

Interaction of Visual Hemifield and Body View in Biological Motion Perception

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Abstract

The brain network for the recognition of biological motion includes visual areas and structures of the mirror-neuron system. The latter respond during action execution as well as during action recognition. Since motor and somatosensory areas predominantly represent the contralateral body-side, and visual areas predominantly process stimuli from the contralateral hemifield, we were interested in interactions between visual hemifield and action recognition. In the present study, human participants detected the facing direction of profile views of biological motion stimuli presented in the visual periphery. They recognized a right-facing body view of human motion better in the right visual hemifield than in the left; and a left-facing body view better in the left visual hemifield than in the right. In a subsequent fMRI experiment, performed with a similar task, two cortical areas in the left and right hemispheres significantly correlated with the behavioural facing effect: primary somatosensory cortex (BA 2) and inferior frontal gyrus (BA 44). These areas were activated specifically when point-light stimuli presented in the contralateral visual hemifield displayed the side view of their contralateral body-side. Our results indicate that the hemispheric specialization of one's own body-map extends to the visual representation of the bodies of others.

Keywords: mirror-neuron; somatosensory; lateralization; hemifield; somatotopic

Introduction

With ‘point-light biological motion’ one refers to a particular class of visual stimuli displaying a human action by presenting just a few moving dots attached to the body. Through this kind of stimuli, human motion is easily and vividly perceived (Johansson, 1973). Brain imaging evidence shows that point-light biological motion is processed by a cortical network of areas that, in addition to extrastriate visual cortical areas, includes the right posterior superior temporal sulcus (Vaina et al., 2001; Grossman et al., 2000; Servos et al., 2002), and premotor and parietal areas belonging to the cortical mirror-neuron system (Rizzolatti and Craighero, 2004; Saygin et al., 2004; Michels et al., 2005).

While centrally presented stimuli are easily detected, the recognition of biological motion presented in the peripheral visual field is considered a quite difficult task (Ikeda et al., 2005). However, the processing of peripheral visual stimuli is more lateralised than that of foveal and parafoveal ones, mainly because of the poverty of callosal connections. Therefore, studying systematically the detection of point-light biological stimuli presented in the peripheral hemifields could help to better understand the functional properties of the neuronal mechanisms underlying the perception of biological motion

The present paper starts from the occasional observation we did when a point-light stimulus representing a human walker was observed from the corner of the eye. The walker appeared more vivid when she faced away the point of gaze than when she faced towards it. We hypothesised that this asymmetric appearance of the facing direction was caused by an asymmetric representation of the human body in the brain (de Lussanet et al., 2004). In the present study, we first carried out a series of psychophysical experiments to systematically explore this facing effect. On the basis of the results of these experiments we formulated a hypothesis to explain the underlying neuronal mechanism. Specifically, we propose that there is an interaction between the visual and motor representations if a side view of a human is seen in the visual periphery, because each visual periphery is best represented in the contralateral visual cortex and each body side is best represented in the contralateral motor and somatosensory cortex. This hypothesis was tested by functional magnetic resonance imaging (fMRI) in a paradigm specifically designed for this purpose.

Materials and Methods

The experiments described in this paper were the following. In the first experiment participants were requested to discriminate the direction of facing of point-light stimuli depicting a side view of human walking. The stimuli were presented either foveally or in the periphery. Experiment 2 was a detection task in which observers were requested to report by key press whether the presented stimulus depicted a human figure or not. The stimuli were presented only in the periphery. Experiment 3 and 4 provided various control conditions. Experiment 5 explored other locomotion patterns and body configurations. Experiment 6 was an fMRI experiment performed with the paradigm of Experiment 1.

Participants

Psychophysical experiments (1–5): Twelve, right-handed, participants (24–35 years, 3 females) took part in the first experiment. Six of them had prior experience with psychophysical experiments involving biological motion stimuli. Six of these twelve volunteers also participated in the detection task (experiment 2). Four of the twelve also participated in the other psychophysical experiments (3–5). One of the authors (MdL) participated in all experiments. Apart from him, the participants did not know the objective of the experiments.

fMRI experiment (6): Behaviourally, there were no significant differences between male and female participants in experiment 1 (ANOVA on proportions correct, with factors gender, stimulus location and facing direction). However, the brains of males and females are known show systematic differences in shape (Kovalev et al., 2003) as well as in BOLD responses to the same stimuli and motor tasks (Kastrup et al., 1999). To avoid such gender variability, we chose to collect data from one sex only. We recruited male participants, because these happened to be better available.

Twelve right-handed, male volunteers (20-35 years) participated in the fMRI experiment. Six of them had participated also in experiment 1. These volunteers had no neurological disorders and had normal visual acuity (1 of them wore non-magnetic glasses of -2 dioptr). Participants gave their written informed consent, in accordance with the guidelines of Helsinki.

