Fachgebiet Psychologie

Cortical activation by a biological motion stimulus with limited lifetime

(Kortikale Aktivierung durch einen biologischen Bewegungsstimulus mit reduzierter lokaler Bewegung)

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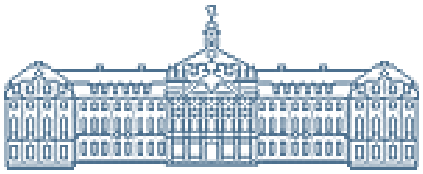

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List of Abbreviations

AC	anterior commissure
BA	Brodmann area
BOLD	blood oxygenation level dependency
BSR	body-selective region
CBF	cerebral blood flow
CS	static Cutting walker
CSF	cerebrospinal fluid
CT	computerized tomography
CW	Cutting walker
EBA	extrastriate body area
EEG	electroencephalography
EPI	echo-planar imaging
ERP	event related potential
FSR	face selective region
FFA	fusiform face area
FG	fusiform gyrus
fMRI	functional magnetic resonance imaging
FOV	field of view
FWHM	full-width at half-maximum
HRF	hemodynamic response function
IFG	inferior frontal gyrus
IPL	intraparietal lobe
ISI	inter-stimulus-interval
ITC	inferior temporal cortex
ITG	inferior temporal gyurs
KO	kinetic occipital region

LG	lingual gyrus
LGN	lateral geniculate nucleus
LH	left hemisphere
MeFG	medial frontal gyrus
MEG	magnetoencephalography
MOG	middle occipital gyrus
MRI	magnetic resonance imaging
MST	medial superior temporal area
MT	middle temporal area
MTG	middle temporal gyurs
OFA	occipital face area
PC	posterior commissure
PG	parahippocampal gyrus
PET	positron emission tomography
PMC	premotor cortex
PPC	posterior parietal cortex
QuP	cerebellar lobule VI, lateral cerebellum
RF	radio frequency
RH	right hemisphere
rTMS	repetitive transcranial magnetic stimulation
rmANOVA	analysis of variance with repeated measures
ROI	region of interest
RT	repetition time
SFG	superior frontal gyrus
SFL	single-frame lifetime
SMA	supplementary motor area
SPL	superior parietal lobe
sPrG	superior precentral gyrus
SRC	spatial stimulus-response compatibility
SS	static single-frame lifetime walker
STG	superior temporal gyrus
STPa	anterior superior temporal polysensory area
STS	superior temporal sulcus

SW	single-frame lifetime walker
T	Tesla
TE	time of echoplanar
TEO	temporal occipital area
TR	time of repetition
V1	visual area 1 (primary visual cortex)
V2	visual area 2 (secondary visual cortex)
V3	visual area 3
V3A	visual area 3A
V3B	visual area 3B
V4	visual area 4
V5	visual area 5
V5A	visual areas 5A

Chapter 1

General Introduction

1.1 General Introduction

From an evolutionary perspective, the ability to identify the movements or intentions of prey and predators and to interact with them in an adequate way is of great importance for animals. Of course, this is less important for humans, but also humans are able to quickly interpret the movements, emotions, and intentions of other individuals. Especially, appropriate judgments of different social contexts can be only achieved when the visual system has analyzed and interpreted the depicted action or mood of other individuals. This analysis process is fast and accurate and is even successful in situations when there is no direct social relation to the other individual, for example, when the individual is unfamiliar to us (Johansson, 1973).

Although humans can discern the affective state of other persons from static pictures, additional motion provides more compelling and reliable information. When humans visually perceive, for example, the movements of the world's number one tennis players Roger Federer or Justin Henin, they can quickly differentiate whether the observed actions depict movements of a man or a woman just from the dynamics of the body movement. Several questions emerge from this remarkable perceptual ability. For example, can the visual system derive the dynamics of the movements from specific single joints or does it maybe integrate structural changes of body configurations over time? Another question is, does the perception of human movements take place in areas that are also engaged in motor preparation and execution? Strongly coupled to questions one and two is the question whether or not the brain possesses a specialized mechanism to analyze human movement patterns?

1.1.1 Biological motion

Johansson (1973) showed for the first time that humans are able to perceive the movements from other human individuals within a fraction of a second even when the visual information is reduced to few moving light-points within a fraction of a second. He called the ability to perceive the actor and its actions the perception of *biological motion*. However, biological motion does not only describe the human body movements but rather all movements generated by living forms or by parts of it such as face or hand movements. In addition, it has been demonstrated that the movement of animals as well can be perceived from point-light displays (Mather and West, 1993). Therefore, the term biological motion refers more to the phenomenon that humans' visual system is able to recover object information from reduced visual input of living forms. Nevertheless, the most intensively studied biological motion stimulus is the point-light display depicting human walking, which will be also investigated in this thesis.

1.1.2 Point-light walker

Johansson (1973) filmed the walking of actors with thirteen light-points attached to the head and the major joints (the head, shoulders, elbows, wrists, hips, knees, and ankles) of the body in an otherwise dark surrounding. Although this walker provides only sparse visual information, observers recognized easily the performed actions such as dancing or walking, as soon the stimulus was set into motion. Johansson called the stimulus the *point-light walker*. The perception of the point-light walker was even possible when presentation times were about 200 ms (Johansson, 1976). Interestingly, static frames of the stimulus typically appear as meaningless assemblages of dots with little information about the underlying configuration, stressing the idea that motion information is essential for the perception of the human gait.

The point-light walker contains different kinds of motion and form information. The illusion of motion when a series of still pictures is shown in rapid succession is called *apparent motion*. Hence, each light-point changes position over time and thence provides apparent motion signals. These signals will be called from now on *local motion* signals. The instantaneous positions of all light-points at any time provide structural information about the momentary posture of the human body. Despite the fact that only few light-points produce the structural information in a single snapshot of the body, temporal integration of the instantaneous positions signals over a sequence of

postures may provide increased structural information. This information is called the *global form* information or sometimes configural information. Of course, changes of the structural information over time yields also motion information. This information will be called the *global motion* information.

Another way to study the perception of the human gait was introduced by James Cutting. He used an algorithm to develop a computer-generated version of the point-light walker (Cutting, 1978). Similar to Johansson's point-light walker, the dots of the – from now on called – *Cutting walker* were positioned on the joints of the major limbs, which results in a constant joint length at each time-point of the presentation so that valid[1] local motion vectors are provided by the single dots. Although this walker appears less natural than its original counterpart, results of different experimental tasks were highly comparable. One advantage of the Cutting walker is that it allows the study of perception under controlled conditions. For example, the number and the position of displayed dots can be easily manipulated with a PC program. Of course, changes could be also applied to the real moving stimuli, but it more complicated, for example, to change the position of the light-points in each frame of the walking cycle manually.

More recently, Beintema and Lappe (2002) asked whether the local motion information provided by the single dots of the point-light walker is essential for its perception or whether observers can detect other individuals on the basis of structural changes of body configurations that is the global form of the human body. To dissociate between position and motion, Beintema and Lappe designed a variant of the Cutting walker in which the dots were not positioned on the single joints, but were rather jumping to a randomly selected location on the limbs in each frame of the presentation. In the new stimulus dots still provide local motion signals, but those are not any longer valid, because their position in each frame of the presentation was unpredictable. Because the dots remained only a single frame of the walking cycle on the joint, that means having a 'lifetime' of a single frame, Beintema and Lappe termed this stimulus the *single-frame lifetime walker* (SFL walker). Despite the absence of valid local motion signals, naive observers were able to perceive the SFL walker to a similar extent as compared to the Cutting walker, although response times were longer (Beintema and Lappe, 2002; Beintema et al., 2006).

[1]The local motion signal is called valid, because the motion from the joints are produced by the consecutive motion signals from the single joints resulting in smooth motion trajectories.

1.1.3 Visual and non-visual features for biological motion perception

When the visual system has to analyze biological motion, it has to deal with a stimulus that contains many degrees of freedom. To understand the processing of the human movement it can be asked: 'What defines the visual input (the stimulus)?' and 'What is the output that means the behavioral response to the stimulus?' In general it could be asked which areas in the brain process biological motion and lead to the vivid visual perception of a human form?

Visual features such as motion and structural information of the stimulus are relevant for the perception of biological motion. Geometrical features, i.e. stimulus depth or size, may also have an influence on its perception. Yet, it is difficult to define the specific visual inputs provided by the biological motion stimulus, because most of these visual features are coupled.

Also non-visual features may be relevant for the perception of biological motion. For example, the stimulus could carry semantic information, such as information about the gender or the emotional state of the observed individual. Indeed, it has been demonstrated that point-light animations provide sufficient information to recognize the gender of a human (Kozlowski and Cutting, 1977; Barclay et al., 1978; Mather and Murdoch, 1994; Troje, 2002; Troje et al., 2005) or the emotional state of individuals (Heberlein et al., 2004).

In addition, motoric and sensory representations may influence the observation of body action. This idea is supported by findings that showed that cortical representations during action observation overlap with motor representation during action planning (Decety and Grèzes, 1999).

In the following section, I will first give a brief overview of the human visual system, because the processing of both form and motion signals are linked to specific areas within this system. I will then summarize the results of psychophysical and modeling, neurophysiological, neuroimaging, and lesion studies that examined the relevance of visual and non-visual features for the perception of biological motion.

1.1.4 The monkey and human visual system

The retina is the first station in the visual processing. When the visual information in form of light passes our eyes, it leads to an electrical excitation of the photoreceptors in

the retina. Each of the two retinae holds a 1:1 copy of the perceived outside world, in other words, each retina possesses a spatial organization of the neuronal responses to visual stimuli (retinotopy). The electrical signals of the photoreceptors are relayed via the ganglion cells and the nervus opticus to the chiasma opticum. From here, the visual information from both eyes is then relayed to the lateral geniculate nucleus (LGN). The LGN receives afferences from the contralateral as well the ipsilateral eye. This ensures that both nuclei possess a full representation of the visual world, maintaining the retinotopy of the retina. From the LGN, the visual information is then relayed via the tractus opticus to the primary visual cortex (V1) and the secondary visual cortex (V2), where the retinotopic organization is still present. After this processing stage, it was believed for a long time[2] that the visual cortex is divided in to two different information processing streams (Mishkin et al., 1983). The streams are known as the ventral and dorsal path. The ventral path processes form and color information, therefore named 'what' path. For example, detection of objects necessarily requires that the form of the object has to be processed. The information from the 'what' path runs via V2 to the ventral part of the higher-level areas V3 and V4 and then to the inferior temporal cortex (ITC).

For the dorsal path it is suggested to process exclusively motion information, therefore it was named the 'where' path. Information in the 'where' path runs from V2 to the dorsal part of V3 (V3A and V3B), and then to area V5, known as the *middle temporal area* (MT) in monkeys, and to area V5A, known as the *middle superior temporal area* (MST).

The information from both pathways is integrated in the superior temporal cortex (termed anterior part of the *superior temporal polysensory area* (STPa) in monkeys). An illustration of the primate visual system is shown in Fig. 1.1.

The receptive field size of the cortical areas[3] enlarges in both pathways with the stage of processing (Bruce et al., 1981; Motter et al., 1987). Additional, the functional properties of the neurons of both streams increases with the stage of processing. For example, whereas V1 processes simple objects features such as the orientation of lines as a result of luminance changes, cells located in monkeys' ITC analyze more complex features such as faces or other objects.

Traditionally, object, face and body-selective regions have been considered as 'non-

[2]Recently, it has been more often demonstrated that the two pathways are heavily connected

[3]The receptive field describes the area where a neuron respond with increased firing rate

retinotopic' areas. However, recently it has been shown that even higher visual areas show sensitivity to various image manipulations like the stimulus position (Niemeier et al., 2005; Hemond et al., 2007; Schmuelof and Zohary, 2005).

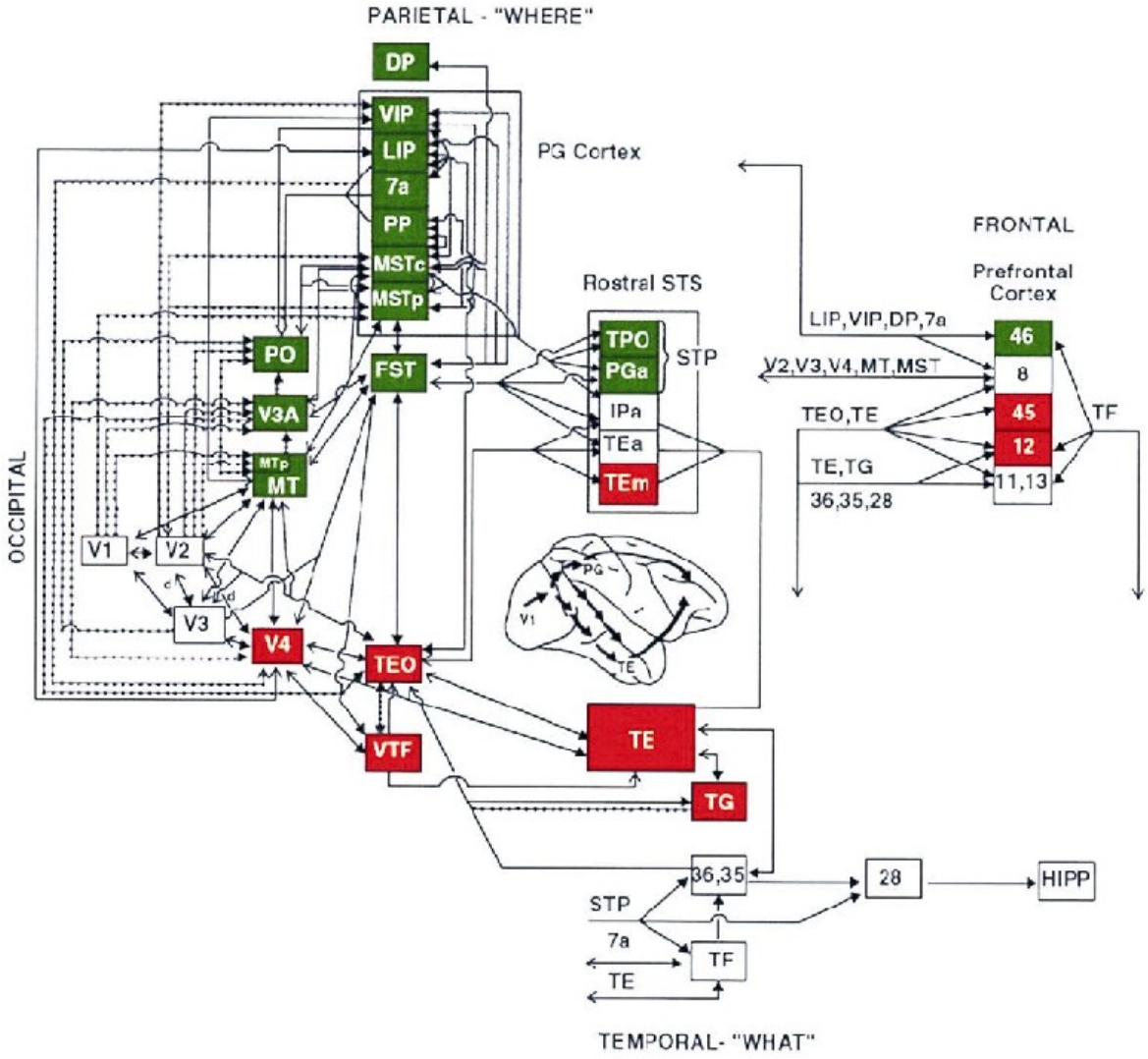

Fig. 1.1: **Illustration of the primate visual system.**The visual cortex is divided in two separate processing pathways, termed 'where' (dorsal) and 'what' (ventral) pathway. Both pathways consist of several visual areas. The 'where' pathway analyses motion signals, the 'what' pathway analyses form and color signals. Adapted from Ungerleider (1995).

1.2 Studies to biological motion perception

1.2.1 Psychophysical and modeling studies

The role of motion information There are different ways to investigate the role of visual and non-visual features for the perception of biological motion. In the next three paragraphs, I will present the results from masking and non-masking studies that investigated the contribution of visual as well as non-visual features for biological motion perception.

In a masking paradigm, the point light walker is embedded in a mask consisting of a field of flickering or moving dots (noise). The mask is designed to render part of the information in the stimulus useless. If the perception of the stimulus is impaired by the mask, the information that had been masked must have contributed to the percept. The observers' perceptual performance in the presence of the mask is usually measured by different psychophysical tasks. For example, in a detection task the presence of a walker has to be discriminated against the presence of other stimuli or against a presentation of the mask alone. In direction discrimination experiments, the walking or facing direction of the walker has to be discriminated. These two tasks were also used in this thesis (although the stimulus was not shown in an array of noise dots).

Mather et al. (1992) tested the necessity of local image motion in biological motion recognition. The authors presented the point-light walker in randomly moving noise dots. The subjects viewed the stimulus frames alternating with a mask of dark frames[4] while they had to discriminate the stimulus' walking direction. The authors varied the duration the mask was presented (60-100 ms). These blanks frames should interfere local motion detectors. Mather et al. demonstrated that the direction discrimination failed if the blank inter-stimulus frames intermit the stimulus in noise. The authors concluded that local image motion information is a requirement for the perception of biological motion.

In addition, Mather et al. showed that the local motion information from single dots provided enough information for a successful discrimination of the walking direction if subjects were trained to see point-light walker. In one experiment, dots from different

[4]If the stimulus is just superimposed with a field of random dots, which change the spatial position in every frame of the animation, the dots that belong to the walker cannot be differentiated from the noise dots on the basis of the information in a single frame. Local motion signals of the walker dots are only available from the apparent motion signal across at least two animation frames

joints were omitted in each single frame of the animation. The result was a strong decrease in the performance level when the dots usually located on the wrists or ankles were omitted. In contrast, no decrease was observed in the performance when the dots of the other joints (shoulder, elbow, hip or knee) were omitted. The result that the local motion signals from the ankles provide enough information for a direction discrimination is maybe not surprising, because the backswing of the legs provides the largest local motion vector (Troje and Westhoff, 2006).

Neri et al. (1998) showed in a detection and discrimination task that observers recognition rates were not significantly different if they had to detect a point-light walker or simple translational motion both embedded in noise. The results showed a linear increase of the detection threshold for increased number of displayed stimulus dots. In a second experiment, the authors found that the discrimination of the walking direction of a point-light walker in noise increased non-linearly with the number of presented stimulus dots, specifically that the perception of biological motion was more robust than the perception of the translational motion for which recognition rates increased linearly with the number of stimulus dots. Neri et al. suggested that common information of the two stimuli in the first experiment (that is motion) is sufficient for the perception of a human walker. From the second experiment, the authors concluded that the motion filters for biological motion perception are flexibly adapted to the stimulus as reflected by the observed non-linearity. The robustness in detecting a point-light walker presented in an array of noise dots was surprising, simply because integration of local motion signals should increase linearly as observed for simply translational motion. The results by Neri et al. suggest that biological motion perception is somehow different from a simple motion detection mechanism.

Biological motion perception should work for the whole visual field, not just for central (foveal) vision. However, recently it was shown that biological motion perception is particularly difficult when it is presented in random noise in the visual periphery (Ikeda et al., 2005). This impairment is not simply attributable to the periphery's reduced visual resolution, because increasing the size of the point-light walker dots and the overall size of the human figure cannot compensate for this loss in sensitivity. Thompson et al. (2007) argued that detection in random dot noise is more difficult in the periphery than under foveal conditions, presumably because of differences in visual grouping processes that are required to join the individual light points into a coherent body structure. In contrast to the processing of central stimuli, processing

of peripheral visual stimuli is more lateralised, because of the few callosal connections. Despite these few connections, perception of peripheral biological motion is nevertheless possible when the stimuli were not embedded in noise (Thompson et al., 2007). To learn more about the functional properties of the underlying neuronal mechanisms for peripheral biological motion perception, a detailed investigation of the perception and brain responses to peripherally presented stimuli may be helpful.

In summary, some of the masking studies may suggest that local motion information is used by the visual system to generate the perception of a human figure. The analysis of common motion directions by the local motion of the single dots may provide information to connect these dots to a rigid element (Ullman, 1984). Hence, the impression of a human form could be based on a mechanism, in which form is derived from the analysis of single (local) motion vectors. This mechanism is termed *form-from-motion-* or *structure-from-motion* mechanism (Johansson, 1973).

In fact, there are several factors that complicate the interpretation of the described masking experiments on the role of local motion for biological motion perception. First, in these studies it was assumed that local motion processes are disrupted when the inter-stimulus-interval (ISI) was > 60 ms (e.g. Mather et al. 1992) or by reversing the dot contrast in the single animations frames. These manipulations, however, may influence not only low-level motion processes, but also other processes, such as form detection. Second, delaying stimulus frames changes the temporal sequence, resulting in an undersampled sequence and therefore in jerky stimuli. Third, the detection of a point-light walker presented in a mask of dots requires a segregation process which profits form local motion signals, but that is not just specific for biological motion.

There are also non-masking studies that investigated the role of motion signals on biological motion perception. Ahlström et al. (1997) showed that perception of biological motion did not rely on first-order motion[5], because their stimulus was also detectable when it was defined by second-order motion[6]. This finding suggests that low-level motion processes probably do not contribute to the perception of biological motion.

But not only the local motion information could be important for the perception of biological motion, but also the global motion information. Shipley (2003) demonstrated that when a point-light walker moved on his hands, the way the display moves had

[5]The motion is defined by luminance changes

[6]The motion is defined by contrast changes

a stronger influence on subjects' responses than the form analysis. Shipley suggested that the dynamics of the stimulus, reflected by the global motion information, provided more information necessary for its perception than the present form information per se.

Giese and Poggio (2003) introduced a model that was motivated by neurophysiological results for the perception of the human body. The proposed model integrated both form and motion information. Their model is based on a *bottom–up* processing of visual signals, which are analyzed in parallel in a motion and a form pathway. For example, they modeled responses of the dorsal pathway by an integration of local motion signals to complex flow patterns, which are then compared to templates of the walking cycle. The core principle of their model is that human motion is represented as learned sequences (snapshots) of human body shapes or the described optic flow patterns. However, their model failed to model the responses of the ventral pathway, presumably because it just connect nearest dots to lines without any prior knowledge about the form of the stimulus. In addition, Giese and Poggio acknowledge that their model remains incomplete, because it does not incorporate *top–down* influences such as attention.

The role of form information Some of the so far described studies suggested that biological motion perception is based on a form-from-motion mechanism. In contrast, it is also possible that the human movement perception is based on a mechanism in which global form information is used rather than local motion information. Indeed, there are masking and non-masking studies that support the existence of such a mechanism, which is called *motion-from-form* or *motion-from-structure* mechanism.

Cutting et al. (1988) and Bertenthal and Pinto (1994) constructed masks by taking multiple copies of the walker and randomly shifting the initial positions or the initial phases of the dots. This type of mask strongly reduces the ability to detect the presence of a walker but recognition rates stayed always above chance level. Bertenthal and Pinto argued that the ability to see the walker at noise threshold must therefore be mediated by a global form recognition process, because the noise dots could only disturb low-level processes involving the processing of local motion signals.

Shiffrar and colleagues investigated the perception of biological motion in context of the aperture problem. The latter is known under the phenomenon that the direction of a unidirectional motion becomes locally ambiguous when the motion is perceived

trough a small hole (that is the aperture). Shiffrar et al. (1997) presented line drawings of biological motion stimuli (stick figures) and non-biological motion objects like cars that subjects saw through small holes distributed over the monitor. Local motion signals in these stimuli were ambiguous, because of the aperture problem. Shiffrar et al. demonstrated that only the perception of the stick figures was possible and therefore biological motion perception is not based on local motion signals.

Thornton et al. (1998) repeated the masking experiment of Mather et al. (1992), but used a longer stimulus display duration. Thornton et al. found that the discrimination performance with inter-frame-intervals became much better for longer stimulus durations, hence, was independent of the inter-frame-interval per se. The authors concluded that the experiments of Mather et al. did not provide enough evidence for the necessity of local motion signals for biological motion perception.

