 2008). Activity was not different in the fusiform gyrus. We thus believe that the fusiform gyrus processes both facing directions similarly and that the different perception of the facing directions is due to different contributions from other areas (BA 2, BA 44).

Our results were obtained with the biological motion stimulus of Beintema and Lappe (2002), which places points on different locations on the body over time. Most fMRI studies of biological motion have used a classic Johansson-type stimulus in which the points are placed on the joints. Both stimuli activate the same network of biological motion analysis (Michels et al. 2005) but the stimulus of Beintema and Lappe provides stronger FG activation making it more suitable for our study. While we cannot, without a direct comparison, be sure that the facing selectivity in FG would be also manifested for a Johansson point-light walker, it is important to note that biological motion perception is truly about perceiving the motion of real living beings and that point-light stimuli are merely intended to study particular aspects of that perceptual capacity. As such, we believe that the existence of form templates in FG that are activated by moving body shapes may be seen as a general part of biological motion perception.

Activation in fusiform gyrus occurred only for stimuli from the contralateral hemifield. This result is in line to recent fMRI studies. For example, a predominantly contralateral activation in the fusiform gyrus was also found for objects (Hemond et al., 2007) and body parts (Shmuelof and Zohary, 2005).

We also observed parahippocampal gyrus activation, most prominent for peripherally presented point-light walkers (Fig. 5). Only few fMRI studies to centrally biological motion processing reported activation in this region (Ptito et al., 2003). Rather, several studies pointed out that the parahippocampal gyrus is specifically involved in encoding new perceptual information about the appearance and layout of scenes (e.g. Epstein et al., 1999). In our study, subjects were not aware about the occurrence of the particular point-light walker in the single trials. Therefore, we suggest that activation in this region is more a result of its specificity to the spatial location of an object than as result of the presence of a point-light walker.

Conclusion

In conclusion, we have shown that the fusiform gyrus contains representations of biological motion stimuli with different facing directions. In particular, the location of the activation with the same facing directions activated different parts of the contralateral fusiform gyrus. Our findings indicate that the fusiform gyrus is, additionally to the processing of face and whole body stimuli, specifically engaged in the processing of point-light walker.

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