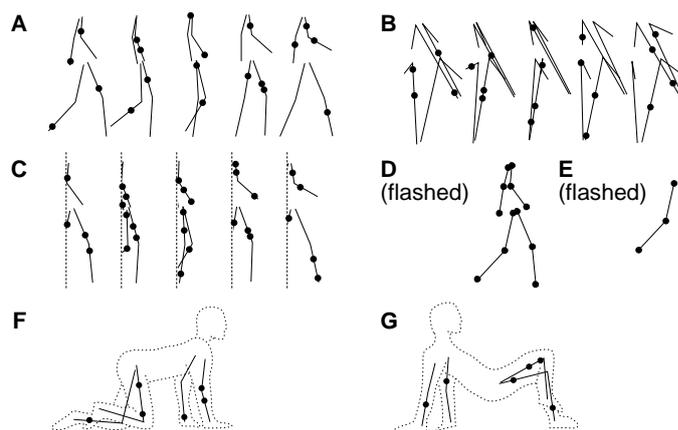


Figure 1: Schematic illustrations of the stimuli, each in rightward facing orientation. The lines connecting the limb segments were not visible in the experiments. (A) An example out of 9 recorded walking cycles. (B) The joints of scrambled walkers received a pseudo-random offset, such that the bounding box remained of the same size, and left and right joints got the same offset. (C) Points in the walker's back half were invisible. The visible front-half was shifted back to be centred at the target position. (D) Example of a walker flashed for 20 ms in a random phase of the walking cycle. Points were located on the joints. (E) A three-point arc flashed for 20 ms. (F, G) The two kinds of recorded crawling movements (examples out of 10 recorded cycles each).

Visual stimuli

Computer-animated point-light stimuli (Fig. 1 A–E) were constructed from kinematic data recorded from 4 females and 5 males (MotionStar WirelessTM, Ascension Technology Corp.) and depicted walking in place. The stimuli consisted of white dots on a dark background. To make the task more difficult to preclude ceiling effects, dots were not presented fixed to joint locations, but were randomly placed, frame-by-frame, along the (invisible) lines connecting the main joints of upper arm, forearm, upper leg and lower leg (Beintema and Lappe, 2002). Thus, the light points did not move and did not reveal the trajectories of the major joints. Therefore, the participants could not rely on local motion cues (such as in Troje and Westhoff, 2006). Moreover, the stimuli thus did not contain motion, and implied motion only after an observer had recognised the presented action.

Unless stated differently, four simultaneous points were presented during each 50 ms frame. A stimulus lasted for 800 ms, which correspond to one step plus 100 ms. The stimuli were presented at -20° , -10° , 0° , $+10^\circ$ or $+20^\circ$ of visual eccentricity in the first experiment, and at -20° and $+20^\circ$ in the other

psychophysical experiments. To compensate for the fact that retinal acuity degrades with eccentricity, walkers presented at 0° were 4° tall (light-point size 0.10°) while eccentric walkers were scaled with factors of 4.5 and 7.7 at 10° and 20° , respectively (Rodieck, 1998). In the subsequent experiments we presented the following stimuli:

Experiment 1 and 1a: Each of the nine walkers was presented twice on each condition. Thus, each location and facing direction was run 18 times for each participant. In experiment 1, the order of trials was randomised (5 locations, 2 facing directions: 180 trials). In experiment 1a, one block of trials only presented to the left visual hemifield (-20°), and another block only presented to the right visual hemifield (20°). The order of the blocks was balanced over participants, and the trial order within each block was randomised (90 trials in each block).

Experiment 2 (detection): In scrambled stimuli (Fig. 1B) the 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 the body motion. Each pair of joints (wrists, elbows, shoulders, ankles, knees and hips) received the same positional offset. As in the normal walkers, the light points were randomly placed, frame-by-frame, along the (invisible) lines connecting the respective scrambled joint positions. In order to be absolutely sure that subjects could not see the facing direction, a scrambled stimulus was derived from a right-facing walker in half the cases; in the other half it was derived from a left-facing walker. Each condition (left or right hemifield, facing left or right, walker or scrambled) was run 72 times for each participant (576 trials, in randomised order).

Experiment 3: Walkers in which the back-half was invisible (Fig. 1C) were derived from walkers with eight simulated light points per frame. Simulated light points were visible only if they were pertaining to the frontal half of the body. The visible part of the stimulus was always centred at the same stimulus location used in Experiment 1, so that a leftward-headed half-walker was shifted to the right with respect to a complete walker, and a rightward one was shifted to the left. Each condition was run 18 times for each participant (72 trials, in randomised order).

Experiment 4: Stimuli were created according to the classical biological motion approach, by positioning dots on the joints (rather than on random places on the limbs) (Fig. 1D). The displayed joints were ankles, knees, hips, wrists, elbows and shoulders. To make this task as difficult as the previous ones, each walker was displayed for 20 ms only. During these 20 ms, 2 frames were shown (frame refresh rate, 100 Hz). The starting phase was chosen randomly. In experiment 4a, the same procedure was used to display the three points of a single leg instead of the full body (Fig. 1E). In both experiments, each condition was run 36 times for each participant (each 288 trials, in randomised order).

Experiment 5: Crawling-in-place movements (Fig. 1F and 1G) were recorded from 4 females and 6 males by using the same method of Experiment 1. Actors used to record the kinematic data were requested to perform crawling on hands and knees (the classical crawling, see Fig. 1F) as well as crawling with stomach-up (spider-like crawling, see Fig. 1G). Point-light stimuli displayed six points simultaneously on random locations of the joint-segments. Cycle periods were 1.2 ± 0.4 s (mean \pm s.d.). Each condition was run 36 times for each participant (two crawling types, two hemifields and two facing directions: 288 trials in randomised order).

Setup, procedure, and analysis

In Experiment 1, stimuli were projected on a large screen positioned 1.90 m from the participant's frontal plane (JVC D-ILA, type DLA-G11E). Further experiments, which only involved the most eccentric conditions ($\pm 20^\circ$), were conducted on a standard 21" monitor at 30 cm viewing distance (Iiyama VisionMaster 505). Participants were requested to fixate a central fixation point (a 0.25° red dot) throughout the whole experiments.