In summary, the masking studies not only demonstrated that the global form information may be sufficient for the perception of biological motion but also showed that the perception may depend on a top-down rather than on a bottom-up process, because the perception was high for different types of masks. In contrast, in a bottom-up process only position and local motion signals can be used for the detection of a point-light walker. This means that only small disruptions of the stimulus, such as inter-joint displays, in which the dots of the walker were not located on the joints but rather between them (Cutting, 1981), should lead to a impaired perception.

There are also non-masking studies that emphasized the role of global form information for biological motion perception. Shiffrar and Freyd (1990) and Chatterjee et al. (1996) studied biological motion perception with displays that are completely devoid physical motion. For example, two static frames can be pulled form a movie of a human action. When these static images are sequentially presented at temporal rates consistent with the amount of time normally required to perform the presented action, observers can perceive biomechanically plausible paths of apparent human motion. This motion percept relates to the global motion of the body and overwrites local motion signals when there is a conflict between consistent and impossible motion path.

Pinto and Shiffrar (1999) used a modified version of the Cutting walker. In their stimulus the common symmetry of the limbs, thus, the correct dynamics of the stimulus was destroyed, because the opposing movements of the limbs were missing. Nevertheless, subjects could still perceive the stimulus. These findings may suggest that the dynamics of the biological motion stimulus plays only a minor role for its perception.

The importance of global form information for biological motion perception is further supported by priming experiments (Verfaillie, 2000). In priming experiments, the reaction time to a test stimulus is shown to be reduced by a preceding prime stimulus due to knowledge about the stimulus. Verfaillie investigated whether the recognition of a point-light walker could be primed by the preceding display of a point-light walker facing and walking in the same or in a different direction. He found priming effects when the follow-up walker faced in the same, but not a different, direction than the preceding one. However, the movement direction (forward or backward walking), and thus the articulated motion, did not exhibit priming effects, because subjects responded faster to walkers that faced to the right if they were primed with a right-facing walker, no matter whether the walker walked forwards or backwards. The results could indicate that the priming effect was contained in the form and orientation of the walker, but not in its motion.

In a study related to apparent motion perception from photographs of human poses, Kourtzi and Shiffrar (1999) investigated priming effects of a sequence of body images on a subsequent pose recognition task. The authors presented two prime views of the human body, followed by a blank screen. Then, a pair of targets appeared until the subjects responded. Subjects carefully observed the prime displays and then pressed a key of the two subsequent targets matched each other. Kourtzi and Shiffrar showed that priming of body poses occured only for poses that lay along the path of body movement that was presented in the primes. The authors concluded that human body movement could be represented as a collection of pose images.

Pavlova and Sokolov (2000) demonstrated that configural information is relevant for the perception of biological motion, because detection of biological motion was not possible anymore when point-light walkers were presented upside-down. Even prior knowledge cannot counteract this 'shape inversion effect', that is, although subjects were informed ahead of time that they will be seeing upside-down versions of the point-light walker, this information did not help them in identifying what they have seen. These results suggest that humans cannot mentally rotate the images, thus, articulated body motion is harder to match to an experience-based template, that is the upright global form of a human body. This shape inversion effect is probably related to the well-known face inversion effect, and also to the more recently reported body inversion effect (Reed et al., 2003). Motion information would only play a role in revealing the articulation of the body from the point-light displays and could as well be replaced by

sticks in a static figure.

Beintema and Lappe (2002) created a novel point-light stimulus (the SFL walker), in which local motion signals were destroyed and only form information was retained in the stimulus. In this stimulus, each of the stimulus' dots were just shown for one frame of the stimulus animation at a fixed location. In the next frame each dot was located on another random position between the joints. Thus, an individual point does not provide a valid local motion signal because it cannot be tracked over frames. The frequent relocation of the dots instead provides increased form information as the limbs are traced over time. Despite the reduction of valid local motion signals naive observers were able to perceive this stimulus with remarkable ease similar to the Cutting walker. The results from Beintema and Lappe suggest that the global form information could be sufficient for biological motion perception. For example, Beintema et al. (2006) showed that the detection performance of SFL walkers is well predicted by the total number of stimulus dots seen in a trial, irrespective of the distribution of theses points over time.

Lange et al. (2006) and Lange and Lappe (2006) proposed a template-matching model of biological motion perception, which consists of two stages. The authors explicitly assume that the human brain already possesses knowledge about the human form, represented by the templates in their model. 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 body postures over time. The first stage requires template cells that are sensitive to the different postures of the gait cycle. The activity of these template cells is then used to calculate the correct percentage level in an orientation discrimination task. The implementation of a second stage was necessary to solve the direction discrimination task, because the model in stage one does not explicitly consider the temporal order of the stimulus frames. The activation in the cells of the first and the second stage were highly comparable with behavioral and physiological responses suggesting that the depicted action (that is a right- or a left facing walker) can be achieved by a temporal integration over body (global form) changes.

The role of the motor system for the perception of biological motion So far I have focussed on the visual sensitivity to human movement perception. Recently, some studies have also investigated the role of the motor system for biological motion

perception (Jacobs et al., 2004; Jacobs and Shiffrar, 2005; Loula et al., 2005; Casile and Giese, 2006). The common theory behind these studies is that action perception and action production share common representations. This means that when an observer performs an action, also its perception to see the activity performed by other individuals is increased. Indeed, Reed and Farah (1995) showed that observers were better able to notice changes in the limb positions of an actor when the observer, too, is moving the corresponding limb. In addition, Jacobs and Shiffrar (2005) demonstrated that the observer's ability to discriminate the gait speeds of point-light walkers depended upon whether the observer is standing or walking.

If motor experience has an influence on the sensitivity to biological motion actions, then the observer's sensitivity should be maximal to actions most familiar to them. Indeed, Loula et al. (2005) showed that observers are especially good at judgments whether a pair of point-light animations depicted the same actor when the animations were created by filming the observer himself some months earlier. In contrast, Jacobs et al. (2004) demonstrated that the perceptual ability discriminating the gait speed of the point-light walker was poor when the spatio-temporal configuration of the walker falls outside the physically possible human gait. Casile and Giese (2006) showed that human's ability to discriminate unusual action styles improved by repeatedly executing these action styles themselves. The perceptual increase was even possible when subjects were blindfolded, thus, the increase was not based on visual cues that could be used to solve the task. This study suggests that simple motor learning dramatically influences the visual perception of learned motor behavior.

1.2.2 Physiological studies

To answer how visual as well as non-visual features of the biological motion stimulus activate brain regions, electrophysiological[7], but also invasive brain imaging methods such as *positron emission tomography* (PET)[8] or non-invasive brain imaging methods such as *electroencephalography* (EEG) and *magnetoencephalography* (MEG)[9], or *functional magnetic resonance imaging* (fMRI) have been used. fMRI measures the *hemodynamic*

[7]Electrophysiology allows to measure the physiological responses at the single cell or at the population level.

[8]Brain imaging technique that uses radioactively labeled tracers to allow visualization of active brain

[9]EEG measures the electrical activity of the brain from electrodes placed on the scalp. EEG traces represent the summation of post-synaptic potential form a large number of neurons. MEG traces

changes associated with synaptic activity (Logothetis et al., 2001; Shmuel et al., 2006) at a spatial resolution of about 1 mm (see section 1.4.3). I will describe the results from electrophysiological, PET, EEG, MEG and fMRI studies to biological motion perception, but focus on fMRI studies, because this is the method that was used in this thesis.

Studies in monkeys As mentioned in 1.1.4, parts of the temporal cortex are convergence point from inputs from areas of the dorsal and also from the ventral pathway. In monkeys, specifically the STPa receives inputs from dorsal MT complex (including area MT and MST) and from areas of the ITC (Felleman and van Essen, 1991). The biological motion stimulus carries form as well as motion cues, hence, a hypothesis, which was first investigated in electrophysiological studies, was that STPa may be a neural correlate for biological motion perception.

The first electrophysiological study that investigated the neuronal responses to body movements was performed by Bruce et al. (1981). The authors demonstrated that some neurons of the STPa were activated by body movements. This finding was replicated by more recent studies (Perrett et al., 1989; Perrett et al., 1990; Oram and Perret, 1994; Oram and Perret, 1996). Perrett et al. (1990) demonstrated that monkeys perceived biological motion even when the stimulus was embedded in an array of noise dots. Oram and Perrett (1996) showed that the STPa consists of different sub-populations which either responded to motion or to form cues, for example to the static view of the body, or to both.

Oram and Perrett (1994) found selective responses in the STPa to centrally, but also for peripherally presented point-light walkers. Furthermore, it was found that STPa cells showed 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., 2002; Jellema et al., 2004; Oram and Perret, 1994; Oram and Perret, 1996).

However, cell responses in the STPa were not only found for whole-body movements per se, but also for the execution of particular actions, such as grasping or the manipulation of objects (Perrett et al., 1989; Perrett et al., 1990). For example, it has been demonstrated that STPa cells preferred articulated body movements in comparison to

represent the magnetic field of a group of neurons. EEG and MEG allow the real time monitoring of brain processes, but provide only a spatial resolution of about 5 mm.

non-meaningful movements (Jellema and Perrett, 2003a), which may indicate that this region shows a selectivity for meaningful human movements.

Moreover, cells of monkey's STPa contain a functional organization for objects of different visual categories (Logothetis et al., 1999; Tsao et al., 2003; Pinsk et al., 2005). For instance, Pinsk et al. (2005) found distinct face and body-selective regions in the STPa.

It was also shown that areas, classically not regarded as visual areas, responded to human bodies or part of human bodies. Specifically, it has been demonstrated that neurons in the ventral and dorsal premotor cortex (vPMC and dPMC), but also in the frontal cortex and in the posterior parietal cortex (PPC), which are heavily connected to the PMC (Rizzolatti et al., 1996; Gallese et al., 1996; Rizzolatti et al., 2002; Rizzolatti and Craighero, 2004), discharged both when a monkey executed an action and when the monkey saw someone else performing the same action. These neurons are called *mirror-neurons*. Interestingly, the visual properties of some of the PMC and STPa neurons show dissimilarities but also similarities. Both neuronal populations are sensitive to body movements, for example, to hand-objects interactions and their causal relation. However, a difference between these two population is that only PMC neurons respond similar strong during the observation and the execution of a movement (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996), whereas STPa neurons do respond more strongly to the observation of a movement. According to Carey et al. (1997), these results could indicate that responses of the so-called mirror-neuron system strongly contribute to the understanding of actions performed by other individuals.

Studies in humans: Activations of the dorsal and the ventral visual pathway
The first human physiological study to biological motion perception was performed with PET (Bonda et al., 1996). In this study two types of point-light animations were used. First, point-light sequences depicted a frontal plane view of a human that moved backward and forwards and from left to right. Second, point-light sequences showing goal-directed actions, i.e. a human hand that continuously performed grasping movements. Bonda et al. reported three findings. First, activation in a limbic structure, called the amygdala, that was only visible for the whole-body movement condition. Second, activation in the intraparietal lobe (IPL) of the parietal cortex that was only present for the hand action. Third, activation in the STS for both point-light animations. This activation was located in the posterior part of the STS (pSTS) as well as

in the adjacent MT area. The finding of pSTS activation was the first evidence for a homologue in humans for the monkey results. From thereon, several human fMRI studies on biological motion reported MT but also activations in parts of the pSTS or the posterior superior temporal gyrus (pSTG) (Howard et al., 1996; Grossman et al., 2000; Vaina et al., 2001; Grossman and Blake, 2001; Grossman and Blake, 2002; Grossman and Blake, 2004; Thompson et al., 2005). An illustration of pSTS activation for biological motion stimuli is shown in Fig. 1.2. However, it can be asked whether or not the activation of MT and pSTS/STG shows a specificity for biological motion.

In the study by Grossman et al. (2000), point-light walkers activated the pSTS region most strongly, whereas coherent motion[10] and motion-induced kinetic boundaries[11] (Malach et al., 1995; van Oostende et al., 1997) showed stronger activation in MT or the dorsal *kinetic occipital region* (KO), respectively. Stronger pSTS activation to biological motion than to coherent motion was also reported by Grezes et al. (2001). These findings suggest that motion areas KO and MT are activated by biological motion, but that they are not specific for it. Rather, it seems likely that activations in these motion areas provide some of the afferent signals innervating STS.

Grossman et al. (2001) showed that pSTS responded as twice as much to upright pictures of biological motion than to inverted biological motion. This result demonstrated that the real physical form of the human body, but not the global motion signals, elicited strong pSTS activations.

Another often observed finding is the dominant right-hemispheric pSTS/pSTG activation for point-light walkers (Bonda et al., 1996; Pelphrey et al., 2003; Puce et al., 1998; Grèzes et al., 1998; Grossman et al., 2000; Grossman and Blake, 2001; Grèzes et al., 2001; Peuskens et al., 2005; Beauchamp et al., 2003; Santi et al., 2003; Wheaton et al., 2004; Grossman et al., 2005). A possible reason for this asymmetric activation pattern could be the known right-hemispheric dominance for socially meaningful stimuli (Perry et al., 2001; Borod et al., 1997). As mentioned, the displayed action or posture in a point-light display can carry information, for example, about the emotional state. The correct interpretation of the action ensures that humans can interact with other individual in a socially adequate way.

[10]Coherent motion characterizes a motion pattern where the single elements (dots) move in the same direction

[11]Kinetic boundaries can be created by differences in direction or speed of motion on either side of the contour as well as by the juxtaposition of coherent and noncoherent motion

In an MEG study, Pavlova et al. (2004) investigated the oscillatory brain activity during biological motion perception. The authors demonstrated that only point-light biological motion elicited an evoked, stimulus onset-related, high-frequency response. In addition, only an upright walker lead to induced (later than the evoked response) responses over parietal and over right temporal lobes. Pavlova et al. concluded that this stimulus-specific time course and the topographic dynamics of oscillatory activity could reflect that the human brain "rapidly dissociates spatial coherence and meaning revealed through biological motion", because the authors did not observed any high-frequency response for scrambled displays. Their finding further indicate that the right temporal cortex is engaged in biological motion perception.

The role of the pSTS in biological motion perception is not fully understood yet, because it is activated not only when human movements are perceived, but also during the observation of mouth and eye movements (Puce et al., 1998). For example, Pelphrey et al. (2005) demonstrated that gaze directions of an observed computer-animated human elicited also strong right pSTS activations, especially when the character was displayed with a midline gaze, thus looking directly to the subjects. In addition it was shown that STS is sensitive to fear-full body expressions when compared to neutral body configurations (Grèzes et al., 2007). These results emphasize that part of the activation in pSTS is not only produced by sensory signals but also by affective signals.

The pSTS region has been also reported to form a possible linkage between visual and motor related actions (Buccino et al., 2001; Iacoboni et al., 2001). Iacoboni et al. demonstrated that parts of the pSTS region were activated by both, visual perception of hand movements and by the execution of same movements without visual feedback. As mentioned in section 1.2.1 observers can best recognize their own movements, which supports the hypothesis that observer's motor system contributes to the visual analysis of human movements. Hence, the importance of pSTS could be that it forms the junction of the cortical network engaged in the perception of biological motion.

However, most studies reported not only activations in the pSTS/STG but also in areas of the ventral pathway. Specifically, an area close to the cerebellum was activated by point-light walker, called the *fusiform gyrus* (Bonda et al., 1996; Vaina et al., 2001; Beauchamp et al., 2003; Peelen and Downing, 2005b; Grossman and Blake, 2004; Grossman and Blake, 2002; Pelphrey et al., 2005; Ptito et al., 2003; Santi et al., 2003). An illustration of fusiform gyrus activation for biological motion stimuli is shown in Fig. 1.3. Beauchamp et al. (2002) showed that static pictures of the

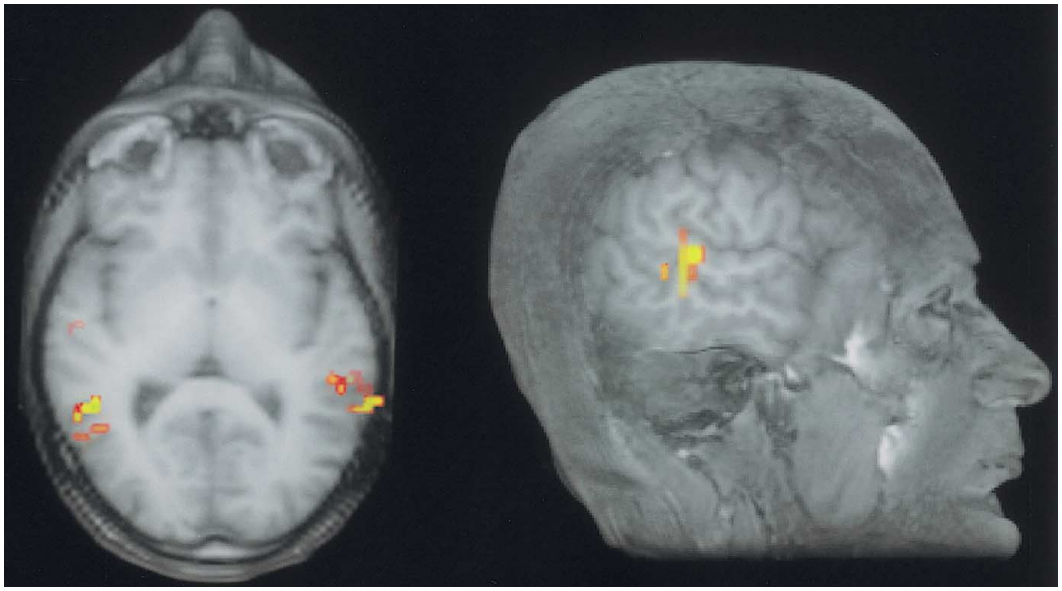

Fig. 1.2: **Illustration of activation in the posterior superior temporal sulcus for biological motion**. The activation of the pSTS (colored patches) is shown on an axial view (left panel) and on a sagittal view (right panel). Adapted from Grossman et al. (2001).

human body activate the pSTS and also the fusiform gyrus. In a follow-up study, the same authors demonstrated that the activation in the lateral fusiform gyrus was stronger for whole-body movements but also for point-light walkers than compared to tool motion, which activated more parts of the middle temporal gyrus (Beauchamp et al., 2003). Activation in the pSTS but not in the fusiform gyrus increased when motion was added. Earlier, it was found that the fusiform gyrus showed sensitivity to pictures of human faces (Kanwisher et al., 1997). The authors observed activations in the lateral and the posterior part of fusiform gyrus, termed the *fusiform face area* (FFA) and *occipital face area* (OFA), that were stronger to images of human faces than to non-human objects. Grossman et al. (2002) found similarly strong responses in the FFA and the OFA for point-light walkers and that these responses were stronger when compared to scrambled displays of point-light walkers[12].

In a similar vein to monkeys' STPa, it was recently reported that whole-body stimuli activated different parts of the fusiform gyrus compared to activation locations found for face stimuli (Peelen and Downing, 2005b; Peelen et al., 2006; Schwarzlose et al.,

[12]In scrambled displays, local motion is kept intact but the single dot-trajectories are randomly displaced within the restricted area of the display, entirely disrupting the shape of the figure. Hence, scrambled motion contains no configural information (but see 3.2.2)

2005). Peelen and Dowing found a lateral region activated by whole-body stimuli and termed this region the *body-selective region* (BSR).

Jokisch et al. (2005) reported in event-related potential (ERP)[13] experiments that upright point-light walkers but not scrambled motion elicited increased amplitudes in an early (180 ms after stimulus onset) and in a late (230 – 360 ms after stimulus onset) right temporo-parietal component. Source localization revealed that the earlier component was located in areas associated with attentional aspects of visual processing, probably reflecting a pop-out effect, whereas the sources for the late component were located in the right fusiform gyrus and also in the pSTS region, probably associated with the specific analysis of the form and motion patterns from the point-light walker.

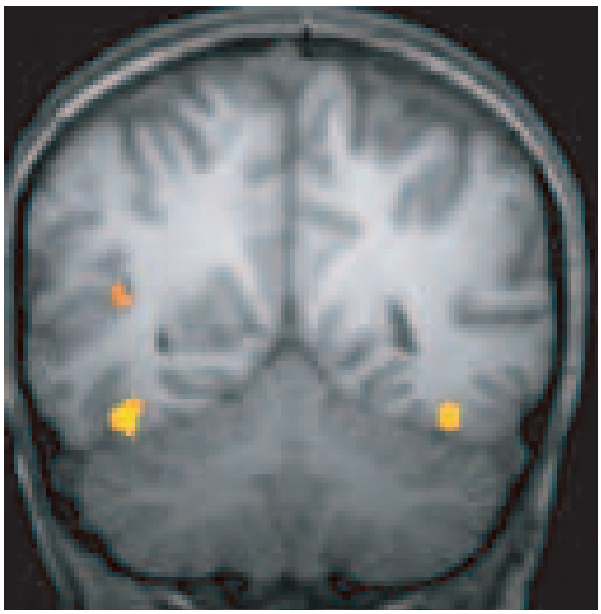

Fig. 1.3: **Illustration of activation in fusiform face area for biological motion**. The bilateral activation of the FFA activation is shown on an axial slice in one observer. Adapted from Grossman et al. (2004).

Peigneux et al. (2000) and Downing et al (2001) demonstrated that pictures of moving and static (the latter one was only investigated by Downing et al., 2001) whole-body stimuli activated not only pSTS or the fusiform gyrus, but additionally a region that is located posterior to MT. Downing et al. termed this region the *extrastriate body area* (EBA). Here, the authors showed EBA activations for point-light walker animations when compared to scrambled motion. Recently, Urgesi et al. (2004) demonstrated

[13]The ERP is the averaged response in the EEG signal.

that repetitive transcranial magnetic stimulation (rTMS)[14] of EBA interferes with the processing of static images of human bodies, i.e. suggesting an active contribution of the EBA in the processing of a human form. Nevertheless, the role of EBA in biological motion processing is not fully understood yet. For example, Grossman et al. (2002) reported EBA activation that was not different for point-light walkers and scrambled motion.

Activations outside the dorsal and the ventral visual pathway Bonda et al. (1996) and Ptito et al. (2003) reported activations in the amygdala as well as in the cerebellum for body and limb movements. Vaina et al. (2001) found activations in the cerebellum when observers had to judge whether the presence of stimulus depicts biological motion or not, but not when they had to discriminate the stimulus' direction. The authors concluded that cerebellar activation could reflect visual-spatial attention as a result of different task instructions rather than the result from perceptual information. Grossman et al. (2000) argued, on the other hand, that cerebellar activation is a result of the cerebellum's general involvement in motor preparation and in motion tasks.

Vaina et al. (2001) and Saygin et al. (2004b) reported also activation in the PPC and PMC for point-light walkers (see Fig. 1.4). For these regions, Buccino et al. (2001) revealed in an fMRI study that the observations of body part (mouth, hand, and foot) actions were represented in a somatotopic manner. Specifically, Buccino et al. found that mouth movements activated the vPMC and vPPC, whereas foot movements elicited more dPMC and dPPC activations. Santi et al. (2003) demonstrated that the observation of point-light speech activated, beside pSTS and the Broca's region, also the PMC . The authors found in addition activation in the inferior frontal gyrus (IFG) for point-light speech and for point-light walkers. A comparison of the IFG activation peaks found for hand actions from other studies (e.g. Decety et al., 1997) to the activation peaks for point-light walkers revealed a large overlap of the activations (Saygin et al., 2004). Taken together, the findings indicate that the human brain possesses a mirror-neuron system (for a review see Rizzolatti and Craighero (2004)).

However, the specific functional contribution of the human mirror-neuron system in the processing of bodily actions is still debated (Urgesi et al., 2004; Peelen and Downing, 2005a; Peelen et al., 2006; Urgesi et al., 2007a; Urgesi et al., 2007b; Gazzola et al., 2007). Urgesi et al. (2007) used rTMS to investigate the causative role of

[14]Technique producing a brief disruption of neural processing

the PMC and the EBA in the visual discrimination task of bodily forms (hand or leg) and actions. The authors found, that when the EBA region was disrupted by TMS, observers were unable to discriminate between the different body forms. When the PMC was disrupted, body actions could not be named anymore. This double dissociation indicates that the PMC is crucial for the visual discriminations of actions.