The capability of participants to keep their gaze fixed was assessed during an eye tracking control experiment with the same setup, task, and length of experiment 1 (EyeLink II, SR Research, Canada). Two participants took part in this control. They both maintained their gaze within 1° of the fixation point throughout the experiment (except for eye blinks) and their responses were fully in agreement with the results of experiment 1.

In all Experiments but Experiment 2 participants were asked to indicate, after each stimulus presentation, the walker's facing direction by pressing the left or right arrow key on a keyboard, using their right hand (Mather et al., 1992; Beintema and Lappe, 2002). A new trial started 500 ms after a response had been recorded. In Experiment 2, scrambled stimuli were randomly mixed with non-scrambled ones. Participants were requested to discriminate between scrambled and non-scrambled.

Data analysis. The mean proportion correct scores were plotted. As proportion correct scores are based on average binomial statistics and therefore follow a Bernoulli distribution, they are by definition not suited for standard ANOVA analyses. As a solution, we performed an inverse-cumulative normal transformation on each participant's proportion correct scores. The thus obtained z-scores were used for statistical testing in repeated-measures analyses of variance (rmANOVAs). In order to assess on a post-hoc basis the statistic validity of the facing effect in each visual hemifield separately, we conducted signed paired t-tests.

fMRI experiment (6)

The sixth experiment was planned according to an event-related design. Each volunteer participated in three consecutive fMRI scans, and underwent a final high-resolution MRI scan to co-register the functional data on the individual anatomy (1.5 T Siemens Magnetom). The stimuli were back projected on a screen located 40 cm from the participant's frontal plane. The projection screen was positioned in the scanner tube and was visible through a tilted mirror. Two participants were rejected from the study: one for technical problems during stimuli presentation, the other because of a claustrophobic reaction. Therefore, 10 out of 12 participants were analysed after the scanning session.

Stimuli were walkers (Fig. 1A) and scrambled versions of the same walkers (Fig. 1B). Each walker was presented in the two facing directions and as a scrambled stimulus, at -20° , 0° and $+20^\circ$ (81 trials per 27-min block). The stimulus duration was 0.8 s, with an inter-stimulus interval of 17.2-21.2 s. Stimulus size was approximately the same as in the previous experiments. Trial order was randomised within each scan (first order randomisation). We verified that performance on the task remained stable both within and between scan sessions, and for each participant.

After each presented stimulus, the observer reported the facing direction by button press with the right index and middle finger. We required observers to provide a facing direction answer also in the case of scrambled stimuli, expecting chance performance. The BOLD signal from the button press was always confined to the left cerebral hemisphere, and was therefore subtracted out in the comparison between the walker's facing directions.

The BOLD signal within the last six seconds before stimulus presentation served as baseline data. We used standard echo-planar imaging (TR 4.09 s, TE 66 ms, flip angle 90° , FOV 192, voxel size $3 \times 3 \times 4.4$ mm); with a standard radio frequency head coil for signal transmission and collection. The whole brain

was covered by 30 transverse slices. The T1-weighted anatomical scan was recorded with a resolution of $1 \times 1 \times 1$ mm. The fMRI data were analysed with BrainVoyagerQX 1.7 (Brain Innovation B.V., Maastricht, Netherlands). The motion-corrected data were smoothed in 3-D (kernel: 4 mm FWHM) and high-pass filtered at 3 cycles per session (after linear trend removal). 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.

For the functional data we first verified that the peripherally presented biological motion stimuli (compared to baseline and scrambled ones) activated the same areas that have been published for centrally presented biological motion. We then contrasted, for each visual hemifield, the two oppositely facing stimuli: For the left visual hemifield, this was the contrast *facing left* versus *facing right*, and for the right hemifield *facing right* versus *facing left*. Only clusters larger than 100 anatomical voxels (2.5 functional voxels) and $t > 3.25$ ($p < .01$) are reported. In order to avoid false positive results, we only report clusters of which one of the compared conditions was significantly activated against the baseline at a Bonferroni-corrected level ($p < .05$).

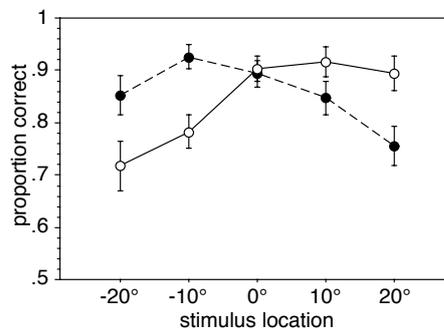


Figure 2: Recognition scores in the first experiment. Stimulus location is given as visual angle with respect to the point of fixation, negative is in the left visual periphery and positive in the right visual periphery. Continuous lines, open symbols: facing right; dashed lines, filled symbols: facing left. Error bars depict standard error of the means (s.e.m.); chance level is at 0.5.

Results

Psychophysical experiments

Experiment 1: The results of the first experiment are displayed in Figure 2. They reveal a strong interaction between visual hemifield and the walker’s facing direction (rmANOVA: $F_{4,44} = 7.4, p = .0001$). The participants discriminated more accurately walkers facing away from the fixation point than walkers facing towards it (post-hoc signed paired t-tests; -20° left hemifield: $t_{11} = 1.8, p = .05$; $+20^\circ$ right hemifield: $t_{11} = -3.2, p = .004$).

One possible criticism to the interpretation of these results in terms of visual processes is that the observed effect might be due to spatial stimulus-response compatibility (Fitts and Deininger, 1954). The spatial stimulus-response compatibility effect (SRC) becomes evident, in terms of reaction times, when the spatial location of a given stimulus is somehow related to the spatial location of the effector chosen to give the response, or to the direction of the response-related movement (e.g. left and right). We consider the SRC explanation quite unlikely for the following reasons: (1) The effect shown by Experiment 1 was related to the participants’ performance and not to reaction time, whereas SRC exerts only a small

influence on performance (Notebaert et al., 2001; Valle-Inclán et al., 2003); (2) in our setup participants were never instructed to respond as fast as possible and, indeed, the median response times did not depend on the walker's facing direction ($F_{1,44} = 0.009, p = .9$); (3) the analysis of reaction times did not show any significant interaction between facing direction and stimulus location ($F_{4,44} = 0.9, p = .4$).

We nevertheless decided to control for the SRC effect by adding a control experiment (Experiment 1a) with the same participants, in which we presented the -20° and $+20^\circ$ conditions in separate blocks (Notebaert et al., 2001). By blocking the location of stimulus presentation (left versus right hemifield), participants could keep their attention directed to a single hemifield, which is known to diminish the SRC (Valle-Inclán et al., 2003). The results of the block experiment (1a) did not show any difference with those of Experiment 1 as demonstrated by the significance of the interaction facing direction versus hemifield (Fig. 3A; rmANOVA: $F_{1,11} = 19.6, p = .001$). The facing effect was again significant in both hemifields ($-20^\circ: t_{11} = 4.3, p = .0006; +20^\circ: t_{11} = -2.8, p = .009$).

Experiment 2: An alternative possibility could be that participants were somehow facilitated in their response by the location of the stimulus in a given hemifield. In other words, that participants were simply more likely to report 'left' when they saw a stimulus in the left hemifield and vice versa. To definitely rule out this possibility we ran an experiment where participants were requested to discriminate between scrambled and normal point-light figures. The task was to press the up-arrow key of a keyboard on the detection of a normal walker and the down-arrow in the case of the scrambled figures. Walkers and scrambled stimuli were presented in random order, with the walkers facing either to the left or to the right. On half the trials the stimulus was scrambled. Although the facing direction was irrelevant to accomplish the task, we found that left-facing walkers were better discriminated from scrambled stimuli when they were presented in the left visual hemifield while right-facing walkers were better discriminated when appearing in the right hemifield (Fig. 3B: rmANOVA on the biological motion trials showed an interaction of location x facing direction $F_{1,5} = 21.9, p = .005$), and this facing effect was significant as a trend in both hemifields ($-20^\circ: t_5 = 1.97, p = .05; +20^\circ: t_5 = -1.8, p = .06$). Hit rates for scrambled were 81% and 83% at -20° and 20° respectively (an rmANOVA on the scrambled trials did not reveal any significant effects: $p > .3$). The result clearly demonstrates the automatic nature of the facing effect, by showing its independence from the type of response given by the participants.

Experiment 3: If we ruled out the SRC effect and other kinds of response-related facilitation, it is still possible to interpret the facing effect in terms of other visual perception-related factors. One possibility is that the participants used the backswing of the lower limb as a cue to discriminate body orientation (Mather et al., 1992; Troje and Westhoff, 2006). In fact, due to the inhomogeneity of retinal acuity, the foot backswing was seen with higher resolution when the walker was facing away from the point of fixation than when facing towards it. To rule out this possibility, we manipulated our stimuli by hiding all the dots behind the body midline (Fig. 1C). Despite this manipulation, the facing effect was not reduced and remained significant (Fig. 3C; rmANOVA on the trials with hidden backside $F_{1,3} = 10.2, p = .04$, which was significant in the right hemifield $t_3 = -3.0, p = .03$ and present as a trend in the left hemifield $t_3 = 1.6, p = 0.1$). In this experiment, half the trials repeated the conditions of experiment 1 for the $\pm 20^\circ$ visual locations, and replicated the facing effect (rmANOVA on the trials with normal biological motion $F_{1,3} = 10.3, p = .04$).

Experiment 4: The facing effect also did not depend on the particular point light walker we used since it was also present for a 'traditional' walker with the light points on the joints (Fig. 3D; rmANOVA, $F_{1,11} = 9.7, p = .01$, significant in the right hemifield $t_3 = -2.4, p = .04$, and present as a trend in the left hemifield $t_3 = 1.8, p = 0.08$). Moreover, the facing effect did not rely on a generic capability to discriminate shape orientation in the periphery as shown by the results of experiment 4a (Fig. 3E), where