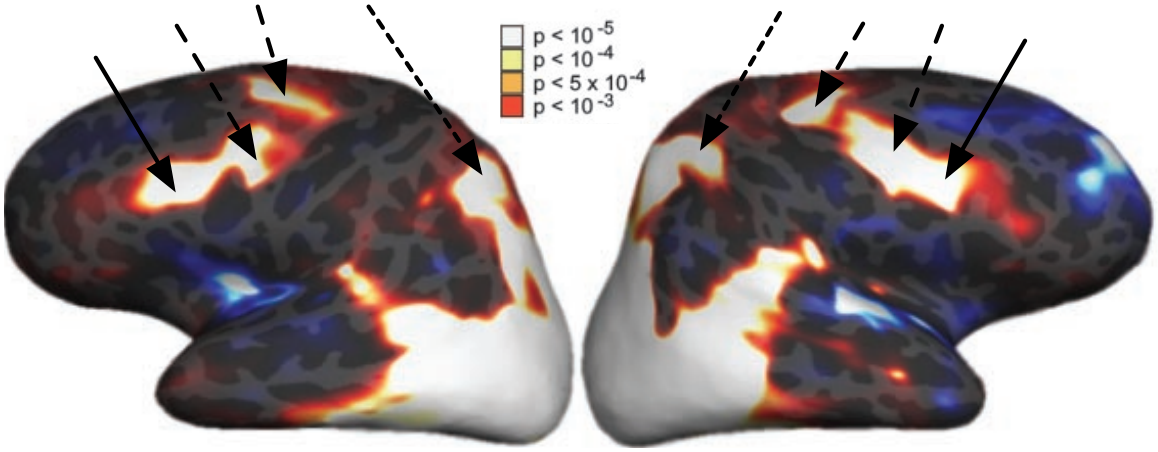

Fig. 1.4: **Illustration of activation in the mirror neuron system(IFG, vPMC, dPMC, PPC)**. Average group results displayed on the lateral views of the inflated cortical hemispheres of a single subject for biological motion versus baseline. The discrete swatches mark colors that correspond to specific p and t-values, respectively. The solid arrows indicate activation in the IFG. The dashed arrows indicate activation of the vPMC and the dPMC dorsal one. The fine-dashed arrows highlight PPC activation. Adapted from Saygin et al. (2004).

1.2.3 Lesion and clinical studies

Biological motion perception was also studied in patients, which had severe visual perception deficits, as a result from an ischemic stroke or a lesion of one or more brain regions. These studies investigated the role of motion and form information or the role of the motor system for biological motion perception.

Of particular importance for studying biological motion perception could be the examination in patients with apraxia (De Renzi and Lucchelli, 1988). Patients with apraxia, have great difficulties in copying and recognizing movements or gestures made by the experimenter. Apraxic patients with lesions that involve the PPC are impaired in discrimination and comprehension of visually presented gestures, whereas patients with lesions in the PMC did not have difficulties in these tasks, but where unable to plan the seen actions. Specifically, Battelli et al. (2003) found that three patients with

PPC lesions achieved normal performance in low-level motion tasks, but failed to see biological motion animations. The authors concluded that biological motion perception is not impaired as a result from the lesion in the PPC but is rather due to observers' inability to pay attention to the biological motion stimulus. This interpretation is consistent with the finding that the PPC is always activated in tasks that need higher attentional demands. The finding by Battelli et al. was corroborated by an earlier study, which reported that biological motion perception was not possible for patients with parietal cortex lesions when a point-light walker had to be segregated from a static or dynamic noise environment. Interestingly, these patients had no difficulties in perceiving point-light animations *per se* (Schenk and Zihl, 1997b).

Vaina et al. (1990) reported that a patient with a lesion in the dorsal occipito-parietal cortex, but sparing the temporal lobe, showed specific deficits in task on early low-level motion analysis, but possessed normal performance in the recognition of whole-body animations and also in other tasks to form perception. In this study, subject's lesion was anatomically close to MT, thus may indicate that this area is involved in the processing of low-level motion information but is not specifically engaged in the perception of biological motion.

Additional support for this idea was given by a study from McLeod et al. (1996). In this study, a patient (L.M.) could identify the motion direction of biological motion animations or other structure-from-motion displays, but was unable to report the direction of a random dot pattern. In an earlier study it was shown that L.M.s' lesion included motion area MT (Zihl et al., 1983).

It was also reported that patients with a lesion, including the STS region, were unable to perceive biological motion, but had normal object recognition rates (Vaina and Gross, 2004). Vaina and Gross suggested that subjects' inability to perceive biological motion resulted from the missing integration step of form and motion information, which takes place in the STS region.

Grossman et al. (2005) revealed that rTMS over the posterior temporal cortex disrupted biological motion perception, but that rTMS over the MT region had no effect on the perception process. These findings are probably the most direct evidence for the necessity of the pSTS/STG for biological motion perception.

Jokisch et al. (2005) examined the perceptual performance in cerebellar stroke patients. In contrast to deficits to discriminate the direction of coherent motion in noise, patients were able to detect point-light walkers in noise. They suggested that the

ventral pathway can compensate for the cerebellar deficits, and hence they concluded that this region is not necessary for biological motion perception. Rather, the cerebellar activations could be produced from areas, which are connected to the cerebellum such as the pSTS or the fusiform gyrus.

There are few clinical studies that demonstrated that the motor system contributes to the perception of biological motion. Saygin (2007) studied the relationship between damaged brain tissue and behavioral deficits in biological motion perception in 60 patients with an unilateral stroke. An anatomical analysis revealed that lesions in the pSTS/STG, but also in the PMC, had the greatest effect on biological motion perception that was a low recognition rate of point-light walkers. The authors suggested that the pSTS/STG and the PMC are not only involved in biological motion perception, but rather that they have a causal relationship to deficits in the perception of biological motion.

Pavlova et al. (2003) demonstrated a strong evidence for the linkage of action perception and production. In this study, biological motion perception was examined in teenaged adolescents, who varied in terms of their locomotion ability. The subjects ranged from normal to those with strong walking disabilities resulting from a lesion in the parieto-occipital region. The sensitivity to biological motion stimuli negatively correlated with the extent of the lesion but was not depended on the severity of motor disorder. The results indicate that the ability to plan a body movement is sufficient for the development of human motion perception, and that perception and production of an action arise from a common coding network that does not require fine motor executions for biological motion perception.

1.3 Objective of this thesis

Being able to recognize people form their actions or movements are important visual abilities. Brain imaging studies revealed a large neuronal network involved in biological motion perception. Biological motion activates visual areas, but also non-visual areas of the human mirror-neuron system. However, the role of these areas within this network is not fully understood yet. Whereas electrophysiological recordings allow the investigation of single areas, fMRI allows a large-scale view of the cerebral cortex in its entirety. Therefore, fMRI was used in this thesis to investigate the neuronal network of biological motion perception.

It is known that the perception and understanding of observed actions has a strong impact on human (behavioral) reactions relating to the depicted action. Understanding the contribution of specific features in biological motion helps to answer the question whether or not the brain uses a specialized mechanism for the perception of the human body. As outlined in section 1.2.1, several psychophysical studies investigated the contribution of motion and form signals for the perception of biological motion by using the Cutting walker. While some studies emphasized the role of motion information, others pronounced the importance of form signals. Beintema and Lappe (2002) developed the SFL walker and provided evidence for a major role of global form information in human movement perception. However, physiological support for this finding has yet to be proven.

In chapter 2, I will therefore examine whether BOLD responses are modulated by different types of point-light walker, i.e. the Cutting walker and the SFL walker, to answer the question of how motion and form information contribute to the perception of a human form.

In chapter 3, I will investigate differences in peripheral and foveal vision of biological motion. The sudden and unexpected appearance of another person rarely originates at the point of fixation. Instead, humans detect most objects and events within more peripheral regions of the visual field and shift attention to them for further scrutiny. As described in section 1.2.1, human observers can nevertheless detect peripherally presented point-light walkers as long as these were not embedded in an array of noise dots. It was also shown that body-like stimuli such as faces showed a contralateral preference in higher visual areas. This contradicts the idea that retinotopy is lost in higher visual areas. Hence, I will compare cortical representations of centrally and

peripherally presented point-light walkers, e.g. to see whether or not higher visual areas show a contralateral bias for the human body.

Once knowing the areas that are activated by centrally and peripherally presented biological motion, it would be then interesting to reveal whether or not brain responses are also specifically modulated by the depicted action of the stimulus. As described in section 1.2.2, humans possess a mirror-neuron system that responds to action execution and observation. By linking the actions of others to the observer's corresponding actions, the existence of the human mirror-neuron system suggests that our understanding of actions of others derives from translating them into the vocabulary of our own actions. Although inherently linked, body form and body action may be represented in separate neuronal substrates. As mentioned in 1.2.2, it was demonstrated that interference with the PMC impaired the ability to discriminate bodily actions, whereas interference with the EBA impaired the ability to recognize a human form.

Therefore, I will compare in chapter 4 brain responses to centrally and peripherally presented point-light walkers to see whether or not brain responses of form-processing areas (EBA, fusiform gyrus) or mirror-neuron areas (e.g. PMC) are modulated by different body views.

Finally, I will compare and discuss the results of the single chapters to psychophysical, physiological and modeling studies of biological motion perception.

1.4 General Methods

"The fluctuations of blood supply followed the state of mental activity almost immediately. We must suppose a very delicate adjustment whereby the circulation follows the needs of the cerebral activity. Blood very likely may rush to each region of the cortex according as it is most active, but of this we know nothing."

William James, The Principles of Psychology (1890)

1.4.1 Localizing brain activity

The idea of localization of function within the brain has only been accepted for the last century and a half. In 1810, Gall and Spurzheim were ostracized by the scientific community for their so-called 'science of phrenology' (Gall and Spurzheim, 1810). They suggested that there were twenty-seven separate organs in the brain, governing various moral, sexual and intellectual traits. The importance of each to the individual was determined by feeling bumps of their skulls. The science behind may have been flawed, but it first introduced the idea of functional localization within the brain which was developed later on by Jackson and Broca.

At this time, most of the information, suggesting a functional specification for a specific stimulus or cognitive task, came from subjects who suffered from various mental disorders, or sustained major head wounds. By examining the nature of the loss of function and the extent of brain damage, it was possible to infer which regions of the brain were responsible for which function.

Patients with severe neurological disorders were sometimes treated by removing regions of their brain. For example, an effective treatment for a form of epilepsy involved severing the corpus callosum, the bundle of nerve fibres which connect the left and the right brain hemispheres. After the surgery patients were tested, using images presented either to the left or to the right visual hemifield. Only if the images were presented to the right visual field, therefore stimulating the contralateral left brain hemisphere, subjects could say what they saw. However, if the same object was shown in the left visual field, then subjects were unable to say what they saw, but they could select an object that was associated with the image. At the time, this lead researchers to suggest that only the left hemisphere is necessary to initiate speech.

Non-invasise investigations of human brain structures could be first achieved with the appearance of computerized tomography (CT) imaging in 1968 and with structural magnetic resonance imaging (MRI) in 1977. With these techniques it was possible to visualize precisely brain structures and brain damages, and thus, to judge the influence of lesions or dissections to the function of specific brain regions. Basically, MRI allows to visualize the different anatomical brain structures, such as the grey matter (the somas of the neurons), the white matter (the axons of the neurons), and the cerebrospinal fluid (CSF), but also to visualize non-brain structures such as bones or cartilage.

It was the advent of functional magnetic imaging methods of PET and fMRI in the mid 80's and early 90's of the last century (Ogawa et al., 1992; Kwong et al., 1992) that allows measurement of activation changes within the brain. Specifically, only fMRI allows the measurement of brain responses to external signals in a non-invasive at a high spatial resolution of about 1 mm^3 and a temporal resolution ranging from few hundred milliseconds up to 1 s.

I will split the method section into four parts. In the first two parts, I will give a brief overview of the physical and physiological principles of MRI and fMRI. I will then explain the general procedure used for the experiment in this thesis. Here I describe the biological motion stimulus, behavioral and functional paradigms, scanning procedure and acquisition parameters. Finally, I will explain the steps required for processing the (f)MRI data.

1.4.2 Magnetic resonance imaging (MRI)

During the scanning procedure, subjects were first exposed to a strong magnetic field. Then a radio frequency (RF) pulse was transmitted to subjects' brain tissue via a head coil[15] , which is attached close to the subjects' head. The RF pulse lead to an excitation process of the brain's tissue. After the radio wave transmitter was turned off a relaxation process started. During the relaxation process, the emitted MR signals for the different brain tissues were recorded via the head coil and could be then visualized as high-resolution structural images of the brain.

I will now briefly describe the physical processes that occur during magnetic field application, excitation, and relaxation process, and MR image visualization.

Biological structures like the human brain compose of molecules that consist of atoms, which are in turn assemblies of neutrons (no charge), protons (positively charged)

[15]A head coil was used, because only MR images of the brain were recorded.

and electrons (negatively charged). For each of these atomic structures, charge and spin are quantized, meaning that they can only possess a positive or a negative charge form. In an externally applied magnetic field, spin orientation also causes a coupling of energy levels. This magnetic-spin coupling is very weak. As a consequence, the preference toward spin orientation persists within a biological sample, but not as a dominant energetic factor. Although most spins pair off in the same way as charge, an unpaired spin is ultimately required in order to magnetically separate either electronic or nuclear populations. Only atoms with an unequal atomic number, such as hydrogen, are suitable for MRI. It is also possible to investigate the brain with MRI, because two-thirds of the brain consists of water. Water consists of two hydrogen atoms and one oxygen atom. The protons possess a nuclear spin (rotation around its own axis) with a rotating mass (m) with an angular momentum M. This spin movement induces a magnetic moment (B). B is influenced by a strong external magnetic field (B_0) and a short electromagnetic wave (RF pulse).

Without B_0, the spins are randomly oriented, but when B_0 is applied, the spins tend to align parallel because it is the energized favorable state. This results in an observable bulk magnetization parallel to B_0 that is the Z-dimension. Hence, the sum of the single angular momentums of each proton get a finite value termed M_z or longitudinal magnetization. In this state the spins rotate with a characteristic frequency ω, called the *Larmor frequency*. When the spins are aligned to M_z, they form a stable system (thermal equilibrium). However, when a short RF pulse with a frequency equal to ω is applied to M_z, this stable system is disturbed and M_z is reduced. After this pulse, the spins do not move any longer in the Z-dimension but rather in the XY-dimension. This tilting process is termed the *excitation process* and induces a magnetization in the XY-dimension termed transverse magnetization or M_{xy}.

However, as soon the spins are turned into the XY-dimension and the RF pulse is switched off, a *relaxation process* takes place with includes two-parallel ongoing processes. First, an exponential recovery of M_z as a result of the strong magnetic field B_0. This means that the spins start to spin at slightly different rates (unequal to ω), each according to the local value of B_0. This process is known as longitudinal relaxation or T1-relaxation. The loss of phase coherence (dephasing) produces a decay of M_{xy}. Therefore, this second process is termed transversal relaxation or T2-relaxation. A sketch of the underlying physical processes of MRI is shown in Fig. 1.5.

During the relaxation process, the different brain tissues emit small voltage changes

(= raw MR signal) that can be detected via the head coil system. When the orientation of the spins' population is randomized, the net vector sum in the transverse plan is zero and no MR signal can be detected any longer. In MRI, so-called gradient coil systems are used, which amplify the received MR signal and encode its spatial position (= MR signal reconstruction).

However, the different tissues of the brain and of the surrounding tissue, possess different relaxation times due to their dissimilar proportion of water. After MR signal reconstruction and several preprocessing steps (see 1.4.4), the MR signals of the different tissues can be visualized in form of different intensity values on MR images covering the whole brain. In the present thesis, T1-weighted MR images were acquired, so that the different tissues are depicted as following: Grey matter appears dark (low intensity values), white matter light (high-intensity values), and CSF black. Bones containing no water are appearing white. An example of a T1-weighted image is shown in Fig. 1.10 A.

The image quality of the MR images does not only depend on the physical and physiological properties of the scanned tissues, but also on the specific scanning parameters. Due to the experimental design presented in chapters 2-4, I used, for example, different *time of repetitions* (TRs), that is the time between two consecutive RF pulses and a different *time of echoplanar* (TE), that is the time period between RF pulse application and the measurement of the MR signal. The specific imaging parameters will be described in the single chapters.

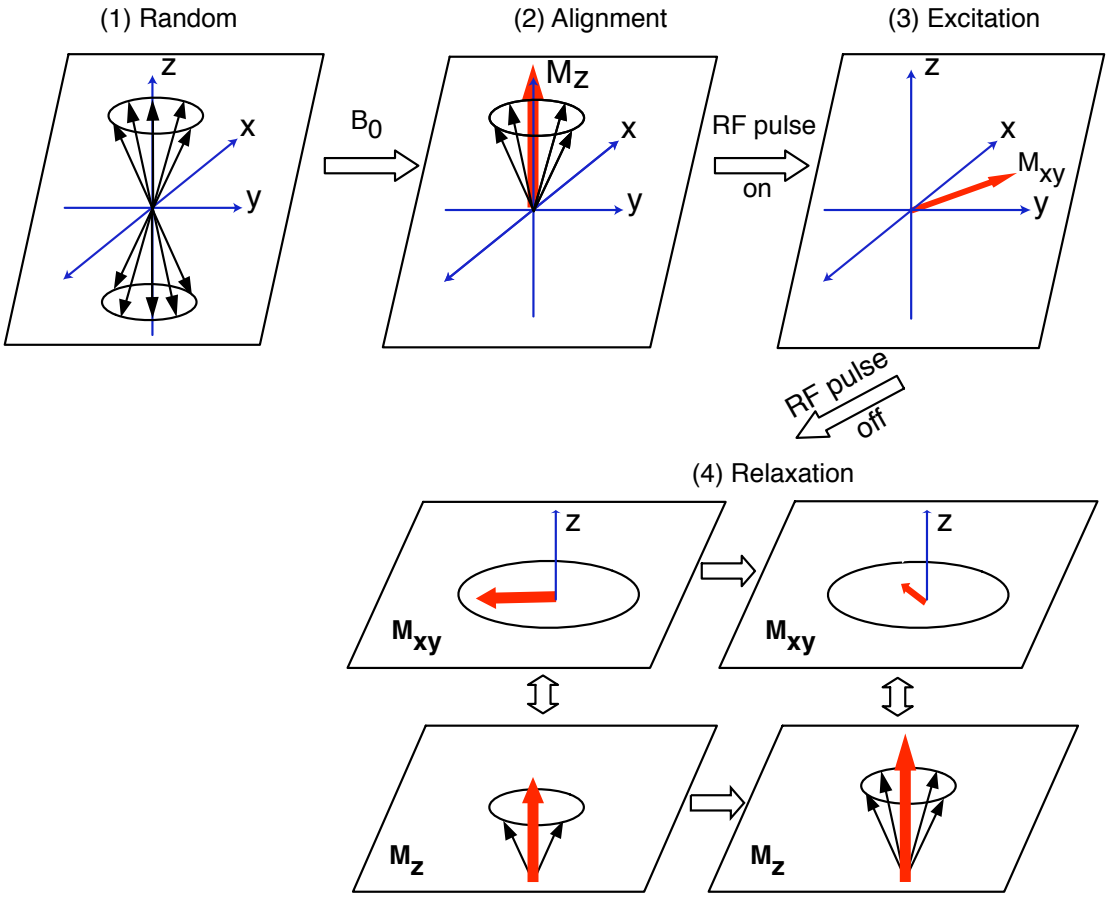

Fig. 1.5: **Illustration of the physical principle of MRI.** Without a strong magnetic field (B_0), the spins of the scanned tissue precess randomly in the Z-dimension (1). When B_0 is applied, the spins tend to align parallel to B_0, because it is the energized favorable state (2). Hence, there is a net magnetization in the Z-dimension (longitudinal magnetization, M_z). After the alignment process, a RF pulse is applied perpendicular to B_0 via a coil system. This process is called excitation (3). The magnetization is now maximal in the XY-dimension (transversal magnetization, M_{xy}). At this state, the spins precess only in the XY-dimensions. When the RF pulse is switched off, a relaxation process starts, which includes two parallel-ongoing processes (4). First, a recovery of M_z (longitudinal relaxation, lower panels) and a decrease of M_{xy} (transversal relaxation, upper panels).

1.4.3 Functional magnetic resonance imaging (fMRI)

As described in the previous section, the strength of the MRI signal does depend on the concentration of water in the particular scanned tissue. In contrast to MRI, the signals measured by fMRI do depend on the level of oxygen in the blood.

The BOLD signal As correctly suggested by the British psychologist William James 'blood very likely may rush to each region of the cortex according as it is most active'. But what are the physiological processes that take place during the activation of a brain region? The vasculature delivers more oxygen and glucose to energy demanding cells within an activated area than to a non-activated area. Metabolically, there is a relation between the cerebral blood flow (CBF), oxygen, and glucose, which is also known as hemodynamics. An increase in the glucose consumption results in a delayed increase of the CBF of oxygenated blood in the activated region. Hence, the net result is that active cortical regions have a higher blood oxygen level than inactive regions (Fox and Raichle, 1986). The outcome of such physiological changes can be measured by the *Blood Oxygenation Level Dependency (BOLD) signal*.

Since oxygen is not very soluble in water, the blood contains a protein that oxygen can bind to, called hemoglobin. When an oxygen molecule binds to hemoglobin, it is said to be oxyhemoglobin, and when no oxygen is bound, it is called deoxyhemoglobin. Deoxyhemoglobin is a paramagnetic molecule whereas oxyhemoglobin is diamagnetic. The presence of deoxyhemoglobin causes a magnetic susceptibility artifact around the cerebral micro-vessels (= field gradient), the venules and the capillary bed (Fig. 1.6 A, left panel), because deoxyhemoglobin induces a small magnetic field. This is generally reflected by a small signal. In contrast, during neuronal activity the CFB increases, which results in a high concentration of oxyhemoglobin (Fig. 1.6 A, right panel) in the veins near the activated area. In the activated state, the oxygen-enriched blood possesses a magnetic susceptibility that closely matches the tissue magnetic susceptibility, resulting in a high signal intensity (= lower field gradient). This is based on the fact that oxyhemoglobin is diamagnetic and does not produce the same dephasing of the signal than deoxygenated blood. The change of the oxygenation level is termed BOLD signal change. The BOLD signal can be either positive or negative, depending upon the direction of change in CBF and oxygen consumption. For example, increases in CBF that outstrip changes in oxygen consumption will lead to an increased BOLD signal. For the functional MR images, T2*-weighted images were acquired in this

thesis, because the changes in the local magnetic fields – induced by changes in the oxyhemoglobin concentration – change the T2* relaxation time.

The time course of the BOLD signal can be divided in five phases (Fig. 1.6 B). First, there is an initial dip of the hemodynamic response after the stimulus presentation which lasts for 2 s (hypo-oxic phase)[16]. This possibly reflects a transient imbalance in the metabolic activity, that means a transient increase in oxygen consumption before any change in the CBF (Menon et al., 1995). Therefore, the amplitude of the BOLD signal is negative. This initial dip starts with a short delay after the onset of the stimulus, because of the delayed CBF and thus blood oxygenation. The second phase of the hemodynamic response (hyperoxic phase) is the rise of the BOLD signal as a result of the vasodilatation of the arterioles and the increase of the CBF. This increase results in a short overshoot (peak), about 5-6 s after stimulus onset, which reflects an over-compensatory response that is more pronounced in the BOLD signal than in the CBF. The overshoot phase is followed by a sustained response that is a saturation phase which lasts until 10 s after stimulus onset. The fifth phase is a decay of the BOLD signal at about 16 s after stimulus onset, paralleled by a slight undershoot of the BOLD signal. The undershoot can be interpreted as a parallel-occurring increase in the CBF and a decrease of the oxygenation level. This leads additionally to local changes in the relative concentration of oxyhemoglobin and deoxyhemoglobin, and to changes in local cerebral blood volume.