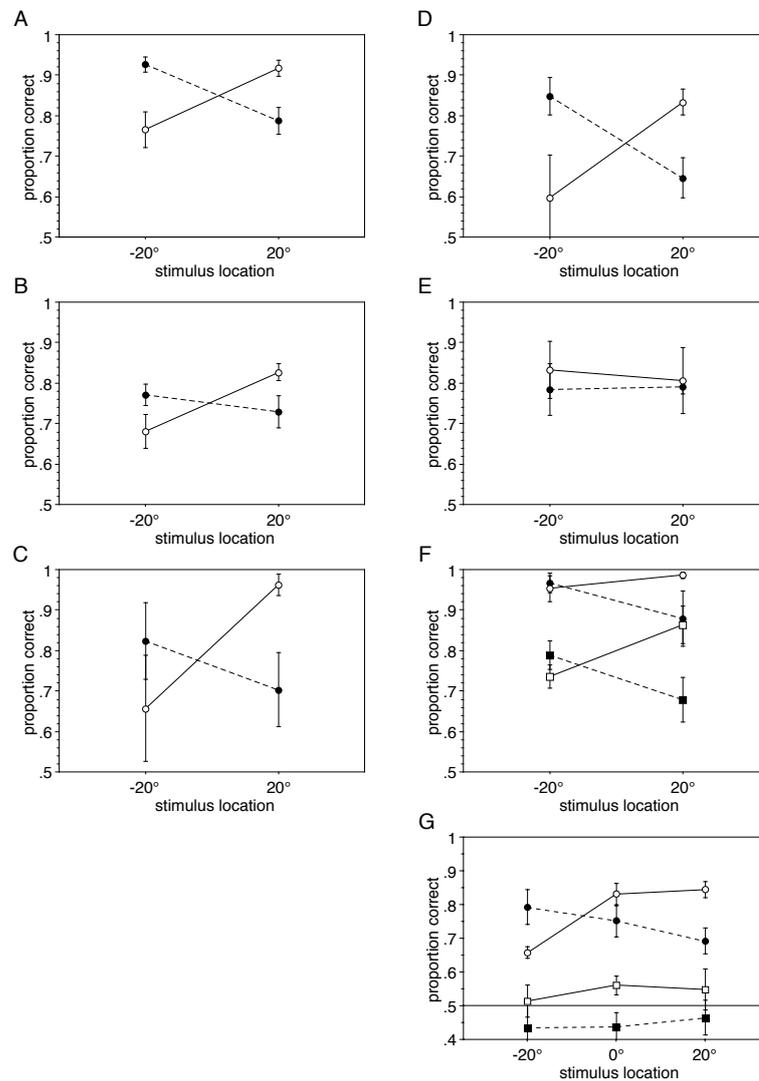


Figure 3: Proportions of correct responses in experiments 2–6. Panels (A) and (C–G) represent recognition scores on the facing direction discrimination task; (B) represents scores for the walker – scrambled discrimination task. *Continuous lines and open symbols*: facing right; *dashed lines and filled symbols*: facing left. Stimulus location is given as the visual angle with respect to the point of fixation. *Error bars* depict s.e.m.; chance level is at 0.5. (A) Experiment 1a, one block presented at -20° and one at $+20^\circ$ visual eccentricity. (B) Experiment 2, walker-scrambled discrimination. (C) Experiment 3, omitted backside (cf. Fig. 1C). (D) Experiment 4 (cf. Fig. 1D). (E) Experiment 4a (cf. Fig. 1E). (F) Experiment 5, two kinds of crawling (*circles*: cf. Fig. 1F; *squares*: cf. Fig. 1G). (G) fMRI experiment: veridical walkers (circles) and scrambled stimuli (squares).

participants performed equally well for both orientations and both hemifields when they were requested to discriminate the direction in which the joint of a three point arc faced (actually the leg of a walker, Fig. 1E).

In experiment 4 the starting frame was randomly chosen from all the frames of the gait cycle. To test whether the starting frame influenced discrimination performance we divided the trials in 6 bins and computed a two-way rmANOVA with factors starting frame and facing direction. Frames close to the maximal extension of the arms and legs gave higher performance than frames close to the minimal extension of the arms and legs ($F_{5,15} = 3.1, p = .03$), presumably because the former provided better form information, which is important for biological motion recognition (Lange and Lappe, 2006). Although performance on inwards facing walkers was worse than for outwards facing, both facings depended on the phase in the same manner (there was no interaction $F_{5,15} = 0.5, p = .7$). Thus, the facing effect was the same, regardless the presented configuration. This confirms the result of experiment 3 showing that the facing effect is not caused by visual cues.

Experiment 5: If one excludes the influence of response biases and low-level perceptual factors, the hypothesis we favour to explain the facing effect is that in order to solve the task participants embody themselves in the presented stimuli. Being this true, the facing effect should remain present also with body configurations others than walking. To test this prediction, we presented participants with two crawling figures (Experiment 5: canonical crawling, Fig. 1F, and ‘spider-like’ crawling, Fig. 1G) in separate blocks of trials. As in the previous experiments, participants were requested to report the direction of facing. Results were twofold: participants performed better in canonical crawling than in ‘spider-like’ crawling, and discrimination of figures facing away from the fixation point was easier than that of figures facing towards it (Fig. 3F; rmANOVA, $F_{1,3} = 10.2, p = .04$). Post hoc signed paired t-tests showed that this effect was significant in both hemifields for the spider-like crawling ($-20^\circ: t_3 = 2.8, p = .03, +20^\circ: t_3 = -2.7, p = .04$), and for the conventional crawling as a trend in the right, but not in the left hemifield ($t_3 = -2.1, p = .06, t_3 = .6, p = 0.3$). The latter lack of facing effect was probably caused by the ceiling effect and by an over-all bias to give more “right” than “left” responses.

The presence of a facing effect for crawling stimuli is in line with the facing effect observed with the walking figures. The effect for the crawling stimuli was much more pronounced when figures were presented in the right visual hemifield, which may have been caused by an overall bias by some of the participants to give “right” responses.

functional imaging

Humans embody themselves in others through the mirror-neuron system (for a review, see Rizzolatti and Craighero, 2004). This system, originally discovered in monkey premotor cortex (Rizzolatti et al., 1996; Gallese et al., 1996), contains neurons that discharge both when we act and when we see someone else performing the same act (see Fadiga et al., 2005; Rizzolatti and Craighero, 2004). The network of human cortical areas activated by action observation comprises the ventral premotor cortex, the inferior frontal gyrus, the superior temporal sulcus and the inferior parietal lobule. In addition, according to some recent fMRI studies, the postcentral somatosensory cortex becomes active in some conditions too (Hasson et al., 2004; Buccino et al., 2001). Given that the action-recognition system contributes to the perception of body movements and given the well-known contralateral organisation of the motor and somatosensory systems, we hypothesise that the lateralised facing effect might result from an interhemispheric interaction between the lateralised visual input and the hypothetical, lateralised embodiment of the seen action.