[16]The duration of the initial dip does depend on the duration of stimulus presentation

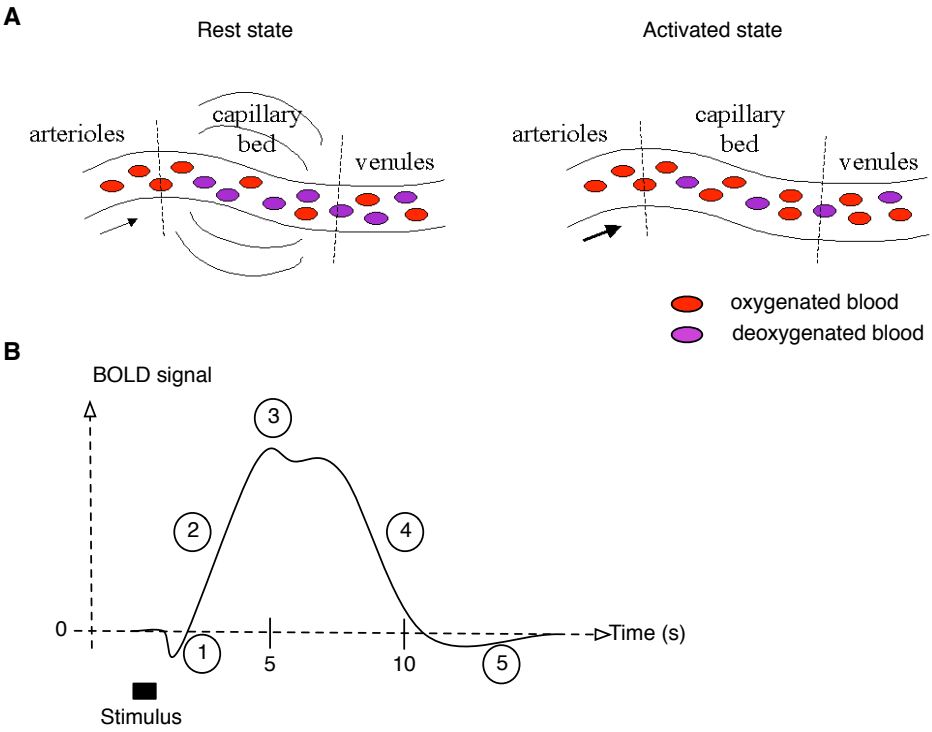

Fig. 1.6: **Illustration of the physiological processes and time course of the BOLD signal. A** Illustration of the physiological process during rest state (left panel) and during an activated state (right panel). In the 'rest state', the CBF concentration of deoxygenated blood (deoxyhemoglobin, filled purple circles) is higher in the venules and the local capillaries than the concentration of oxygenated blood (oxyhemoglobin, filled red circles). The presence of deoxyhemoglobin in a blood vessel causes a susceptibility artifact (indicated by the black curves). In the activated state, the CBF increases (indicated by the larger diameter of the blood vessel) which results in an increase of the oxygenated blood in the venules and the capillary bed. The decrease of deoxygenated blood results in a lower susceptibility. The proportion of oxy- and deoxygenated blood is indicated by the blood oxygenation level dependency (BOLD) signal. **B** Illustration of the time course of the BOLD signal. The BOLD signal can be separated in five phases. (1) the initial dip phase that starts slightly after stimulus presentation, (2) the rise phase, (3) the peak phase, (4) the sustained response phase, and (5) the undershoot phase. The length of the BOLD signal is about 16 s.

1.4.4 General experimental procedure

Subjects Data was recorded from sixteen male subjects (age 19-35 years): Four subjects participated in the experiments of chapter 2 and twelve subjects participated in the experiments of chapters 3 and 4. All subjects gave written informed consent to the study that was approved by an ethics committee. Subjects were paid for their participation in the experiments. None of the subjects showed any neurological disorder. It was ensured that subjects did not carry any metallic materials or tattoos to prevent magnetic field inhomogeneities. If necessary, subjects wore non-magnetic glasses to

correct to normal vision. None of the subjects were informed about the purpose of the study (except the authors). Some of the subjects had never seen point-light walkers before. These subjects participated in a short training session until they were familiar with the stimulus and the task.

Stimuli For the programming and the presentation of the point-light walker, the program *Project Builder* (Apple Computers) was used running on a *Power Mac G4*. Stimuli were displayed outside the scanner on a standard 21-inch monitor (Iiyama VisionMaster 505) with a screen resolution of 1280 x 1024 pixels and a visual field of 30 cm x 40 cm. Depending on the specific monitor that was used during scanning, the vertical refresh rate was either 60 Hz (chapter 2) or 100 Hz (chapters 3 and 4), resulting in different frame durations. The width and height of the stimuli varied from experiment to experiment and will be explained in the specific chapters. If not stated otherwise, the stimulus consisted of white dots (dot size depended on the stimulus size) on a black background and was presented in a frame-by-frame video animation. The stimuli depicted human walking viewed from the side so that the stimulus was facing either to the left or to the right. The point-light walker did not contain any translational, but only oscillatory elliptic motion, giving the impression of walking on a treadmill (walking in place). The starting phase in the step cycle was randomized from trial to trial to avoid spatial cues from familiar positions. The stimuli were presented in a randomized order within an experiment.

Two different types of point-light walkers were used in this thesis. For one stimulus a computer algorithm, adapted from Cutting (1978), was used that mimicked the movements of the walker (Cutting walker). In the Cutting walker, small white dots were presented frame by frame on locations of the major joints (the shoulders, elbows, wrist, hips, knees and ankles). This results in smooth motion trajectories of the single dots as soon as the animation is presented in motion. Structural information about the momentary posture of the human body is provided in this stimulus by the instantaneous position signals of all light points. An example of the walker is shown in 1.7 A.

The other point-light walker was a variant of the Cutting walker. In this stimulus, single dots were not located on the major joints, but were rather located after a single frame to a random position on the limbs connecting the major joints (Beintema and Lappe, 2002). Thus, the dots still provide positional signals, but do not provide any valid local motion signals (Fig. 1.7 B). This stimulus was termed the

single-frame lifetime walker (SFL walker). For the experiments of chapter 2, the stimuli were computer-generated. For the experiments of chapters 3 and 4, walking was recorded from humans with a motion-capture technology so that the walking patterns could be transformed into computer-animated point-light walkers.

Additionally, I used in each experiment different types of scrambled stimuli. Common for all scrambled stimuli was that they contained the same low-level motion cues than the point-light walker, but did not depict human walking. For example, in chapters 3 and 4 the scrambled stimuli were created by randomly shuffling the light points in space, thereby destroying the spatial structure of the body but retaining the height, width, symmetry, rhythm and the local motions of the body (Fig. 1.7 C).

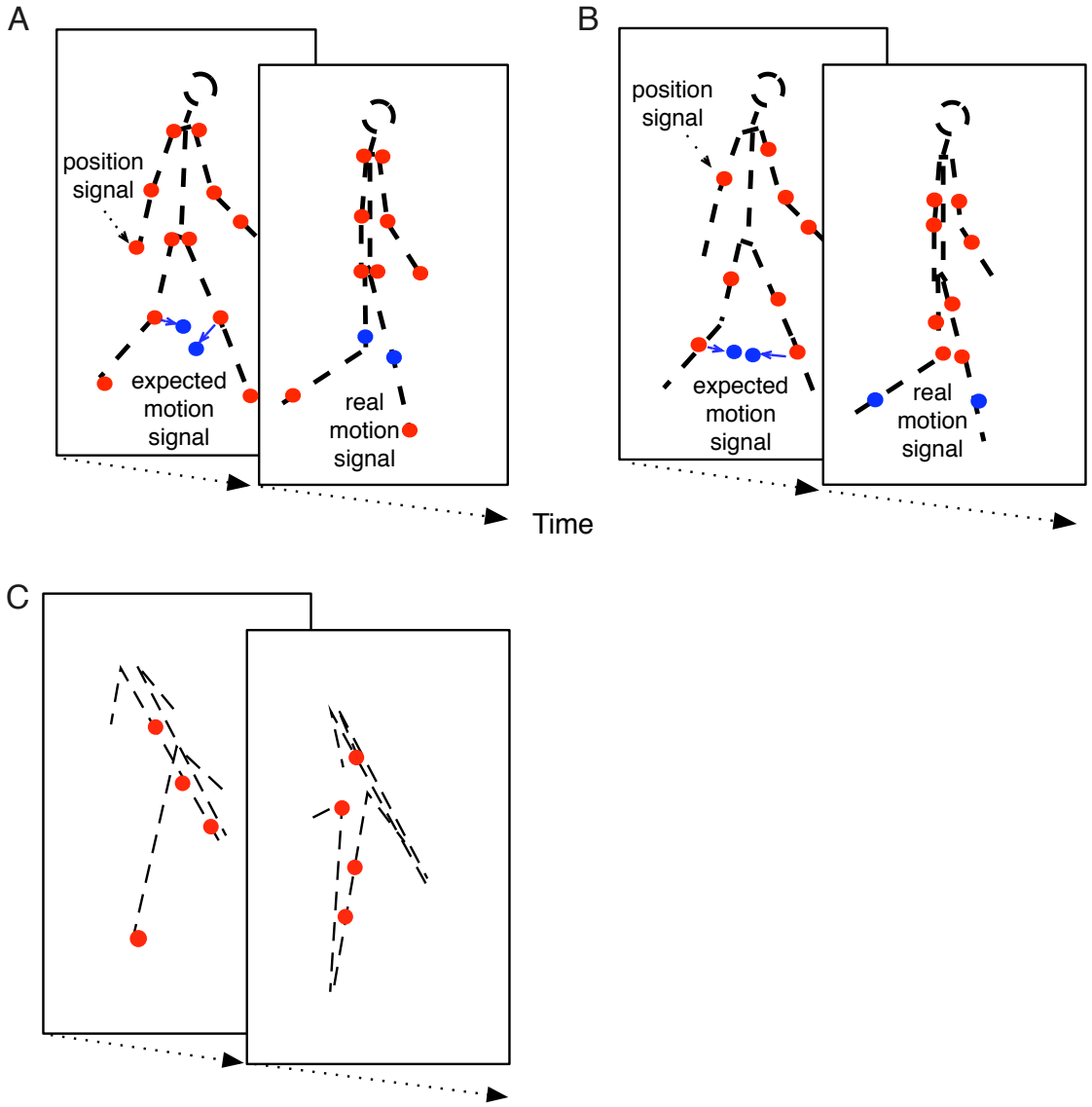

Fig. 1.7: **Illustration of the stimuli that were used in this thesis**. **A** Two consecutive frames of a waking cycle of the Cutting walker. In this stimulus, the dots are located on the major joints (the shoulders, elbows, wrist, hips, knees and ankles) in each frame of the animation. The dashed lines connecting the joints locations were not showed during stimulus presentation. As indicated by the blue dots, the expected local motion signals, shown in frame one, do match the real local motion signals in frame two. Thus, the dots provided valid local motion signals. The instantaneous position signals of all light points at any time provided structural information about the momentary posture of the human body. **B** Two consecutive frames of a waking cycle of the single-frame lifetime walker (SFL walker). In each frame of the walking cycle, dots are not presented at fixed 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. As indicated by the blue dots, the expected motion signals, shown in frame one, do not match the real motion signals in frame two. Hence, the dots of the SFL walker do not provide any valid local motion information, but still provided structural information about the momentary posture of the human body. **C** Two consecutive frames of the scrambled stimulus that was used in chapters 3 and 4. Here, 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. The light points were randomly placed, frame-by-frame, along the invisible lines connecting the joint positions.

Behavioral paradigms In addition to the recording of the brain imaging data, I also recorded subjects' behavioral responses during the different experimental tasks. This was important, because it has been demonstrated in fMRI studies that there is a link between the recognition rates and the activated brain regions (Grossman and Blake, 2004; Grill-Spector et al., 2004). For example, Grill-Spector et al. (2004) showed that the BOLD responses were higher when subjects detected and correctly identified stimuli compared to undetected stimuli. In the experimental conditions of this thesis subjects either had to respond to blocks of trials containing point-light walkers (detection task, chapter 2) or they had to report the stimulus facing direction (discrimination task, chapters 3 and 4) via key pressing on a non-magnetic response button box. During a so-called baseline condition, subjects had either to report the luminance direction of an array of dots (chapter 2), or they had to fixate on a cross in the center of the screen (chapters 3 and 4).

fMRI paradigms In this thesis, I used two different fMRI paradigms to record the functional MRI data. In fMRI, a distinction is made between the *block design* and the *event-related design*. In the experiments of chapter 2 of this thesis I used a block design. Here, the trials of the specific stimulus type (Cutting walker, SFL walker) were presented within so-called on-blocks (Fig. 1.8 A). The single trials were only separated by an inter-stimulus interval (ISI). This resulted in one (averaged) BOLD signal, because the length of the BOLD signal to a specific stimulus is about 16 s, and hence, will be not separable anymore if the ISI was shorter than 16 s (which was the case in this experiment). Within each block not only biological motion stimuli were presented, but also scrambled motion. These trials were included for two reasons. First, scrambled motion was included to prevent subjects from drowsiness as a result from trial repetition. Secondly, to prevent from BOLD adaptation effects (Grill-Spector and Malach, 2001)[17]. Although this means that the activity of an on-block reflected averaged activity from biological motion stimuli and scrambled motion, it has been shown in many studies that the BOLD responses to scrambled motion were statistically

[17]The adaptation paradigm is used to study neural sensitivity to feature differences that mediate discrimination between stimuli, as neurons responding to these features are intermingled within each voxel (see paragraph Image acquisition), and thus, could not be measured at the standard fMRI resolution. This means, that repetition of the same stimulus results in reduced BOLD responses as long as no different stimulus will be presented

lower compared to biological motion stimuli (Bonda et al., 1996; Grossman et al., 2000; Grossman and Blake, 2002; Grossman and Blake, 2004; Saygin et al., 2004; Peelen et al., 2006).

Each on-block was separated by so-called off-blocks, which served as the baseline condition. As for the on-block, the off-blocks lasted for about 16 s to ensure that the first trials of the follow-up on-block were not contaminated by the BOLD signal from the preceding on-block.

In chapters 3 and 4, I was interested in BOLD responses to the same type of biological motion stimulus that differs only in two particular features: the presentation location and the facing direction. Therefore, I used the event-related design (Fig. 1.8 B). In this design, each stimulus (= event) was separated by an off-block with lasted for about 16 s. This ensures that the BOLD responses were attributable to single events, and do not represent averaged activity over trials.

The temporal order of the onset and offset on a block or single event was stored as number of scans in a text file (protocol file, upper panels in Fig. 1.8). In the brain imaging software, the protocol file was linked to the anatomical images of the brain, so that BOLD signal changes of a block or event could be attributed to brain regions.

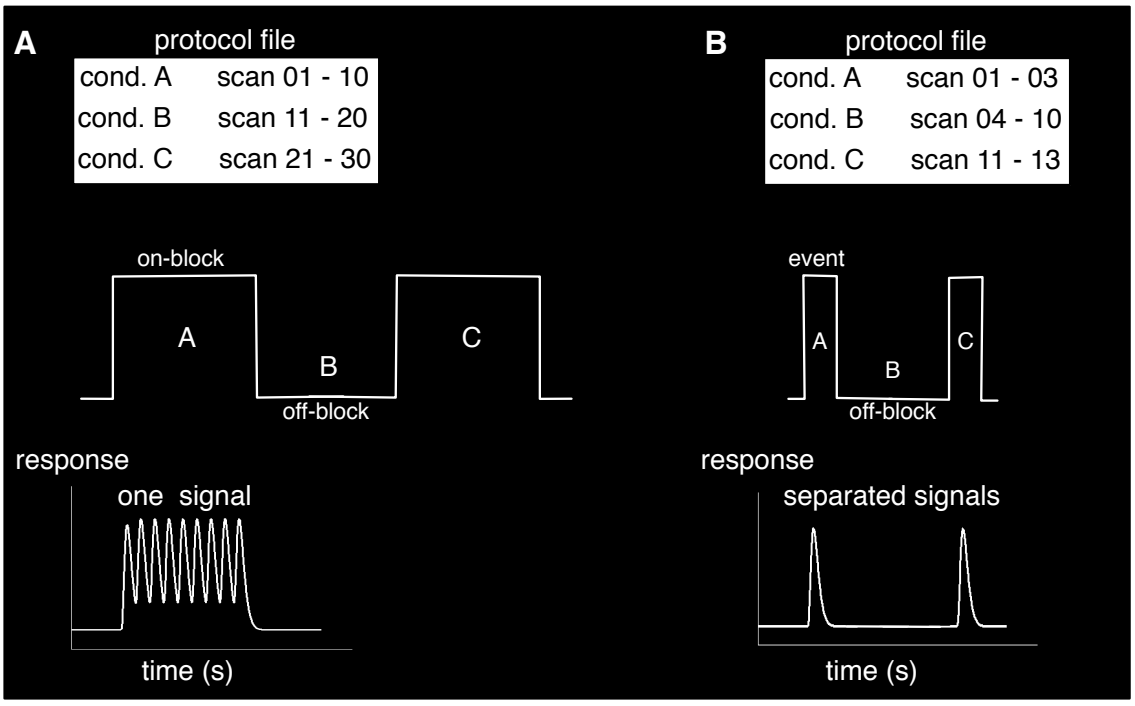

Fig. 1.8: **Illustration of the two fMRI design types used in this thesis.** To define the particular design design, the precise timing of the onset or offset stimuli has to be defined. The timing was stored in number of scans in a protocol file (upper panels in A and B). **A** In the block design, alternating on-blocks (A, C) and off-blocks (B) were presented, whereby each on-block contains more than a single trial/event. In the on-block, the condition of interest was presented, whereas the off-block served as baseline condition. Due to the slow nature of the BOLD signal (about 16 s) and the short inter-stumulus interval (<16 s), activity within the on-block reflected averaged activity over all trials (lower panel). The duration of the off-block was about 16 s, to ensure that the follow-up on-block was not contaminated by BOLD signals from trials of the preceding on-block. **B** In the event-related single trials/events (A, C) were separated by an off-blocks (B). As for the block design, each off-block lasted for about 16 s. The event-related design ensures that the BOLD responses could be attributed to single trials/events, and thus do not represent averaged activity.

Scanning procedure Within the scanner tube the subjects lay in a supine position. A head clamp, attached to the head coil, restricted head movements. Via a mirror, which was attached to the head coil, subjects could watch the visual stimuli inside the scanner tube. After the mirror system was attached, subjects were placed inside the scanner tube and waited for further instructions via headphones, that were also used to minimize the strong scanner noise. Outside the scanner room, first a reference scan was acquired to detect the subject's head position. Next the scanning parameters were specified, for example, the field of view (FOV, determines the scanning area), the number of slices to be acquired, or the spatial resolution of the (functional) MR images.

The visual stimuli presented during the scanning session were generated on a stimulus PC that was located outside the magnetic shielded room (stimulus PC). At the same time of stimulus generation, stimuli were presented via a projector onto a translucent screen and then to the mirror. Before scanning was initiated, the task was explained to the subjects and they were instructed not to move during the whole scanning session. Additionally, subjects were told to focus on correct behavioral responses rather than to respond as fast as possible. Subjects used a non-magnetic response button box to report their responses. Another PC outside the scanner room was connected to the stimulus PC, and was used to store subjects' behavioral responses (control PC). This PC also stored the time points of the stimulus generation, so that it was possible to control offline whether the time points for stimulus generation and occurrence on the mirror matched (but see chapter 3). An illustration of the MR scanner and environment is shown in Fig. 1.9.

Image acquisition In this thesis a 1.5 T (Tesla) GE Horizon EchoSpeed (GE Medical Systems, Milwaukee, Wisconsin, USA) or Siemens Magnetom Vision (Erlangen, Germany) scanner were used for collecting the structural and functional MR images. Echo-planar imaging (EPI) with a RF head coil was used for (functional) MR signal transmission and reception. A gradient coil system was used to amplify the received signal and to encode its spatial position on each single acquired image. A conventional volume was acquired by using contiguous oblique slices oriented parallel to the anterior-posterior commissure (AC-PC) plane to cover the whole brain. Next, a high-resolution T1-weighted structural scan was acquired during the same scanning session for each participant (spatial resolution: $1 \times 1 \times 1.5$ mm^3).

To collect the functional MR images, different EPI parameters for the TR, TE and the FOV were used. The values of the specific parameters are described in the chapters 2-4. The spatial resolution of a structural and functional image was defined by the *voxel* size. In contrast to a 2-D pixel (= smallest presentable unit of an 2-D image), that contains only spatial information in the x- and y-dimension, the voxel is a cubic (3-D) structure that possesses in addition a z-dimension (Fig. 1.10). The z-dimension gives information about the depth of an anatomical region of the brain with respect to the AC-PC plane. To report BOLD changes in the brain, it was necessary to acquire the functional MR images as fast as possible. To do so, less images were recorded compared to the number of recorded structural images. This however results in a lower spatial resolution of the functional MR images. In the experiments of this thesis, the voxel resolution was about $3 \times 3 \times 4$ mm^3 (see chapters 2-4). An illustration of structural and functional MR images are shown in Fig. 1.10.

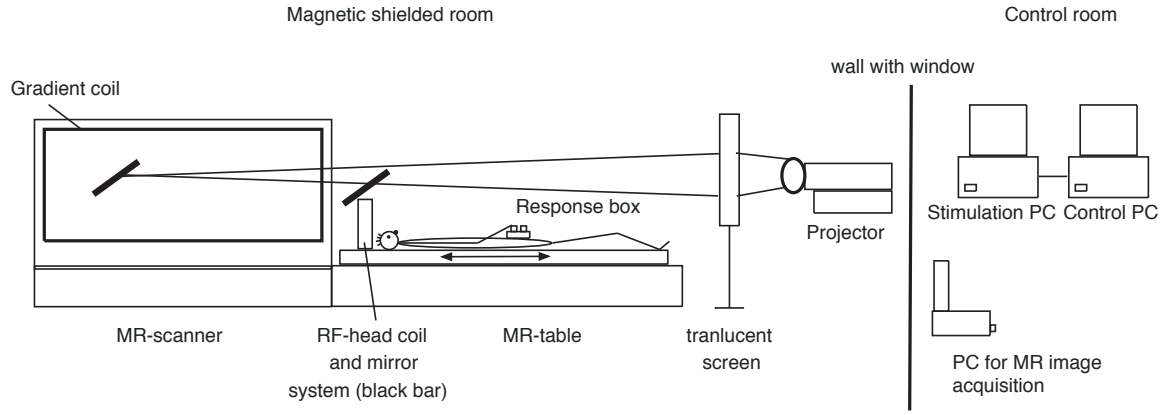

Fig. 1.9: **Schematic drawing of the scanner and environment.** Inside the magnetic shielded room, the subjects were positioned supine on a movable table (indicated by the black arrow), so that they could be placed inside the scanner tube. Subjects were lying on the table so that the position of the head was close to the head coil system for RF pulse transmission and signal reception. On the unit with the head coil system, a mirror system (black bar) was attached, directly in front of the subjects eyes. The mirror could be tilted so that the subjects could see the visual stimuli. The final position of the mirror inside scanner tube is indicated by the black tilted bar. Subjects gave the behavioral responses via key-press on a non-magnetic response box that was connected to the control PC outside the magnetic shielded room. The stimuli were generated on a stimulation PC, which was connected to a projector and to the control PC. The control stored the time points of the stimulus generation. The stimuli were projected from the projector to a translucent screen and then to the mirror inside the scanner tube. A further PC was used for the setting the specific scanning parameters. A gradient coil system was used to amplify the received (functional) MR signal and to encode its spatial position.