The goal of the fMRI experiment was to test this hypothesis and to find patterns of activity that could have caused the facing effect. If a peripheral visual stimulus is processed best in the contralateral visual cortex and if a side view of a walking human is better represented on the cortical side that is contralateral to the corresponding side of ones own body, this could lead to a locally increased cortical activation.

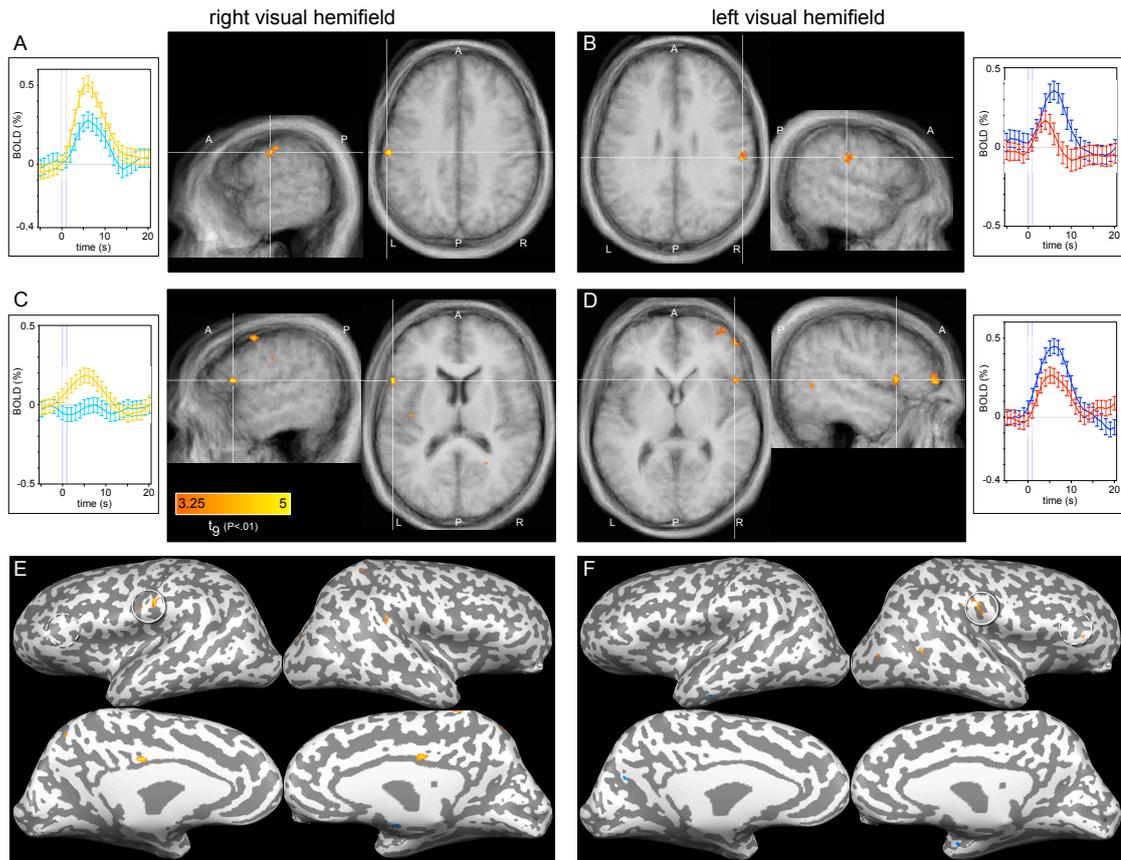


Figure 4: Statistical activation maps and BOLD responses for the two sites that show the facing effect (group random effect analysis, $t > 3.25$: $p < .01$). (A), (C), and (E): The right visual periphery: facing right > facing left (yellow and turquoise BOLD curves). (B), (D), and (F): The left visual periphery: facing left > facing right (blue and red BOLD curves). (A) left BA 2 (Talairach coordinates $-59, -16, 36$); (B) right BA 2 (Talairach $55, -21, 29$); (C) left BA 44 (Talairach $-54, 16, 13$); (D) right BA 44 (Talairach $48, 17, 7$). The underlying anatomic image is the average T1 scan of all participants. (E and F) The same contrasts on a inflated brain. Circles depict the BA 2 regions of (A) and (B), dashed circles depict the BA 44 regions of (C) and (D). The inflated brain was computed from the border of grey and white matter of the T1 scan of one of the participants. Dark and light grey regions represent sulci and gyri respectively.

Specifically, we selected bilateral regions where figures presented in each respective contralateral visual hemifield caused more activity when facing away from the fixation point than when facing towards it.

The behavioural results achieved during the fMRI experiment confirmed the facing effect for the participants also in the fMRI study: walkers facing away from the fixation point were recognised more accurately than walkers facing towards the fixation point (82% vs. 64%: Fig. 3G: circles). The facing effect was significant for the veridical walkers (rmANOVA, $F_{1,9} = 40.4, p = .0001$), and was significant for both hemifields (post hoc signed paired t-tests: -20° : $t_9 = 2.5, p = .02$, $+20^\circ$: $t_9 = -3.1, p = .007$). Performance was at chance level for the scrambled stimuli, regardless the presented location and regardless the facing direction of the walker the stimulus was derived from (Fig. 3G: squares).