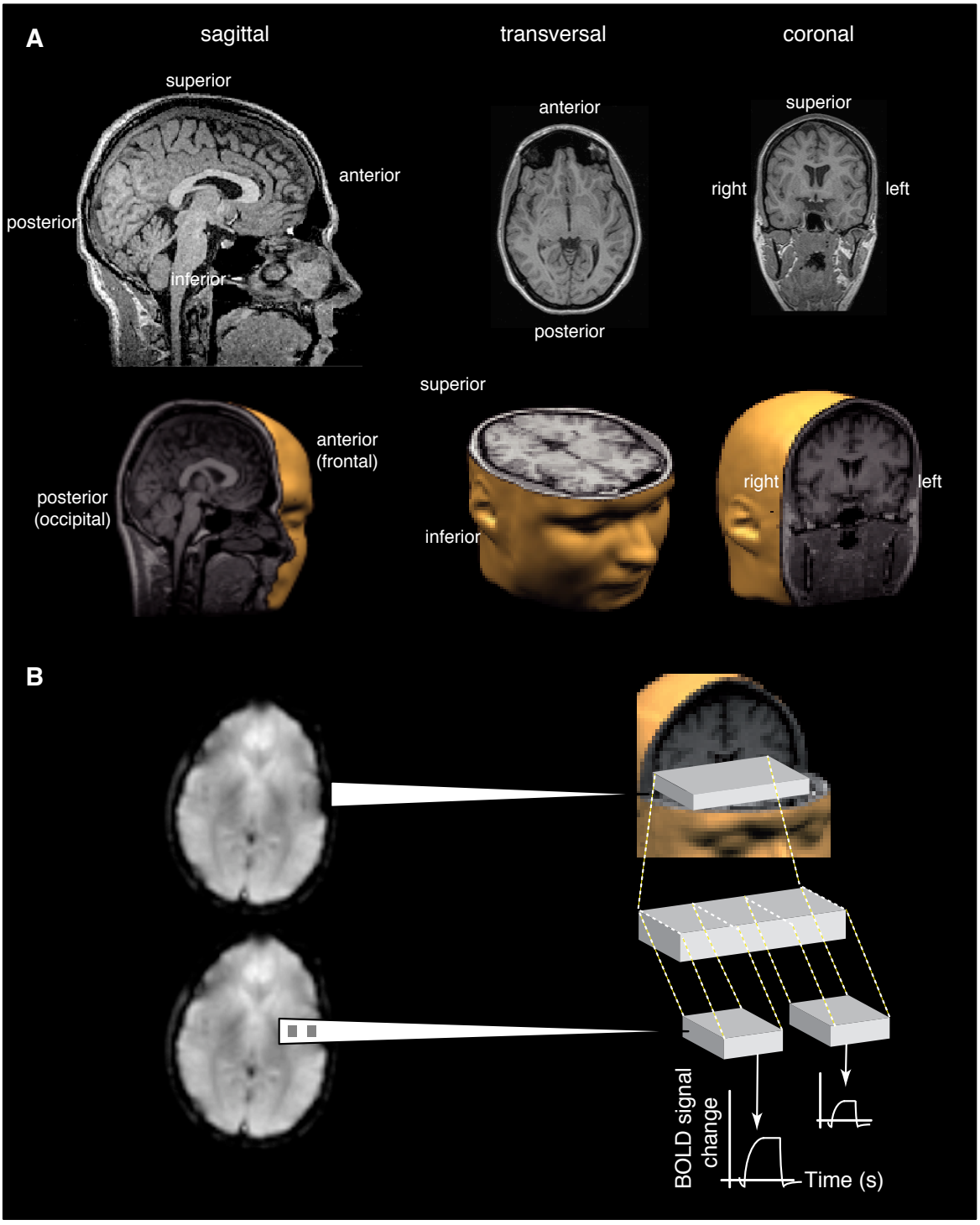

Fig. 1.10: **Illustration of structural and functional MR images**. **A**: High-resolution structural MR images of the brain shown in different section planes. Left panels: sagittal section, middle panels: transversal section, and right panels: coronal section. Please note that right and left are given in neuroradiological conventions. **B**: Low-resolution 2-D functional MR images (left panels). The single functional MR images were aligned to the structural MR images, as schematically shown in the upper right panels (functional MR image is shown as the grey 3-D object). The functional MR images are subdivided into small sub-units, termed voxel, as shown in the lower part of the left panel in a 2-D view and in the right panel as a 3-D view. For each voxel, BOLD signal changes were calculated.

1.4.5 Data analysis

Data preprocessing After the structural and functional MR images were recorded and reconstructed, they were processed with a particular brain imaging software (see chapter 2-4). First, functional MR images were motion corrected. Although the subjects were instructed not to move the head (and body) during the scanning session, small movements still occurred. Therefore, an additional realignment of the MR images was necessary, first, because motion artifacts could lead to false-positive activations, and secondly, to ensure that the relative position of the MR images was constant throughout the scanning procedure. For the motion-correction, a specific algorithm was used to correct for head movements in the six possible degrees of freedom, that are three translational and three rotational.

Then, temporal smoothing was applied to the functional data that included two steps. First, slow[18] linear signal drifts were removed by high-pass filtering. Second, fast changes, possibly occurring from respiration or from the RF pulse, were removed.

The next preprocessing step was spatial smoothing of the functional MR images. The idea behind spatial smoothing is that neighboring voxels are not independent. Spatially smoothing, therefore, causes activations around the peak voxel to be smoothed to a single activation cluster. Specifically, spatial smoothing leads to more robust statistical results, because less independent statistical tests are performed for the single voxels and therefore, a reduction of the percentage of false-positive activations can be achieved. For the spatial smoothing a temporal low-pass filter was used, where all voxel-values are re-calculated by replacement of the unfiltered voxel-values by a weighted average-value for each old voxel and its neighboring voxels. The weighing was done by a 3-D Gaussian filter (kernel)[19].

Next, functional MR images were anatomically aligned to the structural images, which is known as co-registration. The co-registration is the first step that allows the linkage of BOLD signal changes for the specific experimental tasks to brain regions. For the co-registration, an algorithm was used that translated and rotated the functional MR images until its anatomical borders (superior-inferior, anterior-posterior, and left-right) match those of the structural images. The second step is the so-called

[18] slower than the temporal characteristic of the BOLD signal

[19] A good estimate of the extent of the spatial smoothing is given by the full-width at half-maximum (FWHM). The FWHM indicates the spatial distance between neighboring voxels from which the voxels are implemented in the smoothing with half-weighting

Talairach transformation where the structural images were spatially transformed into the Talairach space (stereotaxic space). Talairach and Tournoux (1998) were the first who presented a normalization method that allows reporting of anatomical coordinates of activation in a common stereotaxic space that compensates for the size differences of individual brains. This transformation was done in two steps. First, the structural MR images for each subject were rotated into the AC-PC plane. The AC defines the origin of the Talairach coordinate system and has the coordinates: x = 0, y = 0, and z = 0. Then, the anatomical borders of the brain, that means the anterior, posterior, inferior, superior, left and right border, was defined. With respect to the AC-PC commissure, a brain region with a positive x, y, and z-coordinate indicates an anterior brain region in the right hemisphere, which is additionally located superior to the AC-PC plane. An illustration of a talairached brain is shown in Fig. 1.11.

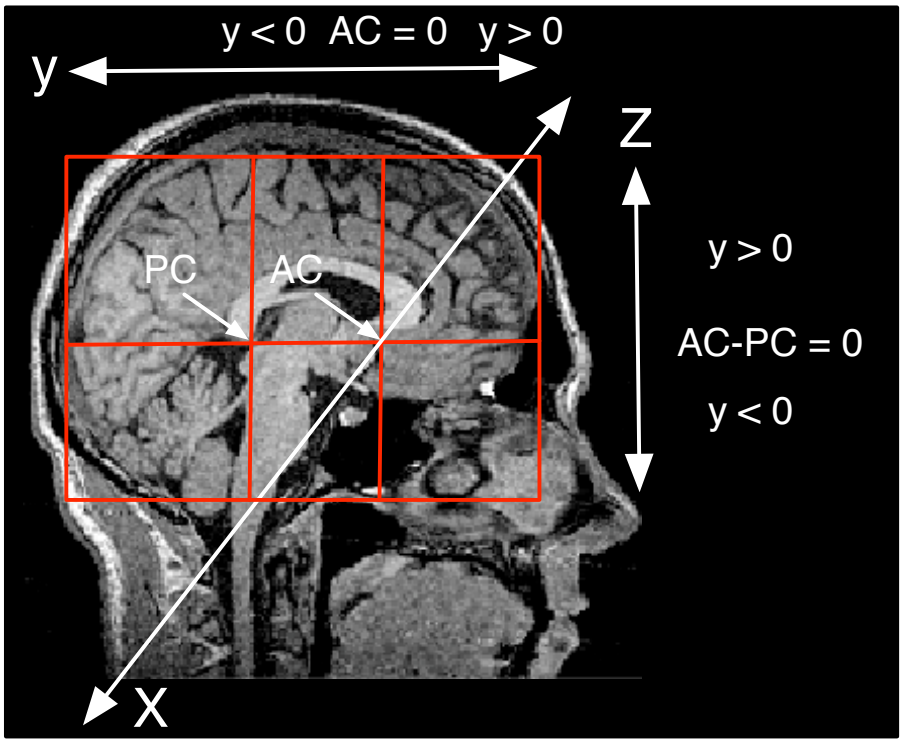

Fig. 1.11: **Illustration of the Talairached brain**. The red rectangle indicates the anatomical borders of the brain. In this sagittal slice, the anterior-posterior and the inferior-superior borders are visible. Brain regions and activations are reported in x, y, z Talairach coordinates. With respect to the AC-PC (anterior commissure-posterior commissure) plane, a brain region with a positive x, y, and z-coordinate indicates an anterior brain region in the right hemisphere, which is additionally located superior to the AC-PC plane.

Postprocessing of fMRI data (I): The General Linear Model To calculate the BOLD changes between two conditions of interest in this thesis, statistical tests were applied. In fMRI, the *General Linear Model* (GLM) is used, which is mathematically identical to a multiple regression analysis. Briefly, the GLM aims to 'explain' or 'predict' the variation from a dependent variable (the condition of interest) in terms of a linear combination of several reference functions (= predictors). The dependent variable corresponds to the observed BOLD signal and the predictors correspond to the expected (idealized) BOLD signal, for the different conditions of the experimental paradigm (design matrix). A predictor time course is obtained by convolution of a condition box-car time course with a Gaussian hemodynamic response function (HRF) that means which has a similar shape than the real BOLD signal. A condition box-car time course is defined by setting values to 1 at time points at which the modeled condition is defined, like the onset and offset of a block or event, and 0 at all other time points, such as the duration of the off-block. Each predictor time course has an associated coefficient *beta weight*, quantifying its potential contribution to explain the measured BOLD signals for the different conditions. A large positive (negative) beta weight indicates a particular region of strong brain activation (deactivation) during the modeled experimental condition relative to the baseline condition. All beta values together characterize, therefore, a preference of one or more particular brain regions for one or more experimental conditions.

Comparisons of conditions can be formulated as contrasts, which are linear combinations of the beta values to null hypotheses. To test, for example, whether or not activation for condition 1 is significantly different from activation of condition 2, the null hypothesis is that the beta values of the two conditions do not differ. The linear combination defining a contrast (condition 1 - condition 2), can be written as the scalar product of vector c and beta (values) vector b. The results of these statistical tests, that means the statistical BOLD signal differences between (at least) two conditions, are expressed in t- and p-values respectively.

As mentioned in 1.4.4, I used in the experiment of this thesis either a block design or an event-related design. According to the GLM, trials within each block were modeled with boxcar predictors that are convolved with the synthetic HRF. In the event-related design, each event was modeled with a boxcar predictor by convolving the event with the synthetic HRF.

Postprocessing of fMRI data (II): Group analysis and single-subject analysis In the present thesis, I analyzed the brain activation for biological motion stimuli on single-subject as well as on group level. To test for quantitative inference of the average effect in a large sample of subjects (> 8 in recent fMRI studies), I used in chapters 3 and 4 the random-effect analysis (Holmes and Friston, 1998; Friston et al., 1999). Basically, in the random-effect analysis the contrasts of parameters estimated from a first level analysis (indicating within-subject variability) are then entered into a second-level analysis to statistically test for the between-subject variability.

For two reasons, I also investigated the single-subject results. First, small but statistically robust effects may be hidden when averaging over a large sample of subjects, especially when a large kernel for spatial smoothing is used. Secondly, in the experiments with only few (< 8) subjects (chapter 2) calculating the mean activity across subjects could lead to an over-interpretation of the data. For example, activations in a particular brain region can be small or absent in the majority of subjects, but strong in a single subject.

Postprocessing of fMRI data (III): Whole-brain analysis and Region of Interest Analysis One approach in this thesis to investigate brain activations was the so-called *whole-brain* analysis. In this analysis, multiple statistical comparisons between two or more conditions are performed for each single voxel of the brain. Therefore, this approach is also termed voxel-by-voxel analysis. This analysis is useful when there is no specific a-priori assumption about the expected location of brain activation.

However, there is the so-called multiple comparison problem whenever the whole-brain approach is employed. When functional MR images for the whole brain are acquired, statistical tests must be performed for a large sample of voxels (> 100000 voxels). Due to the large number of voxels, some are falsely treated as significantly activated by chance. To compensate for this problem, the α-level has to be adjusted to a higher statistical threshold. An α-level of 5% is equivalent to a p value of $p = 0.05$. However, this adjustment often results in the activation of only a few voxels, thus only strong effects will be visible.

The second approach used in this thesis was the *region of interest* analysis (ROI analysis). It involves identifying a priori defined functional region, and then calculating the BOLD responses in that region. To define the spatial extent of the ROI, either so-called functional localizer scans can be used, or anatomical borders of the area.

A localizer scan may be useful, when it is known that a particular stimulus will only activate a specific brain region (see chapter 2). The definition of the ROI was performed for the brain of each individual subject, to compensate for the slight activation and anatomical differences for the individuals. In the ROIs, I first calculated the mean BOLD signal changes and then compared these changes for the different experimental conditions statistically.

Chapter 2

Visual areas involved in the perception of human movement from dynamic form analysis

2.1 Introduction

One of the most compelling examples of the visual system's ability to recover object information from sparse input is provided by the phenomenon known as biological motion. People can recognize actions performed by others, even when these movements are portrayed by a stimulus that consists of just light points attached to the major joints of the body (Johansson, 1973). It is often assumed that the recognition of biological motion is a highly specialized part of motion analysis that leads to a perception mechanism, called form from motion mechanism.

Recent studies of biological motion showed the involvement of brain areas that underlie the perception of biological motion (Grossman et al., 2000; Grossman and Blake, 2002; Vaina et al., 2001; Bonda et al., 1996; Saygin et al., 2004; Beauchamp et al., 2003; Thompson et al., 2005). The brain activation was located in the posterior superior temporal sulcus (pSTS). STS receives projections from both pathways of the visual system: the dorsal pathway that processes primarily motion information and the ventral pathway that processes mainly color and form information. Reciprocal connections within the dorsal pathway connect pSTS with the motion responsive areas MT

and MST. The input from the ventral pathway into STS comes from form responsive areas V3 and V4. Therefore STS activation can result from analysis of either form or motion signals in the visual input. Similarly, biological motion recognition could be derived from form or motion cues. Vaina et al. described a patient (AF) with bilateral motion impairment (Vaina et al., 1990). AF could not solve basic motion tasks, but was however able to perceive biological motion. Furthermore, McLeod studied a patient (LM) with bilateral lesions along the dorsal pathway (including MT) who was almost 'motion-blind', but able to recognize human actions in point light displays (McLeod et al., 1996). Schenk and Ziehl described two patients with normal sensitivity to coherent motion, but with strong inability to perceive biological motion figures portrayed against a background of a static noise pattern (Schenk and Zihl, 1997a; Schenk and Zihl, 1997b). These studies indicate that biological motion perception differs fundamentally from other kinds of motion perception. Specifically, global form information may be used in biological motion perception by integrating the static form information of individual frames of the stimulus sequence over time (Beintema and Lappe, 2002; Beintema et al., 2006; Lange et al., 2006; Lange and Lappe, 2006). In this view, the visual system would first analyze the shape of the human figure from form cues such as the distribution of light-points on the body. Subsequently, the motion of the body is derived from an analysis of the transformation of the shape over time. This procedure eventually captures both form and motion aspects of biological motion but the motion is derived from form analysis rather than from low-level motion perception. A computational model using this approach quantitatively captures many of the properties of biological motion perception (Lange et al., 2006; Lange and Lappe, 2006). Imaging studies support this idea showing that biological motion selectivity is not just restricted to pSTS but involves also two areas of the ventral stream: the occipital and the fusiform face area (OFA and FFA), which are part of the fusiform gyrus (Grossman et al., 2000; Grossman and Blake, 2002; Vaina et al., 2001; Bonda et al., 1996; Saygin et al., 2004; Beauchamp et al., 2003; Downing et al., 2001). Whether the extrastriate body area (EBA), which responds to bodies or body parts, is selectively activated by biological motion, is not fully clear yet (Grossman and Blake, 2002; Downing et al., 2001).

Beintema and Lappe (2002) have introduced a variant of the classical point-light walker – termed single-frame lifetime (SFL) walker – to investigate the role of form information in the perception of biological motion. This stimulus provides a way to study

the perception of biological motion when it is not supported by low-level motion signals. In this chapter I will investigate the neuronal network engaged in the perception of biological motion for stimuli with local motion (Cutting walker) and without local motion signals (SFL walker). Based on the psychophysical findings from Beintema et al. (2002), I hypothesize that the brain activation to the SFL walker is stronger in form-processing areas than in motion-processing areas. I would regard this as evidence for a route to biological motion perception that bypasses the dorsal visual pathway.

2.2 Methods

2.2.1 Stimuli

In the Johansson's classic point-light walker one light point is placed at each of the major joints of the body. I used a computer algorithm, first introduced by Cutting (1978), which simulates a walker that walks in place on a treadmill (Cutting walker, CW) and consists of 10 dots located on the ankles, knees, hip, wrists, elbows and the shoulder (Fig. 2.1 B and 2.2 A). In the SFL walker (SW, Fig. 2.1 B and 2.2 C), eight light points appear at random locations on the imaginary lines connecting the major joints (e.g. between shoulder and one elbow) of the walker's body. Each point was shown for just one frame of the stimulus animation (frame duration = 54 ms). In the next frame, it is relocated to another random position between the joints. Thus, an individual point does not provide a consistent motion signal because it cannot be tracked over frames. The frequent relocation of the dots instead provides increased form information as the limbs are traced over time. Observers recognize this new stimulus spontaneously as a walking human figure (Beintema and Lappe, 2002). The starting phase in the sequence of each step cycle for both walkers was varied randomly from trial to trial. For each walker type, I also included a static condition (CS and SS, respectively) in which the walker was presented in a single static condition (Fig. 2.1 B and 2.2 B, D). For the CS stimulus, one randomly chosen static frame of the CW stimulus was shown throughout the trial. For the SS stimulus, the walker remained in a single randomly chosen posture throughout the trial, but the dots were relocated in each frame of the animation to new positions between the limbs. Together, I therefore presented four conditions (CW, CS, SW and SS). All stimuli subtended 5° by 11° of visual angle and were composed of luminous (red/green) square dots (0.2°) presented

on a black screen (visual field 40° x 25°, frame rate of 60 Hz).

2.2.2 Experimental Design

The fMRI experiment was done in an on-off block design. Study participants performed two discrimination tasks while fixating a green fixation dot (0.2°) in the center of the screen. Each on-period contained one of the four experimental conditions. Subjects saw blocks of 60 s duration, in which half of the trials presented the specific walker (CW, CS, SW or SS) and the other half presented phase-scrambled versions of the same walker type. In the phase-scrambled stimuli, the starting phase of each joint angle was randomly chosen. The resulting stimuli contain local motion of the limb segments similar to a normal walker but in a configuration that is inconsistent with the human body structure. Previous studies using this scrambled stimulus pointed out that the outline depicting a human figure were not visible in this condition (Bertenthal and Pinto, 1994; Grossman et al., 2000; Grossman and Blake, 2002). Subjects had to respond about whether the stimulus depicted as a human figure. The blocks were presented in pseudo-randomized order and were repeated three times during scanning. Duration of a single trial was 1.6 s with 1 s stimulus presentation (= 0.625 of a step cycle). In half the trials, stimuli were facing to the left, and in the other half to the right. An illustration of the experimental design is shown in Fig. 2.1.

In the off-period (baseline, 30 s/block), subjects saw eight stationary dots at random positions within an area of the same width and height as the walker stimulus. Four of the dots changed luminance to an increased or to a decreased level at a random time of 0.4 – 0.7 s after trial onset. The direction of the luminance change was determined randomly. The task was to maintain attention and detect a luminance change in an array of the dots. After 1 s stimulus presentation the screen turned dark for 0.6 s except the fixation dot. Participants responded whether the four dots became brighter or darker on a keypad connected to the computer.

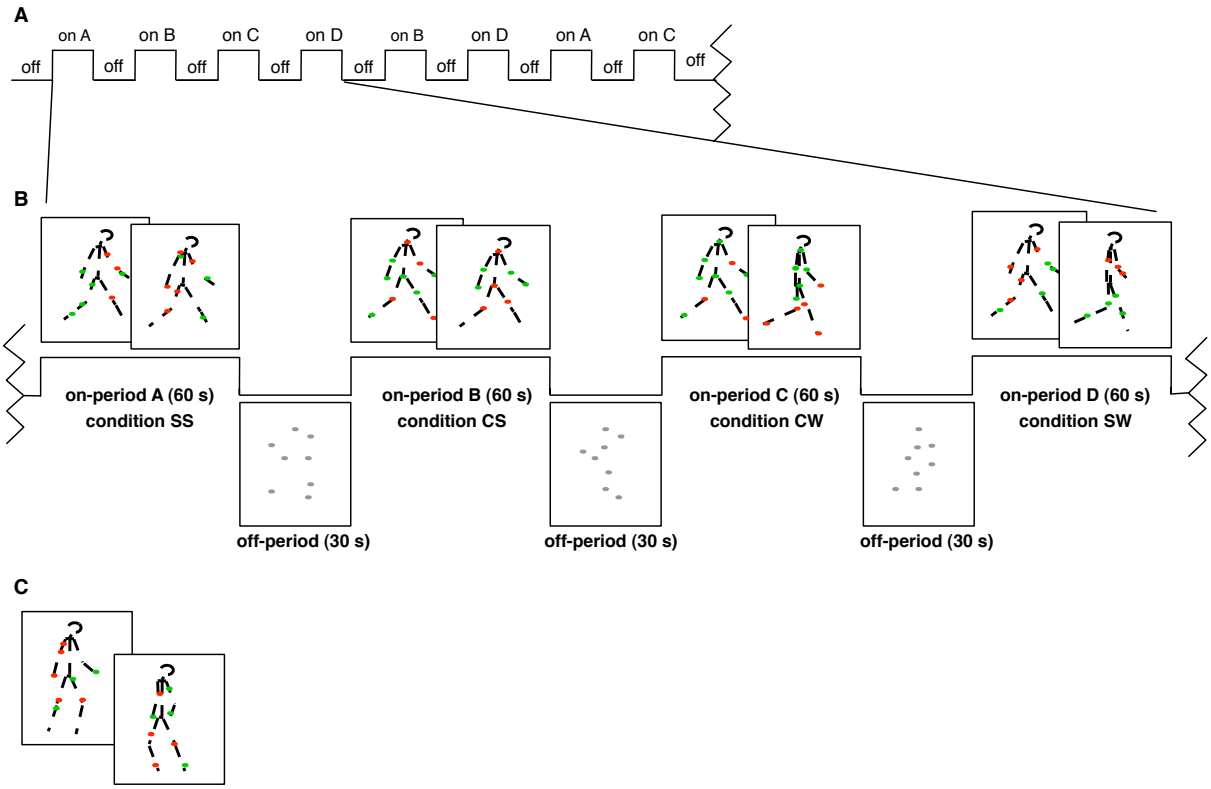

Fig. 2.1: **Illustration of the experimental design during the scanning session**. Each condition (CW, CS, SW, SS) was shown in an on-off block design (A, B). Trials of the on-period (60 s) contains either one type of the point-walker or scrambled version of the point-light walker. Each on-period was separated by an off-period (30 s). In the off-period eight grey dots were presented at random positions within an area of the same width and height of the walker. Each on-block was repeated three times and was presented in pseudo-randomized order. In C, two frames of the SS condition are shown. In the first frame the SS stimulus is shown, whereas the second frame portrays a scrambled version of the SS stimulus. For SW and SS, dots lived only one frame and were then relocated to a random position between the joints. The dashed lines of the body and the head were not shown in the experiments. In the scrambled display, local motion signals were kept intact, but the single dot-trajectories were randomly displaced within the restricted area of the display, thus, entirely disrupting the shape of the figure. The color of all stimulus dots changed each frame of the animation.