Figure 4 plots the contrast between leftward facing and rightward facing walkers in the left visual hemifield and between rightward facing and leftward facing walkers in the right visual hemifield. Two cortical regions showed symmetric activations in both hemispheres. The first one was in the ventral portion of Brodmann area 2 (BA 2), located on the surface of the postcentral gyrus in the primary somatosensory cortex. The second region was BA 44 located in the inferior frontal gyrus (IFG, pars opercularis).

A further area of activation in the medial frontal gyrus (MFG) in the right hemisphere (Fig. 4D: the activity anterior the cross) did not have a counterpart in the left hemisphere, and could therefore not account for the facing effect. A region in the pre-supplementary motor area (pre-SMA, Talairach coordinates $-2, 13, 65$) was better activated by rightward-facing walkers in the right visual hemifields, but the activation difference in the left hemifield did not reach the significance criterion (data not shown).

Since the participants responded with their right hand, a strong activation occurred in the primary somatosensory and motor regions on the left side, when compared to baseline activity (Fig. 5A). This activity was clearly separated from the region showing the facing effect (cf. circles in Fig. 4 E, F). Finally, the right superior temporal sulcus (STS) was activated by biological motion when contrasted against the scrambled controls (Fig. 5B; similar to previous studies: [Vaina et al., 2001](#); [Grossman et al., 2000](#); [Servos et al., 2002](#); [Michels et al., 2005](#)), but not differentially activated by outward versus inward facing walkers, suggesting that it cannot account for the facing effect.

Discussion

In the present study we showed that rightward facing point-light walkers were better recognised than leftward facing walkers in the right visual periphery, and that leftward facing walkers were better recognised than rightward facing walkers in the left visual periphery (experiment 1). The asymmetry was not caused by the spatial stimulus-response compatibility (experiments 1a and 2), it did not depend on local cues (experiments 3 and 4), and was specific for stimuli depicting biological motion (experiment 2, 4 and 5).

Experiment 4a showed that the facing effect was absent for non-biological stimuli. The facing effect was not restricted to human walking figures, since it occurred also when the displayed actions and body posture differed strongly from walking (experiment 5).

From an ecological point of view one could speculate about functional advantages of better recognising a human figure oriented away from the point of looking. However, depending on the starting point of such an argument, one can make opposite ecological predictions (for example, for a hunter and for a social interactor). In our opinion, a more sensible approach is to focus on brain asymmetry in embodiment via the mirror-neuron system.

Two areas of the mirror-neuron system, the ventral region of BA 2, and BA 44, matched the selectivity of the facing effect in that the induced activity in these areas was larger for walkers facing away from the fixation point than for walkers facing towards the fixation point. These areas receive direct input from the ipsilateral visual cortex (e.g. [Rizzolatti and Matelli, 2003](#)). Information from the contralateral visual cortex must pass the corpus callosum, which predominantly connects homotopic areas ([Aboitiz and Montiel, 2003](#)) and which will therefore be less rich than the ipsilateral visual information.

It should be made clear here that this does not mean that only these two areas are activated by the observation a human walker. In fact, what we discuss here are just the results of the very specific interaction: that between right-left facing and right-left visual hemifield.

In more general terms, we thus propose the following to explain the facing effect. The body-form is processed in the visual cortex, such as extrastriate and fusiform visual areas, and the STS ([Grossman and Blake, 2001](#); [Vaina et al., 2001](#); [Peelen et al., 2006](#)). Premotor and somatosensory areas are involved in the embodiment of other persons' actions ([Rizzolatti and Craighero, 2004](#)). Thus, given that the visual system and the motor/somatosensory system both contribute to the perception of body movements, and given that both systems possess a lateralisation, the perception of peripheral stimuli will benefit if both

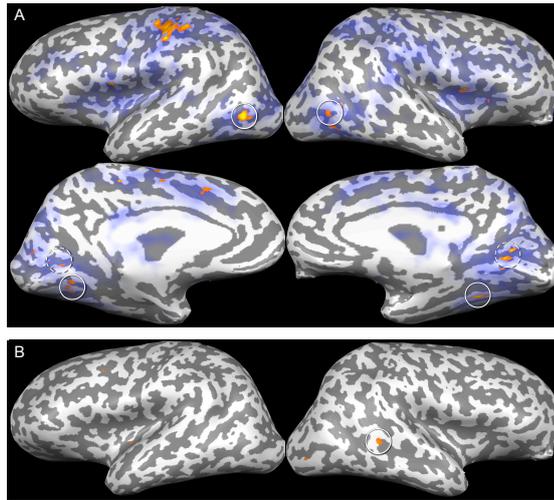


Figure 5: (A) Overview of activation in trials with correctly identified biological motion compared to baseline activity (orange-yellow: $8.0 < t < 15.0$, transparent blue: $t > 2.0$). The largest activity is motor and somatosensory activation in the finger-region of the left M1 and S1, contralateral to the hand used for responding. Bilateral visual activation by the biological motion stimuli can be seen in the side views in insula and medio-temporal gyrus (circle) and in the medial views in V1 (dashed circles) and fusiform gyrus (circles). (B) Activation in trials with correctly identified biological motion compared to the scrambled control conditions ($t > 3.25$; $p < .01$). Biological motion specific activity can be seen in the right STS (circle) and middle occipital gyrus, as well as in the left premotor and anterior STG regions. Both panels include only the trials with a correct response of the four biological motion conditions that the participants recognised well (presented centrally, and presented facing away from the fixation point).

lateralised representations are located in the same cerebral hemisphere. This is the case if the presented stimulus faces away from the point of fixation, for then it presents the body side that matches the side of one's own body in the sensori-motor central system to the side in which the visual stimulus enters the visual system.