2.2.3 Subjects

Four neurologically healthy males (mean age 22 years) with normal vision gave their informed consent for the experimental protocol approved by the Massachusetts General Hospital Human Subjects Committee. The subjects were naive with respect to the hypothesis of the study.

2.2.4 MRI scanning

A 1.5 T GE Horizon EchoSpeed (GE Medical Systems, Milwaukee, Wisconsin, USA) scanner was used, retrofitted for echo-planar imaging (EPI). A conventional volume was acquired by using twenty-two 6-mm-thick contiguous oblique slices (3.13 x 3.13 mm in plane) parallel to a line drawn between the AC-PC commissure, sufficient to cover the whole brain. A flow series was obtained in the oblique planes selected for functional scanning to detect major blood vessels, followed by a T1-weighted sagittal localizer series (repetition time (TR) = 6 s, field of view (FOV = 20 cm^2). Functional images acquired using the BOLD technique were obtained by applying an ASE pulse sequence (22 axial slices, TR/TE (time of echo-planar) = 2500/30 ms, flip angle = 90°). A high-resolution 3-D structural scan for each participant was also acquired during the same session (114-slice sagittal partitions, TR/TE = 2500/4 ms, in-plane resolution: 1 x 1 x 1.5 mm^3, FOV = 20 cm^2.

2.2.5 Data analysis

Echo-planar images were post-processed with MEDX 3.3 software (Sensor Systems, Sterling, Virginia, USA). The first four functional images of each run were excluded from analysis to avoid differences in T1 saturation. Motion correction was performed by registering all functional scans to the same reference scan. The reference scan was calculated as the mean over all functional images.

Functional images were spatially smoothed with a three-dimensional Gaussian filter of 10 mm full-width at half-maximum (FWHM) to accommodate anatomical variations between subjects (kernel size 3.13 x 3.13 mm). For temporal smoothing of the time series 3 cycles per run were applied. For each subject, the combined z maps (of each condition of the on-period) were set to a voxel activation threshold of $p < 0.05$ ($z = 3$) and were superimposed onto the subject's high resolution MRI in Talairach space (Talairach and Tournoux, 1988). Similar to Vaina et al. (1998, 2001), the z-maps were

taken from the subtraction of the averaged signal of the off-period from the averaged signal of the on-period (the averaged signal of all biological motion and scrambled events within a block) . For the group analysis, the Talairach registered z-score maps images of all runs and subjects were summed and then divided by the square root of the total number of scans, providing a group z-score map (corrected for multiple comparisons) for each condition. The cluster threshold for later analysis was set to a minimum of > 25 activated neighboring voxels.

I examined the mean percent signal change of the BOLD signal in specific region of interests (ROIs). The dimension of a ROI (MT, pSTS, EBA, FFA/OFA, LG (lingual gyrus), IFG (inferior frontal gyrus), QuP (cerebellar lobule VI,) sPrG: (superior precentral gyrus, part of the premotor cortex), and KO (kinetic occipital area)) was defined as follows. For each subject the location of a ROI was identified based on anatomical landmarks. Then a mean (fixed) Talairach coordinate for each ROI was determined across subjects. The depth and the size of a ROI varied between areas. The statistical threshold for activations within the ROIs was set to $p < 0.05$ (corrected for multiple comparisons). The spatial extent was within accepted and published ranges for each ROI. Because the activations to biological motion in FFA and OFA were very similar (Grossman and Blake, 2002), I averaged the signals of both ROIs and report a combined activity for FFA/OFA.

Additionally, I performed an MT localizer test for each subject. Here, subjects saw alternating blocks (60 s, 3 repetitions) of contracting and expanding dots (200 dots, average speed 8.0°/s, black dots on white background) with the focus of expansion and contraction at the center of the display (Fig. 2.4 A) while fixating a central fixation dot. On the basis of the activation map from of the localizer test, I adjusted the size of the anatomically predefined MT ROI.

2.2.6 Prescan

For later analysis of the fMRI signal, it was necessary that the off- and the on-period had the same difficulty in decision making. Therefore, subjects were trained prior to scanning for both discrimination tasks. The collected data of both tasks were analyzed to compare the percent correct ratio. The training phase was repeated until the subjects reached a stable performance level of at least 80% correct for both tasks. This took on average 245 trials per condition and subject. After the subsequent scanning session

a two-way repeated measures ANOVA (rmANOVA) with the factors condition and time (before and during scanning) revealed no significant difference in the performance among the four conditions of the on-period ($F_{31,1} = 2.5$, $p = 0.13$) or the off-period and no training effect comparing the performance before and during scanning ($F_{28,3} = 0.48$, $p = 0.7$ for the on-period).

2.3 Results

I examined the functional brain activity among four contrasts (CW, CS, SW and SS versus baseline). The whole-brain analysis revealed significant effects of stimulus type in several regions (Table 2.1). Part of the averaged activity maps for the group is shown in Fig. 2.2 with the foci on some of the ROIs. In Fig. 2.3, the group mean percent MR signal change (with SEM) from baseline for the ROI templates is plotted.

functional	right hemisphere			CW	CS	SW	SS	left hemisphere			CW	CS	SW	SS
area	x	y	z	max Z-score				x	y	z	max z-score			
EBA	40	-69	4	15.7	6.8	10.9	12.5	-41	-68	3	14.8	5.1	10.9	10.1
MT	42	-62	2	13	5.8^{2}	13.9	12.8	-42	-64	1	14.4	3.6^{1}	14.9	12.1
KO	29	-86	1	5.4	5.4^{3}	10.1	11.7	-27	-84	2	4.6	4.2^{2}	7.5	7.3
FFA	40	-41	-14	8.3	5.1	9.9	11.4	-34	-40	-14	9.1	5.7^{2}	7.4	7.6
pSTS	52	-43	12	5.8	3.5^{2}	5.5^{3}	5.4	-44	-50	11				3.8^{1}
QuP	32	-68	-19	6.9^{2}	3.8	8.7^{2}	10	-31	-72	-18	8.1^{2}	5.1	10.1^{2}	8.7
IFG	42	32	12	5.1	9.3	7.8^{3}	11.3	-41	24	10	4.1^{3}	5.2	5.5	6.2
sPrG	32	5	52	4.9	8.1	7.2	6.9	-36	3	55	4.1	6.3^{3}	6.5	8.1
LG	16	-84	0	8.4	4.7	8,7	10.4	-12	-86	0	8.1	6.3	10.3	8.7

Table 2.1: Activations referring to maxima z-values (> 25 activated neighboring voxels; corrected $p < 0.05$, corrected for multiple comparisons) in ROIs. The superscript digits indicate that activation could not be found in all subjects. For example, a superscript digit of 1 indicates activation was found only in one subject.

Group results Activation was obtained in FFA/OFA in all conditions bilaterally compared to baseline. A repeated-measures ANOVA with the factors condition and ROI revealed a significant effect ($F_{31,3} = 4.6$, $p < 0.03$). Further, Fisher's post-hoc tests showed that SW and SS were significantly higher activated compared to CW (SW to CW: $p < 0.05$; SS to CW: $p < 0.04$) and CS (SW to CS: $p < 0.02$; SS to CS: $p < 0.02$). No significant differences were obtained comparing CW to CS ($p < 0.56$) and SW to SS ($p < 0.97$). Similar to earlier studies of biological motion (Grossman et al., 2000; Grossman and Blake, 2002; Vaina et al., 2001; Bonda et al., 1996; Saygin et al.,

2004; Beauchamp et al., 2003; Thompson et al., 2005), activation occurred in the right pSTS (bilateral in one subject in the SS), which was significantly higher for CW, SW and SS compared to CS (see Fig. 2.2). In all conditions tested, comparison in the ROI of EBA revealed significantly stronger activation for SW and SS compared to the CW and CS (see Fig. 2.2).

The activation in frontal regions, especially in the left IFG, was significantly higher for CS compared to CW ($p < 0.02$, post-hoc test). Also, weak but significant activation was found in the premotor cortex in the inferior and the superior precentral gyri bilaterally for all four experimental conditions. I observed robust activation in the cerebellar lobule VI (QuP)(Vaina et al., 2001; Schmahmann et al., 1999). Activation in motion-sensitive areas of the dorsal pathway (MT and KO) was strong but showed no significant differences between CW, SW and SS (repeated-measures ANOVA). Comparing SW with CW, the effect in the left KO was marginally significant ($p = 0.058$). The CS condition gave significantly lower activation. Further, post-hoc analysis showed that this was true for the right and the left hemisphere (all $p < 0.05$).

Single-subject results The group results demonstrated that the activation in ROIs of the ventral pathway (FFA/OFA and EBA) was stronger for the static and moving versions of the SFL walker as compared to the (moving) Cutting walker. In contrast, activation was not significant different in the dorsal ROIs (MT and KO). Next, I investigated whether the stronger activation in the ventral pathway for the new biological motion stimulus was also visible on the single subject level. In Table 2.2, single subject peak activation locations are reported for the four conditions (CS, CW, SS, and SW). In addition, in Fig. 2.5 the BOLD signal changes in the different ROIs for the four subjects are shown. As observed on group activation level, single-subject analysis revealed for all subjects that BOLD signal changes in bilateral EBA and fusiform gyrus were stronger for SW and SS conditions compared to the CW condition. The EBA activations – which were anatomically different from the MT activations – for the four experimental conditions are shown in Fig. 2.4 for a single subject. In contrast, activation strength in dorsal pathway areas was similar for all four subjects when SW was compared to CW (Fig. 2.5). In Fig. 2.6 and 2.7 activations are shown for the four experimental conditions for a single subject.

ROI area	anatomical area	Brodmann area	subject	Talairach coord. (right hemisphere) x	y	z	Talairach coord. (left hemisphere) x	y	z
EBA	inferior temporal gyrus/ middle occipital gyrus	19	1	34	-72	0	-40	-72	2
			2	34	-72	2	-38	-74	2
			3	38	-70	2	-44	-68	2
			4	36	-72	0	-41	-71	-2
KO	middle occipital gyrus	18	1	30	-84	0	-26	-86	2
			2	30	-86	4	-26	-84	2
			3	26	-88	-2	-26	-80	2
			4	30	-84	2	-28	-86	2
FFA/OFA	fusiform gyrus	37	1	40	-46	-14	-34	-48	-14
			2	42	-38	-16	-36	-38	-14
			3	40	-38	-12	-30	-36	-12
			4	38	-41	-14	-36	-38	-15
pSTS	posterior superior temporal sulcus	42/41	1	54	-34	10			
			2	58	-44	12			
			3	48	-38	12			
			4	49	-44	10			
LG	lingual gyrus	17/18	1	18	-80	-2	-12	-86	-2
			2	16	-86	4	-13	-84	2
			3	14	-85	-2	-12	-88	2
			4	15	-86	0	-12	-86	-2
MT	middle temporal area	37	1	46	-58	2	-42	-64	2
			2	36	-60	0	-40	-62	1
			3	42	-66	2	-46	-64	1
			4	41	-58	4	-42	-66	1
QuPO	cerebellum	19	1	30	-71	-18			
			2	26	-72	-20			
			3	34	-60	-18			
			4	33	-66	-18			
IFG	inferior frontal gyrus	46	1	40	33	12	-38	31	12
			2	40	32	14	-38	22	14
			3	42	31	12	-44	28	12
			4	47	30	12	-42	24	10
sPrG	superior precentral gyrus	6	1	30	0	55	-32	3	55
			2	34	4	52	-36	2	54
			3	32	7	52	-35	2	57
			4	31	7	31	-39	3	52

Table 2.2: **Peak ROI Talairach coordinates for the individual subjects.** Activation locations of the ROI are given by anatomical names and Brodmann areas. Peak coordinates are reported only for activation at a statistical threshold of $p < 0.05$ (corrected for multiple comparisons).

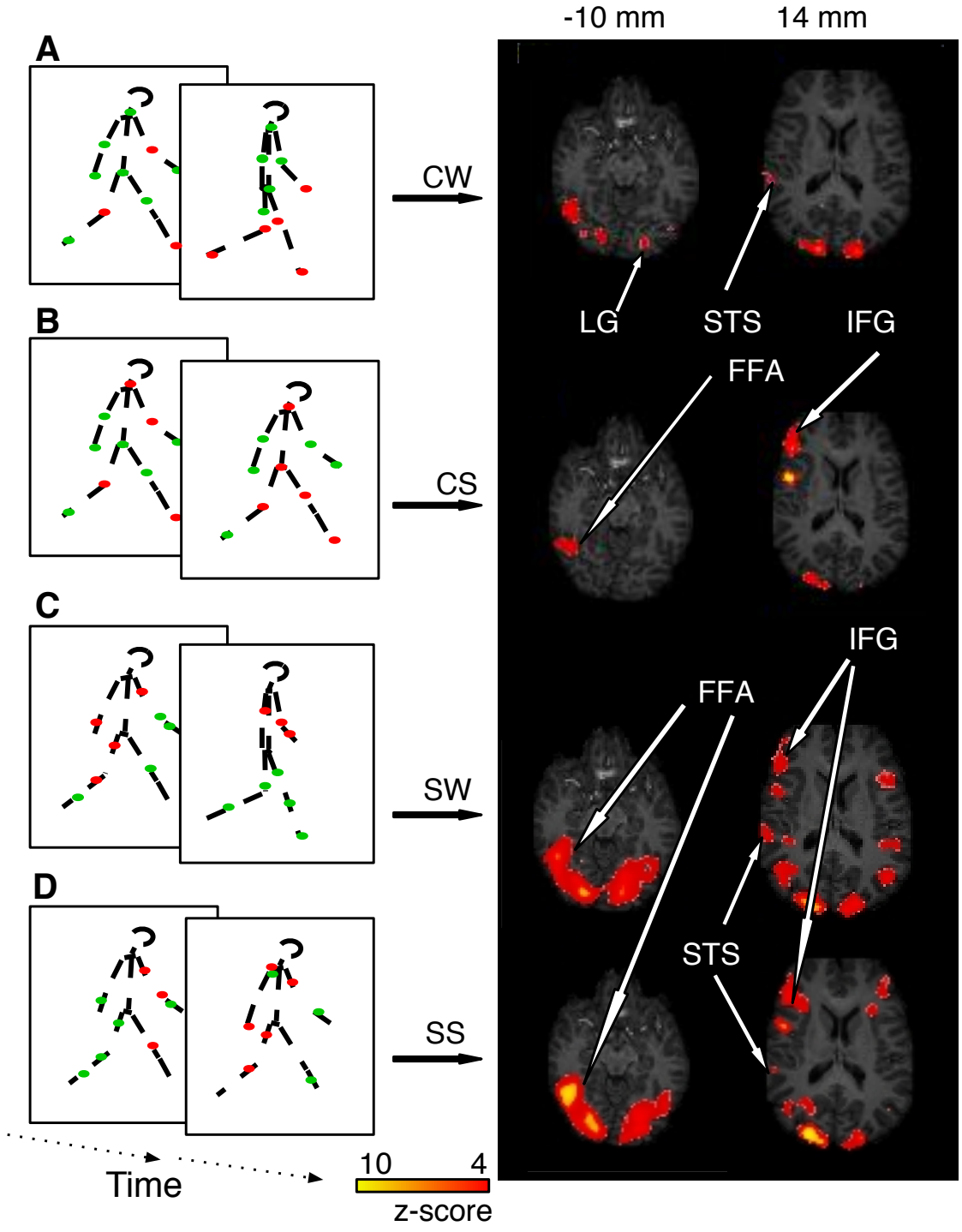

Fig. 2.2: **Group activation map for each contrast (CW, CS, SW, and SS versus baseline) in two different axial slices.** Subfigures A-D show the stimulus properties in two consecutive frames. Activation was strong in areas of the ventral stream for the new stimulus (e.g. FFA in subfigures C and D). Right in the images corresponds to left in the subjects. Color scale represents z-score. LG, lingual gyrus; FFA, fusiform face area; STS, superior temporal sulcus; IFG, inferior frontal gyrus.

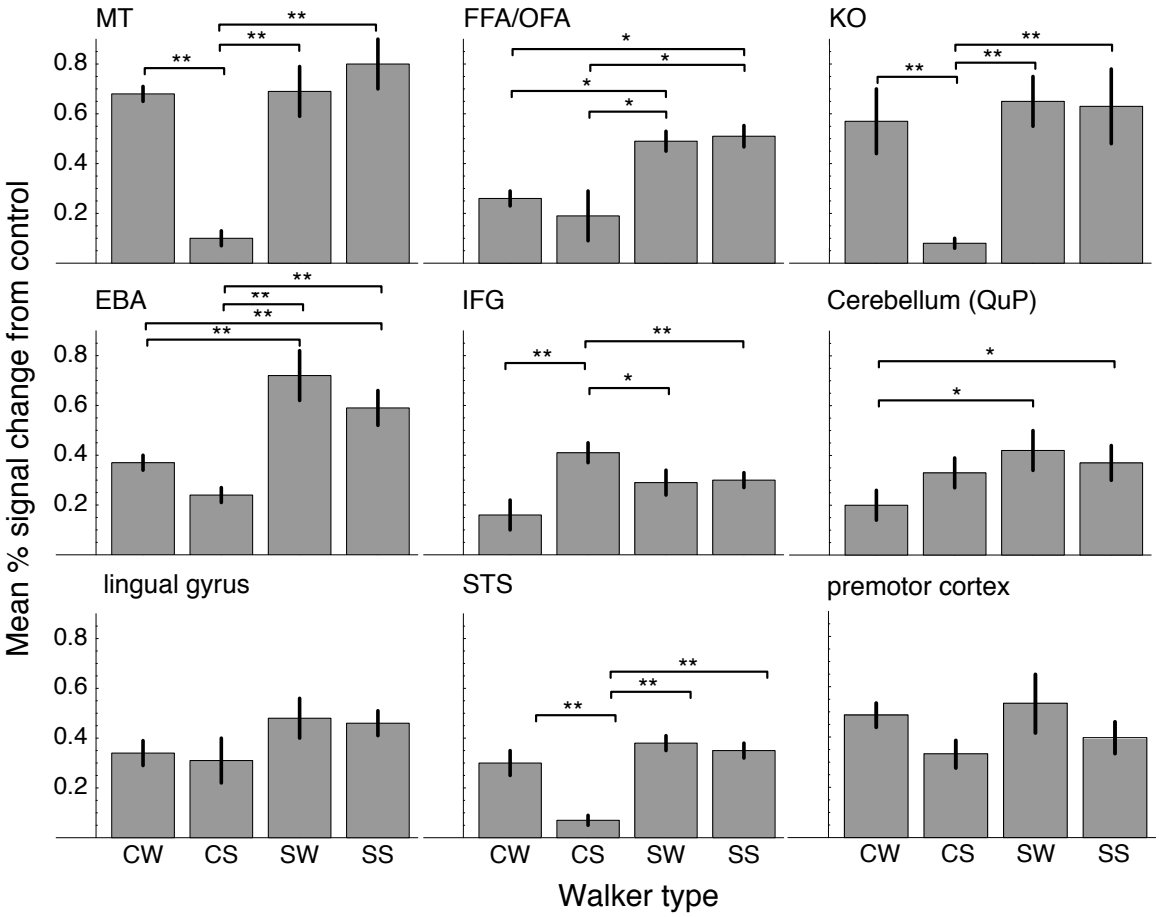

Fig. 2.3: **Mean percent signal change for the group (with SEM) for the specific biological motion conditions (CW, CS, SW, and SS) versus baseline in ROIs**. The results were averaged across both hemispheres (pSTS only activation in the right hemisphere, except for one subject). * highlights significant differences at $p < 0.05$, ** at $p < 0.01$.

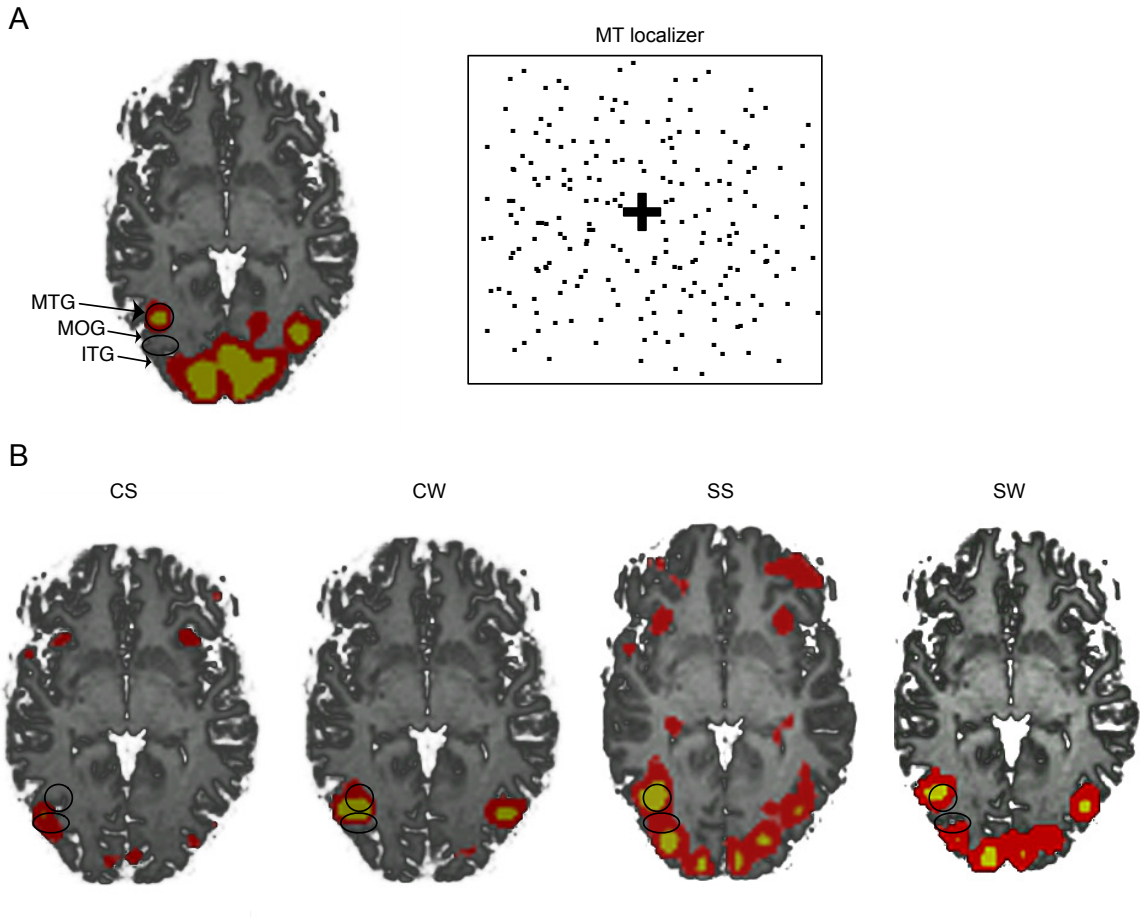

Fig. 2.4: **Single subject activation for the MT localizer test (A, left panel) and for the different types of point-light walker (B)**. During the MT localizer, subjects saw a radially contracting and expanding dot pattern with the focus of expansion and contraction at the center of the display (A, right panel) while fixation on a central fixation dot. In B, activation is shown on axial slices with a similar anatomical z-Talairach coordinate. For MT, the ROI (black circle) was defined by the gravity center of activation from the localizer scan (middle temporal gyrus, MTG). The size of the other ROIs was defined on anatomical criterions. For example, the EBA ROI (black ellipsoid) was defined as a region between the middle occipital gyrus (MOG) and the inferior temporal gyrus (ITG). For this subject, activation for EBA occurs for all four experimental conditions.

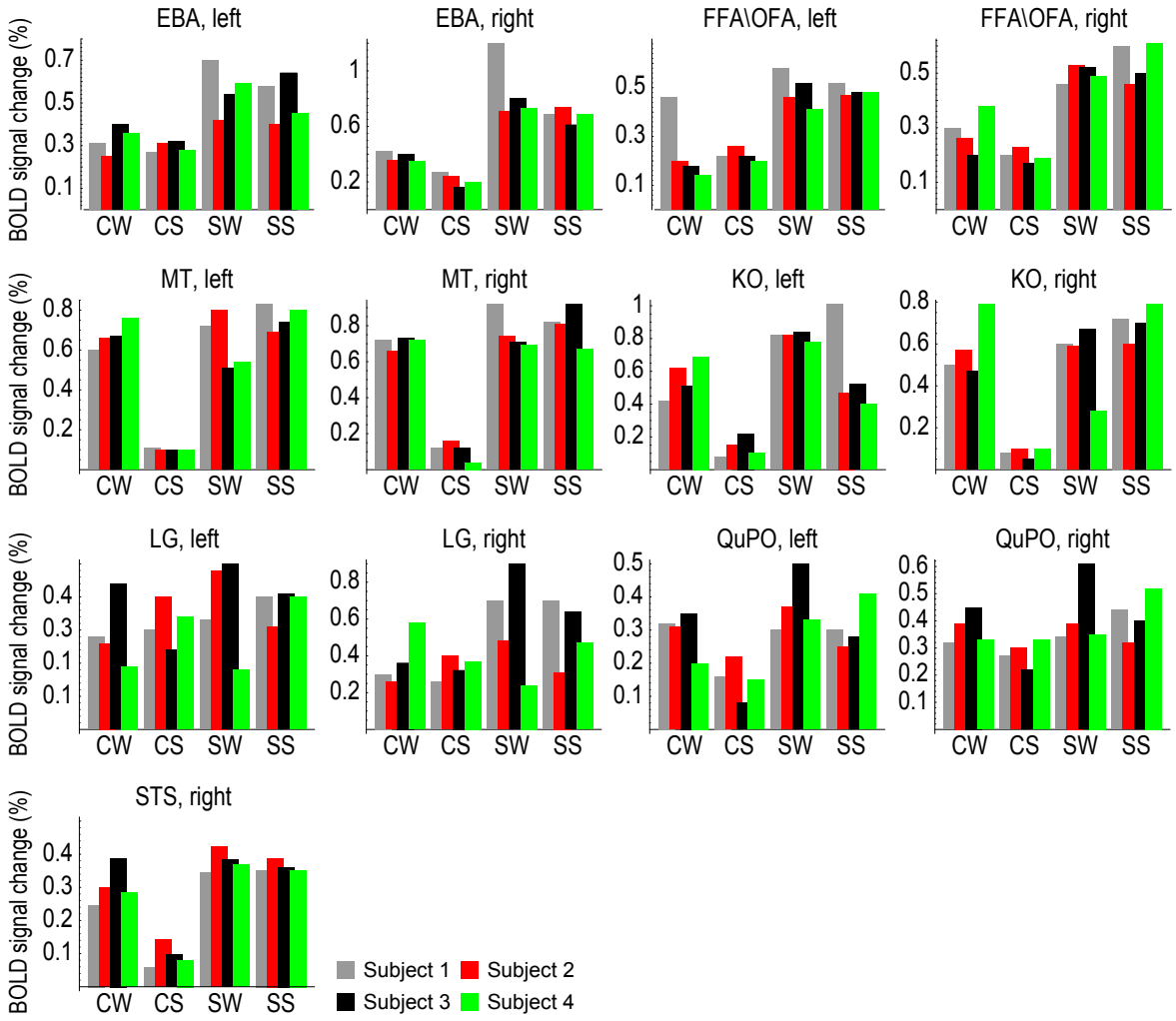

Fig. 2.5: **BOLD signal changes (%) for the different ROIs (except for sPrG) and point-light walker types for each subject**. BOLD changes are reported for both hemispheres (except for STS).

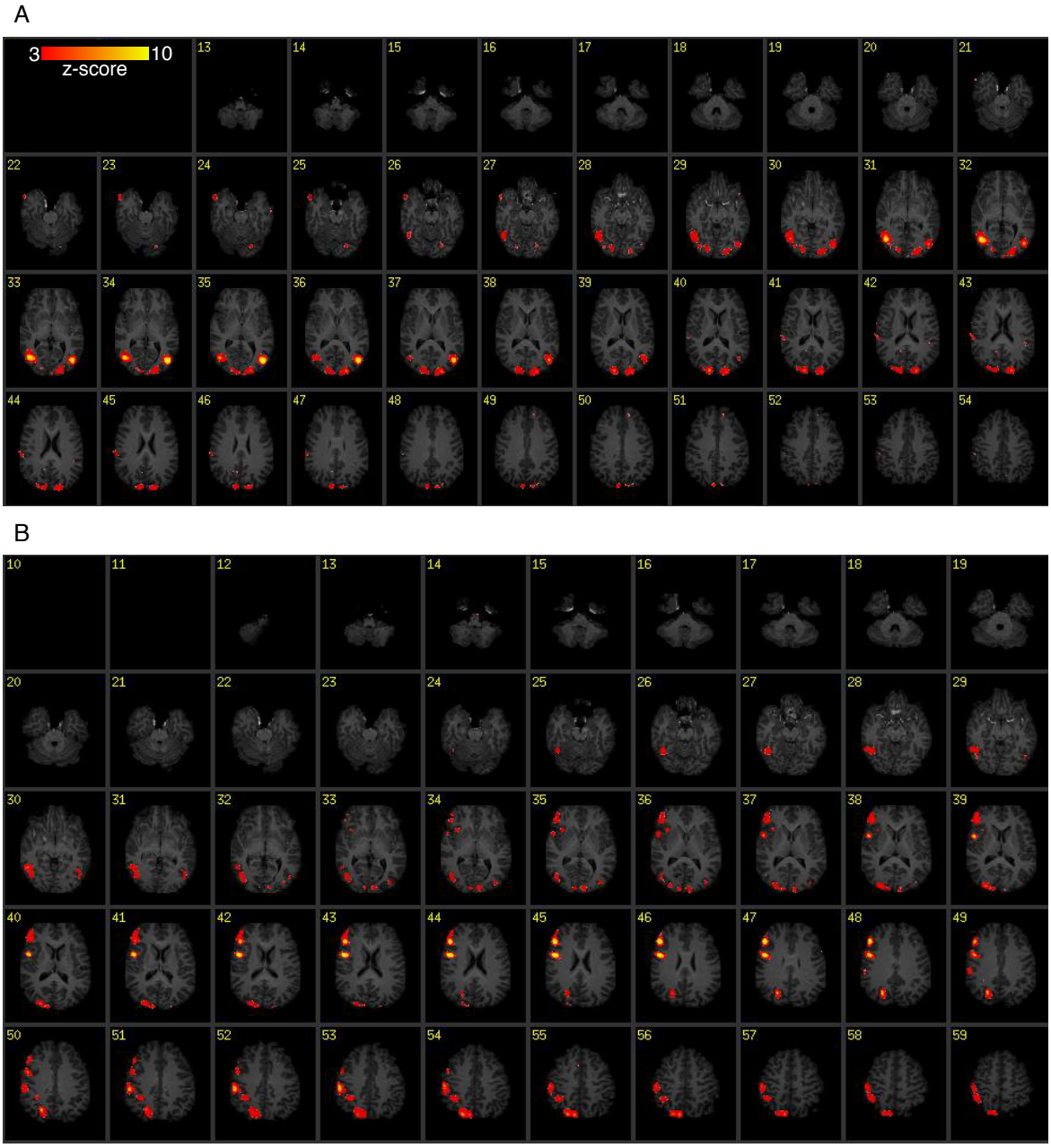

Fig. 2.6: **Activation map for a single subject for the Cutting walker (A) and the static Cutting walker (B).** Activation is shown on axial slices from inferior (scans with lower number) to superior (scans with higher numbers) brain regions. Activation is shown at $p < 0.05$ ($z = 3$).

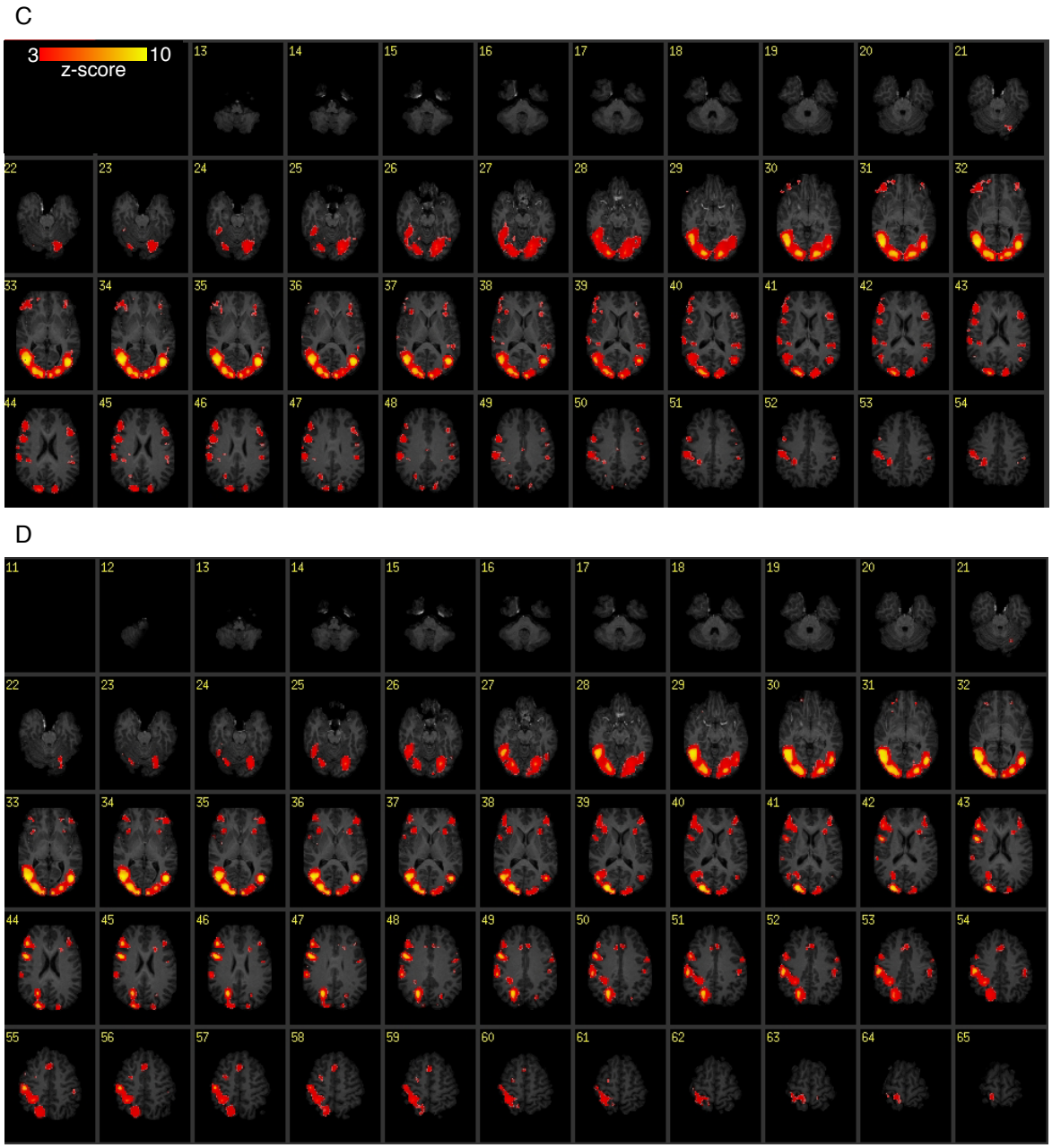

Fig. 2.7: **Activation map for the same subject for the SFL walker (C) and the static SFL walker (D).** Activation is shown on axial slices from inferior to superior, and at $p < 0.05$ ($z = 3$).

2.4 Discussion

2.4.1 The SFL walker

In this chapter, I investigated the BOLD responses to both the Cutting and the SFL walker. In contrast to the Cutting walker, the dots of the SFL walker jumped after a single frame to a new location between the major joints of the body. As a consequence of the rapid positional change of the dots, the stimulus possesses a high temporal frequency of about 20 Hz. One could argue that the SFL walker is flickering, which is produced by the fast re-appearance of dots on random positions on the body. Therefore, the SFL walker may provide more form information compared to the Cutting walker so that the stronger EBA and fusiform gyrus activity for the SW and the SS condition could be a result of flickering. Specifically, flickering could emphasize the illusionary contours between the joints and thereby promotes two processes, the perception of form and in consequence possibly also the local motion of a contour. I will discuss this hypothesis in the next section.

2.4.2 The role of form information in biological motion perception

Like most previous neuroimaging studies of biological motion, I found activation in the pSTS (Grossman et al., 2000; Grossman and Blake, 2002; Vaina et al., 2001; Bonda et al., 1996; Saygin et al., 2004; Beauchamp et al., 2003; Downing et al., 2001). I provide three new findings for pSTS. First, the right pSTS responds significant lower to stimuli without motion information (CS), probably because of the missing dynamic signal. Second, pSTS activation was similar to biological motion stimuli that contain local motion (CW) and to stimuli that contain no local motion information (SW, SS). Third, pSTS responds similarly to biological motion stimuli with different amounts of form information (comparing SW and SS to CW). This suggests that pSTS, on the one hand, discriminates between biological motion and non-biological motion, but is not dependent on local motion signals in the biological motion stimulus. I primarily found right pSTS activation (except in one subject, see Table 2.2). This is in good agreement with other studies to biological motion (Bonda et al., 1996; Santi et al., 2003).

A major conclusion of my experiments is that form-processing areas are differentially activated by different biological motion stimuli. I found increased activation in

the FFA/OFA and EBA for stimuli possessing primarily form information (SS and SW) compared with stimuli with less form information (CW and CS). This finding was corroborated by the results on single subject level. These findings on group and single subject level are consistent with earlier studies showing form-based activation of the fusiform gyrus in the perception biological motion (Vaina et al., 2001; Downing et al., 2001; Peelen and Downing, 2005b; Beauchamp et al., 2003). For example, when fMRI responses to video and point-light displays of moving humans were compared, strong activations in the ventral temporal cortex occurred for human videos and weak activations occurred for point-light animations of biological motion, especially in the lateral fusiform gyrus (Beauchamp et al., 2003). The authors suggested that the global form, but not motion, contributes to the activation in the ventral cortex.

I found that in EBA, which is also activated by biological motion, activation was dependent on the type of biological motion stimulus (Downing et al., 2001; Peelen and Downing, 2005b). Activation was significantly stronger for point-light walkers that possess strong form cues (SW, SS) than for the two types of the Cutting walker (CW, CS). As mentioned earlier, the SW and SS stimuli convey stronger form information by tracing the outline of the figure due to the high temporal frequency of SW. I suggest that this additional global form information could be responsible for the higher activation in EBA compared to CW, where no contours were visible. Furthermore, EBA responses were similar to moving and static stimuli of each respective stimulus type (CW similar to CS, SW similar to SS). This is consistent with previous work showing that EBA is activated by both moving and static human figures (Downing et al., 2001).

Unlike ventral stream areas, the CW, the SW, and the SS stimulus similarly activated motion-sensitive areas KO and MT. Similar activation by CW and SW may occur because both stimuli present a moving walker. The motion of the limbs may drive MT and KO responses even if local motion signals are missing as in the SW case. However, this does not explain the activation for the SS stimulus. Activation by the SS stimulus (and also possibly the SW stimulus) could result from the flickering of the dots, which may induce illusionary contours and possibly some apparent motion along the limbs. Dorsal stream areas are known to respond to flicker revealed by fMRI (Tootell and Taylor, 1995; van Oostende et al., 1997). However, Lagae et al. (1994) demonstrated that the responses in monkeys' MT complex to flickering dots are lower than responses to real motion. Furthermore, the effectiveness of flicker stimulation decreases very much in higher dorsal areas (e.g. V3A and lateral occipital sulcus)

(Murray et al., 2003). This is also true for the ventral pathway, for both apparent and real motion (Liu et al., 2004).

I also obtained activation in frontal regions, here in the IFG and the superior precentral sulci (part of the premotor cortex). Higher activation of the (left) IFG could be due to the comparison of possible human figures with impossible ones (Stevens et al., 2000). Although the performance level for the four conditions was very similar, it seems plausible that stimuli containing intact motion information (CW) or strong form information (SW, SS) are much more vivid than CS. Possibly, subjects were simply faster in decision-making, which could results in less IFG activation. Indeed, a two-way repeated measures ANOVA with the factors condition and ROI showed that there was an effect of response time ($p = 0.034$, post-hoc test).

The responsiveness to biological motion in the premotor cortex could result from the involvement of the premotor cortex in action observation (Gallese et al., 1996). Several studies revealed that monkey's area F5 (the putative homologue for the human premotor cortex), respond to an executed hand movement and also to the same or a similar observed action (Grafton et al., 1996; Gallese et al., 1996; Rizzolatti et al., 1996). These neurons are called mirror-neurons. The mirror neuron system is also activated by biological motion as observed in an fMRI study from Saygin et al. (2004b). The authors concluded that the observer's motor system is recruited to fill in the simplified biological motion displays and that the motion information in body actions can drive frontal areas. In my data, premotor cortex activation in the static CS and SS conditions also occurred, although this activation was less extensive compared with the moving conditions. This difference could possibly explain why Saygin et al. found activation when they compared biological motion with static point-light figures.

2.5 Conclusion

In summary, I revealed that the activations to biological motion in areas of the ventral stream (FFA/OFA and EBA) were depended on the amount of form information in the stimulus and were not driven by local motion signals. The SFL walker, which contains form but lacks motion information, activates these areas more strongly than a stimulus that contains local image motion or a stimulus that is presented in a specific static posture (static Cutting walker). This suggests that these areas are recruited for biological motion perception, particularly in the absence of local motion signals.

Chapter 3

Brain activity for peripheral biological motion in the posterior superior temporal gyrus

3.1 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) (Bonda et al., 1996; Saygin et al., 2004; Grossman and Blake, 2001; Grossman and Blake, 2002; Grossman and Blake, 2004; Grossman et al., 2005; Beauchamp et al., 2003; Santi et al., 2003; Peuskens et al., 2005; Pelphrey et al., 2003; Puce et al., 1998; Grèzes et al., 2001; Thompson et al., 2005) and gyrus (pSTG) (Vaina et al., 2001; Servos et al., 2002; Santi et al., 2003; Grèzes et al., 1998; Howard et al., 1996) and the fusiform gyrus (Bonda et al., 1996; Vaina et al., 2001; Beauchamp et al., 2003; Peelen and Downing, 2005b; Grossman and Blake, 2004; Grossman and Blake, 2002; Pelphrey et al., 2005; Ptito et al., 2003; Santi et al., 2003). Most of these studies reported stronger activation in the right pSTS/STG than in the left pSTS/STG (Bonda et al., 1996; Pelphrey et al., 2003; Puce et al., 1998; Grèzes et al., 1998; Grossman et al., 2000; Grossman and

Blake, 2001; Grèzes et al., 2001; Peuskens et al., 2005; Beauchamp et al., 2003; Santi et al., 2003; Wheaton et al., 2004; Grossman et al., 2005). A possible explanation for this asymmetric activation pattern is a functional lateralization. However, previous imaging studies have used only foveal and 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 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); and also the motion-induction mechanism, in which a point-light walker induces a motion percept in background stimuli, works for peripheral presentation. 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 (see chapter 4).

The processing of peripheral visual stimuli is organized retinotopically in lower and mid-level visual areas (Engel et al., 1997; Sereno et al., 1995; Huk et al., 2002) and the strongest activations occur usually in the hemisphere contralateral to the stimulus. Higher visual areas, such as pSTS/STG, 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 Perret, 1994). Here I use the BOLD activations in posterior temporal cortex to investigate the organization of pSTS/STG for peripheral biological motion stimulation.

3.2 Methods

3.2.1 Participants

Twelve right-handed, neurological healthy males (mean age 29.4 ± 5 years) from the University of Münster and from the University of Düsseldorf participated in the study. Two of them wore non-magnetic goggles to correct for shortsightedness. The study was

approved by the Ethics Committee of the Heinrich-Heine-University Düsseldorf and all subjects gave written informed consent. Apart from the experimenters, they were not informed about the purpose of the study. Three of the participants were unfamiliar with point-light biological motion. I recruited only males, because it was shown that brains of males and females 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).

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 pSTS/pSTG. Thus, the data of nine participants are presented in this study. The same group of subjects participated in the experiments described in chapter 4.

3.2.2 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. 3.1 A) or to the right (Fig. 3.1 B). 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 (SFL walker, Beintema et al. (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 800 ms, which corresponded to one step plus 100 ms.

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 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. Three red dots were continuously present, and marked the centers of the possible the stimulus locations. These locations were at visual eccentricities –20° (i.e. to the left), 0°, and +20° (i.e. to the right; Fig. 3.1 C). 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. I recorded three functional runs resulting in 27 trials per condition. The order of the 81 trials within a functional run was randomized.

3.2.3 Procedure and Experimental design

The fMRI experiment was performed in an event-related design. Each subject participated in three consecutive fMRI scans and had a final high-resolution MRI scan.

Throughout fMRI scanning, subjects fixated a red dot in the center of the screen (Fig. 3.1 C). 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 inter-stimulus-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.

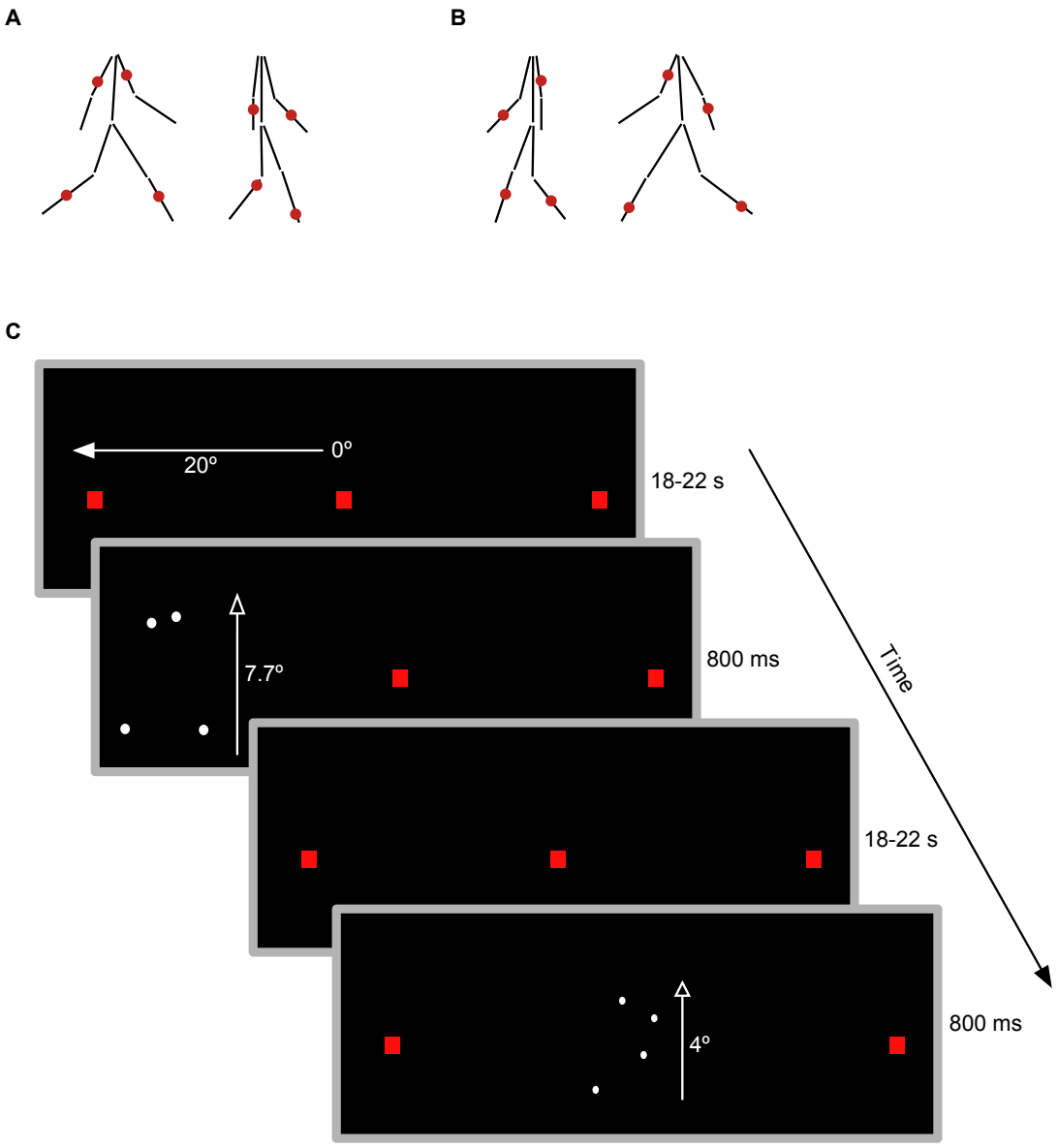

Fig. 3.1: **Illustration of the biological motion stimulus and the experimental design.** The stimulus was either rightward facing **(A)** or leftward facing **(B)**. Stimuli were presented as white dots on a dark background in a frame-by-frame video animation. Four light-points were presented for each stimulus frame. The dots were located on random positions between the main joints of the arms and legs (black lines, not visible during the experiment). **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 a baseline 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.