BA 2 is the most caudal part of the somatosensory cortex and processes somatosensory information from the contralateral body-side. If observers embody themselves in point-light walkers, then the right BA 2 should correspond to the left body side of the visual stimulus and the left BA 2 should correspond to the right body side of the visual stimulus. A rightward facing walker presents its right body side to the observer. This is consistent with the selectivity of the left BA 2. If we assume that BA 2 contributes to the recognition process, then this contribution should be most effective for visual stimuli that are processed predominantly in the same cortical hemisphere, i.e. stimuli from the right visual hemifield for the left BA 2.

Facing-related activity occurred ventrally from the hand/finger region (which was activated on the left by the right-handed response presses, see Fig. 5A) and dorsally and anteriorly from the secondary somatosensory cortex, SII (which is usually found activated by touch or rubbing of the skin (Eickhoff et al., 2006; Seitz and Binkofski, 2003)). Although the walking stimuli did activate the arm and leg regions of dorsal BA 2 with respect to the baseline, the pattern of activity in these regions did not correspond with the facing effect. Instead, the differences in activity related to the facing effect were located on the ventral-most part of BA 2. Sacco et al. (2006) found this part of BA 2 activated by visual imagery of walking. However, on the somatosensory homunculus the ventral BA 2 corresponds to the face. An activation of the face region is not inconsistent with our explanation of the facing effect. The face region

is relevant for the task, since facing direction is linked to the orientation of the head. The head was not represented by light points, but mirror neuron activity has been reported for invisible actions and objects for which the observer knew the actor or object must be present (Umiltà et al., 2001; Graziano et al., 1997). We may speculate that the facing activity in BA 2 reflects a completion of the information about body orientation for the parts not visible in the stimulus. For example, in expert piano players observing one hand playing a piano (without hearing it), the ventral BA 2 contralateral to the non-seen hand is activated in addition to the more dorsal somatosensory hand area contralateral to the seen hand (Haslinger et al., 2005). Since piano playing is a bimanual task, these expert players may have automatically generated activity associated to the unseen hand. Similarly, our participants may have generated activity for the unseen head of the walker. Further research may clarify this issue.

It has been shown that humans can recognise the facing direction from the motion trajectories of just the feet (Troje and Westhoff, 2006). These authors reported recently that they possibly reproduced the facing effect for this task, at least in the right visual hemifield (Williamson et al., 2007). As these stimuli thus not only missed the head but even the entire body, these results might be interpreted as a more extreme case of completion. Thus in order to get the facing effect, two conditions must be fulfilled. First, the task must involve the recognition of a body structure, and second, a body structure must be recognisably present in the stimulus.

The second activation consistent with the facing effect was located in BA 44. This area is activated in action recognition, imitation and biological motion recognition (Rizzolatti and Craighero, 2004; Goldberg and Karnath, 2006; Binkofski et al., 2000; Saygin et al., 2004). The activation shown by our study supports an involvement of BA 44 also in the facing effect, although it is not clear whether BA 44 contributes to the generation of the facing effect or reflects the better embodiment for outward facing walkers. Further experiments are needed to clarify this issue.

Several recent studies support our view that the mirror-neuron system contributes in a somatotopic manner to interpersonal body representation. First, the mirror-neuron system contains somatotopic body-representations (Buccino et al., 2001; Aziz-Zadeh et al., 2006; Sakreida et al., 2005). Second, Michelon et al. (2006) found a contralateral organisation of imagined body-actions during both the imagining and the preparation of movements. This lateralisation was strongest in the pre- and postcentral gyrus. The latter region is in accordance with our findings. Third, Thomas et al. (2006), showed that a visual cue presented on a limb of a person who is sitting opposite the observer, advances a response to a sensation on the corresponding limb of the observer. Fourth, Aziz-Zadeh et al. (2006) measured simple reaction times to the presentation of images of hands. Reaction times were shorter for left compared to right hand images in the left visual field and for right compared to left hand images in the right visual field.

An important issue is why other regions of the mirror neuron system were not selectively activated for the facing effect. Possible reasons fall in two categories. First, it is known that laterality effects in the pre- and postcentral gyrus for activity other than motor execution is generally small Michelon et al. (2006). Also, mirror-neuron activity appears to be generally lower for filmed actions than for real actions (Jarvelainen et al., 2001). Secondly, the task was unusual. Whereas studies on the mirror-system typically find a coding in terms of action understanding with respect to the goal (Rizzolatti and Craighero, 2004), in our task the performed action was known to the observers and did not represent any particular goal. Instead, the observers' task was related to understanding the presented body configuration. This task was more strongly related to the somatosensory than to the motor representation of the action.

The perception of the movements and actions of others is the result of a complex capability that takes information not only from visual input but also from other sensory signals and from one's own vocabulary of motor representations. Our findings lend support to the view that somatosensory and motor structures contribute to visual action recognition. Moreover, they enrich this hypothesis by providing evidence that the representation of other people's body-sides is achieved through an embodiment on the somatosensory map of our own body.

Abbreviations

BA, Brodmann area; BOLD, blood oxygenation level dependency; fMRI, functional magnetic resonance imaging; FOV, field of view; FWHM, full-width half maximum; IFG, inferior frontal gyrus; MFG, medial frontal gyrus; rmANOVA, analysis of variance with repeated measures; s.d., standard deviation; s.e.m., standard error of the mean; SMA, supplementary motor area; SRC, spatial stimulus-response compatibility; STS, superior temporal sulcus; TE, echo time; TR, time of repetition.

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