3.2.4 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 home-written 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 slices (interslice gap 0.1 mm, sag-cor-trans-orientation) were acquired oriented parallel to the anterior-posterior commissure plane to cover the whole brain. 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 view): 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).

3.2.5 Image processing and data analysis

Standard preprocessing was performed, including motion correction, slice time scan correction, and linear trend removal, as implemented in the BrainVoyagerQX 1.6/1.7 software package (Brain Innovation B.V., Maastricht, Netherlands). For each subject, the 3-D images were transformed into Talairach space. Anatomical locations of the position of activation was estimated with the reference to the standard stereotaxic atlas (Talairach and Tournoux, 1988) and a brain atlas (Mai et al., 2004). 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, I applied a spatial smoothing in 3-D (kernel: 4 mm full-width at half-maximum), linear trend removal and temporal high-pass 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 six seconds before stimulus presentation served as baseline data.

3.2.6 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 Hochberg, 1995; Genovese et al., 2002). For the group analysis, I first contrasted the biological motion conditions at –20°, 0°, and at +20° against baseline and against scrambled controls, respectively. Note that this comparison included all biological motion stimuli, hence irrespectively whether correctly identified or not (see 4.3 for the contrast correctly identified biological motion versus scrambled controls). Next, I compared each of the biological motion conditions to the specific scrambled control conditions, e.g. –20° versus scrambled controls at –20°. Finally, I contrasted the stimuli with different facing directions for each of the biological motion condition versus baseline.

For single-subject analysis, I performed a peak activation analysis in the pSTS/STG. Here, I used the same contrasts as for the group analysis (except of the contrast biological motion versus scrambled controls). I 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 pSTS/STG region was defined by anatomical criterions. For statistical comparisons outside BrainVoyager I used ANOVAs or two-tailed paired t-tests.

3.2.7 Behavioral data analysis

To check fixation control, for three 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 I determine trials in which a saccade occurred during the stimulus presentation. This was less than 1% of cases. The other subjects were tested for their ability to fixate before they entered the scanning session and showed similar fixation ability.

The analysis of the behavioral responses of the 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 (82% versus 64%, rmANOVA, $F_{1,60} = 12.5$, $p < 0.001$).

3.3 Results

3.3.1 Group activation

Figure 3.2 shows flat maps of BOLD activation against baseline for stimulation in the left, central, and right visual field. There were significant activations in several early visual areas (V1, V2, MT) and in biological motion related areas (pSTS/STG, fusiform gyrus, Insula (Pelphrey et al., 2005; Saygin et al., 2004), premotor and (inferior) frontal gyrus (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 early visual areas. pSTS/STG activation occurred only in the right hemisphere. Figure 3.3 shows the activation by peripheral stimulation in sections through early visual cortex, fusiform gyrus, and pSTS/STG. For early visual areas and the fusiform gyrus, stimulation in the left visual field (blue) activated more strongly the right hemisphere, and stimulation in the right visual field (yellow) activated more strongly the left hemisphere. In pSTS/STG, 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). A similar area was also activated for central stimulation (x = 63, y = –37, z = 16). For central as well as for peripheral stimulation activation was stronger than for scrambled controls in the right pSTS/STG (Fig. 3.4). Note that the activation location for this contrast was slightly different than for the condition to baseline comparisons. No activation was found in the left hemisphere at the statistical threshold for the different experimental conditions.

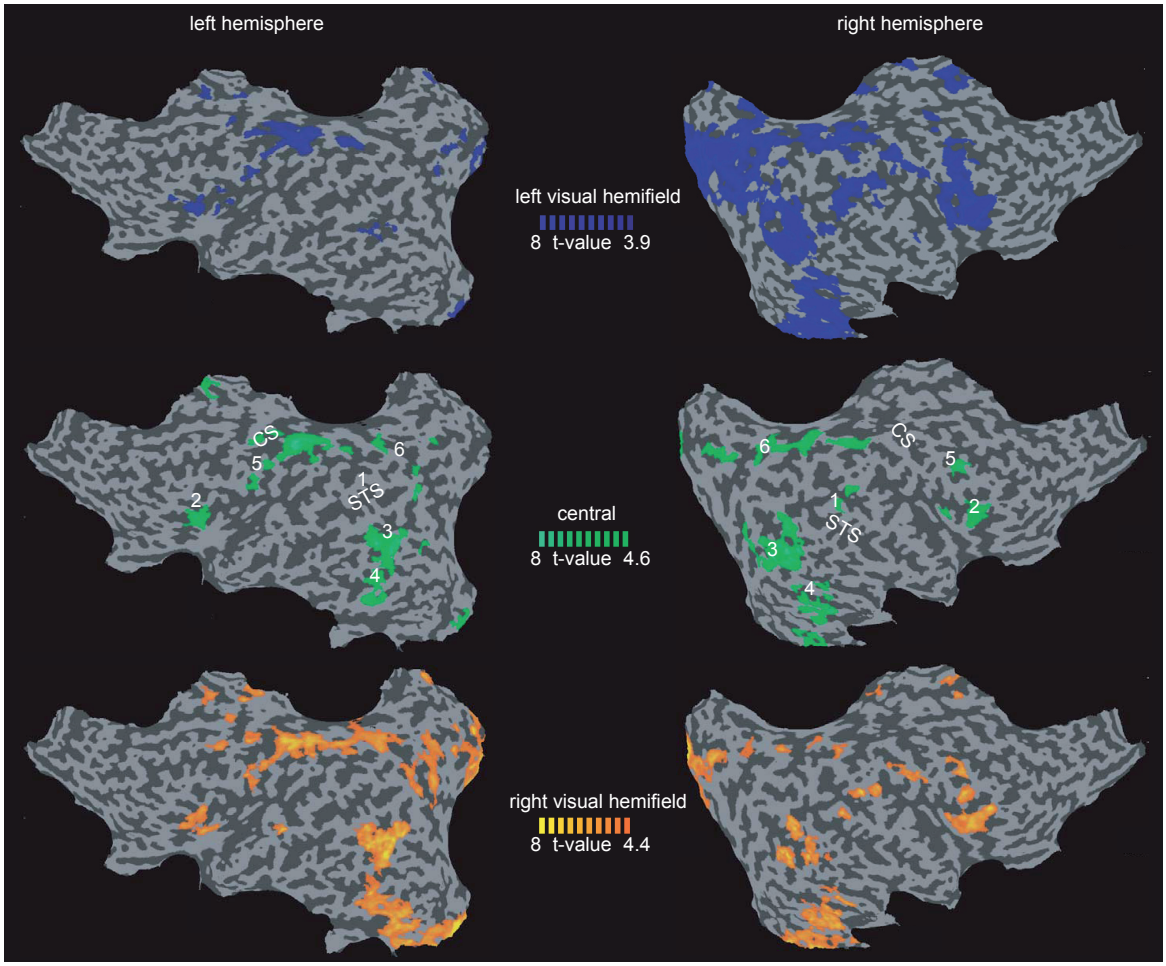

Fig. 3.2: **Group activation map (random effect analysis; p $<$ 0.0001, corrected for multiple comparisons) for biological motion presented in the left visual hemifield (blue), central (green), and in the right visual hemifield (orange) versus baseline on a flattened Talairach-normalized brain of one subject.** Numbers plotted on the flatmaps for centrally presented stimuli correspond to pSTS/STG **(1)**, Insula **(2)**, middle temporal (MT) area and extrastriate body area (EBA) **(3)**, fusiform gyrus **(4)**, premotor cortex **(5)**, and parietal cortex **(6)**. Dark and light grey regions represent sulci and gyri respectively. STS, superior temporal sulcus; CS, central sulcus. Activation for peripheral biological motion conditions is stronger in the contralateral hemisphere. Note that in all conditions pSTS/STG occurred only in the right hemisphere.

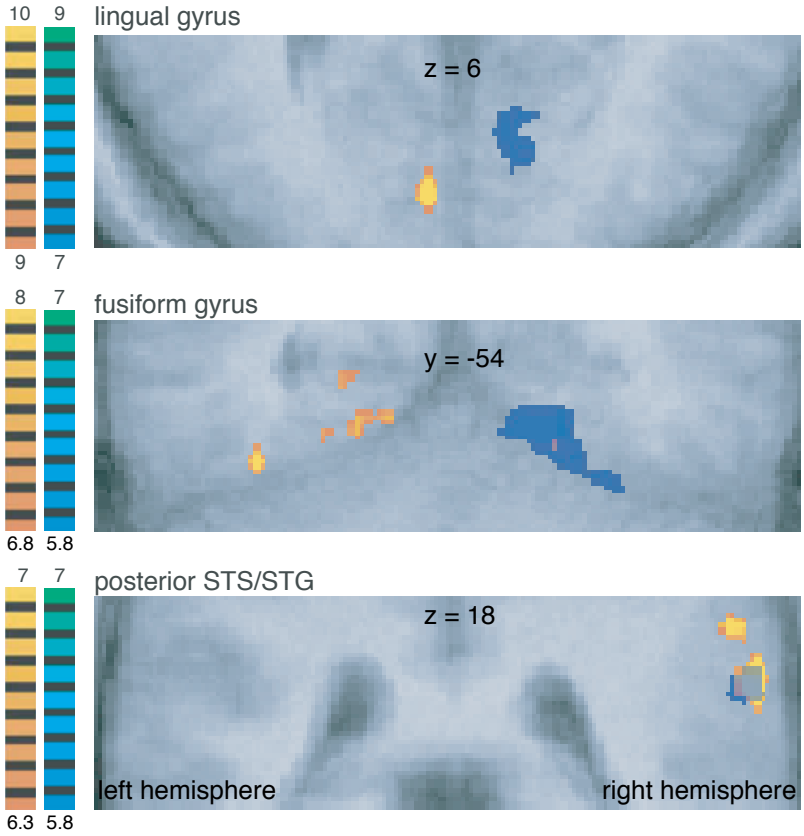

Fig. 3.3: **Group activity (all p < 0.001) evoked by peripheral biological motion in three visual regions.** Condition-specific t-values for two peripheral biological motion conditions are indicated by the different color-bars. In blue colors, activation is shown for stimuli presented in the left visual hemifield. In orange colors, activation is shown for stimuli presented in the right visual hemifield.

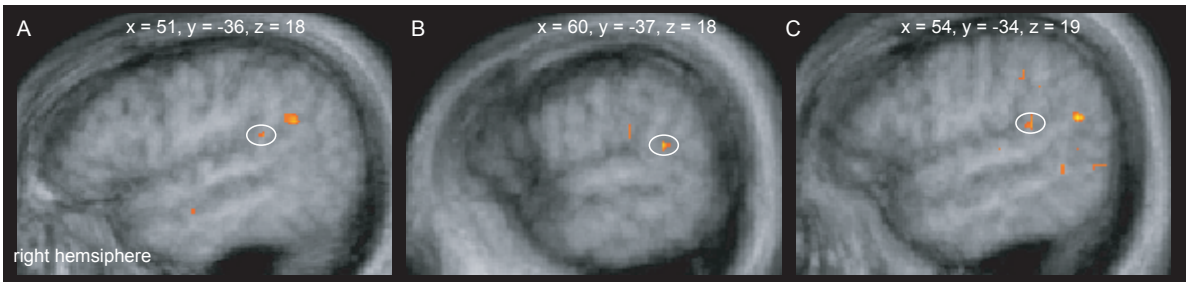

Fig. 3.4: **Statistical activation maps for the contrast biological motion versus scrambled controls (t > 2, p < 0.05, random effect analysis).** Results are shown for biological motion stimuli presented in the left visual hemifield **(A)**, for centrally presented stimuli **(B)**, and for stimuli presented in the left 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 pSTS/STG close to the fissura lateralis (white circles).

3.3.2 Single-subject analysis of hemifield organization in right pSTS/STG

In the group data, activations of the right pSTS/STG by stimulations in the left and right visual field appeared largely overlapping. However, the single-subject analysis revealed a consistent difference in the representation of the left and right hemifields in the right pSTS/STG. Figure 3.5 shows the activations for the different hemifield stimuli (blue: left, yellow: right) in coronal slices through the pSTS/STG for each of the nine participants. All of them show distinct activations for left and right visual field stimulations, respectively. The peak locations for each hemifield stimulus are listed in Table 3.1. Paired t-tests revealed a significant difference in x-Talairach coordinates ($p < 0.05$), showing that activation to left hemifield stimulation was more lateral than activation to right hemifield stimulation. Although 7/9 subjects showed more lateral activation for stimuli presented in the left hemifield and more medial activation for stimuli presented in the right hemifield it is noteworthy that the effect in pSTS/STG is small. Specifically, the mean difference for the two experimental conditions was only 4 mm and therefore only slightly larger than the functional voxel resolution (3 mm). In terms of this, the results rather reflect a statistical trend. The hemifield organization observed for biological motion was not found for scrambled controls.

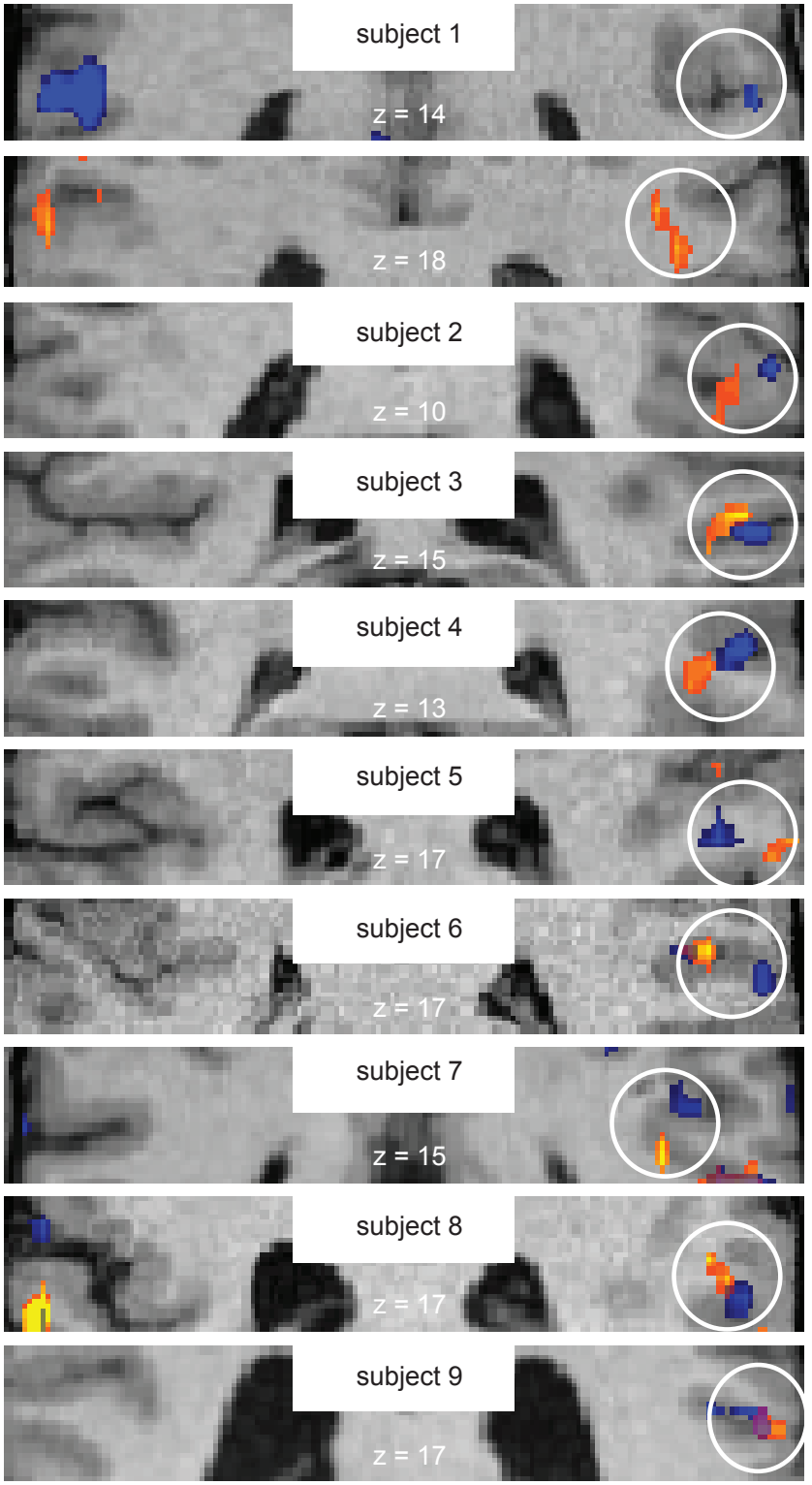

Fig. 3.5: **Activation patterns in the right pSTS/STG for the two peripheral biological motion conditions versus baseline for the nine subjects.** Peak activations for stimuli presented in the left visual hemifield are shown in blue and for stimuli presented in the right visual hemifield are shown in orange. For subject one, two coronal slices are shown. All activation clusters have a size of > 10 mm^3 and are shown at $p < 0.05$ (for exceptions see Table 1).

right hemisphere

stimulus location	left	right	left	right	left	right	left	right
				Talairach coordinates				
subject	x		y		z		t-max	t-max
1	**54**	**46**	-46	-39	14	18	3.2*	3.1*
2	**60**	**51**	-42	-40	13	10	7.1	7.3
3	**59**	**55**	-33	-34	13	15	5.8	5.1
4	**57**	**51**	-38	-37	16	13	7.5	4.1
5	**52**	**59**	-35	-34	18	15	4.4	4.8
6	**61**	**50**	-36	-33	16	18	6.4	6.1
7	**48**	**42**	-48	-45	18	15	4.9	5.2
8	**57**	**54**	-35	-35	16	19	5.9	4.3
9	**61**	**61**	-43	-43	18	17	6.1	5.5
paired t-test	p = .039		p = .056		p = .827			

Table 3.1: **Talairach coordinates and t-values of the activation peaks in right pSTS/STG for biological motion stimuli presented in the left and in the right visual hemifield.** t-values are reported at $p < 0.05$ corrected for multiple comparisons (* $p < 0.01$ uncorrected). The difference in the location of the activation peaks for stimuli from different visual hemifields was significant only for the x-Talairach coordinate.

3.4 Discussion

The results of the present investigation are twofold. First, peripheral biological motion stimuli from both visual hemifield activate, beside other areas, the right pSTS/STG. Second, within the right pSTS/STG, stimuli from the two visual hemifields activate different sub-fields.

The result for right pSTS/STG activations are in accordance with functional brain imaging studies that investigated the neuronal correlates for biological motion with parafoveal stimulation. Most studies have found only right-hemispheric activation (Bonda et al., 1996; Puce et al., 1998; Grossman et al., 2000; Hirai et al., 2003; Pelphrey et al., 2003; Beauchamp et al., 2003; Santi et al., 2003; Grossman and Blake, 2004; Pavlova et al., 2004; Grossman et al., 2005; Peelen et al., 2006). This experiment adds to this data that the lateralization is also present for peripheral stimulation. This is indicative of a functional lateralization of biological motion perception, but the nature of this lateralization remains a matter of speculation.

I further found that the hemifield of origin of the stimulation is preserved within the right pSTS/STG. This not only shows that right pSTS/STG indeed receives input

from both hemifields but that this input is represented in different sub-fields of the right pSTS/STG. This result is not expected on the basis of electrophysiological studies, because higher areas in monkey's STPa do not show any retinotopic organization (Bruce et al., 1981; Motter et al., 1987; Perrett et al., 1989), and because receptive fields in monkey's STPa are very large and often include ipsilateral as well as contralateral areas of the visual field. However, in the monkey both left and right STS show responses to biological motion (Oram and Perret, 1996; Jellema and Perrett, 2003a; Jellema and Perrett, 2003b). The sub-fields observed in human pSTS/STG may be related to the lateralization of biological motion processing in humans.

The sub-fields of pSTS/STG were found consistently on individual subject analysis, but were not reflected in the group analysis. The reason for this is that the small differences in the relative locations of these sub-fields disappear in the average clusters due to inter-individual differences in brain anatomy (c.f. Fadiga (2007)). This difference underscores the importance of single-subject analyses for the interpretation of functional imaging data. Nevertheless, the results observed on single-subject level were small and it needs additional research to support my interpretation of the data.

3.5 Conclusion

The results of this experiment demonstrated that the neuronal network for peripheral biological motion shows similarities, but also dissimilarities, when compared to central biological motion. One similarity was that for different stimulus locations areas of the ventral as well as areas of the dorsal pathway were activated. However, one major difference was that the peripherally presented point-light walkers activated different regions of the pSTS/STG. This suggests that not only early visual areas but also specific higher visual areas are organized retinotopically. However, this result does not provide a physiological explanation for the observation that subjects recognized peripherally presented point-light walkers with a facing direction away from the central fixation dot more often than when those were facing towards the fixation dot. In addition, it needs to be established whether or not the contralateral preference of the fusiform gyrus (for peripherally presented biological motion stimuli) may indicate that this hemisphere is specifically engaged in biological motion perception. I will investigate these two topics in the following chapter.

Chapter 4

Interaction of visual hemifield and body view in biological motion perception

4.1 Introduction

4.1.1 Is there a link between the perception and cortical activation for peripheral biological motion stimuli with different facing directions?

The idea for this fMRI experiment started from the observations from colleagues in the lab. de Lussanet and others found that when a point-light walker was observed from the corner of the eye, it depicted more natural and vivid when it faced away the point of gaze than when the stimulus faced towards it. One hypothesis by de Lussanet et al. was that this asymmetric appearance of the facing direction could be caused by an asymmetric representation of the human body in the brain. They tested this hypothesis systematically by subsequent psychophysical experiments. In the first experiment observers were requested to discriminate the direction of facing of point-light stimuli depicting a side view of human walking. The stimuli were presented either centrally (= foveally and parafoveally) or in the visual periphery. They found a strong interaction between visual hemifield and the walker's facing direction. Subjects' response rates were better for walkers facing away from the fixation point than walkers facing towards it.

The results could not be explained by the so-called stimulus-response compatibility (SCR) effect (Fitts, 1954). For example, the SRC is expressed by shorter reaction times, as a result either from a coupling of the spatial location of the stimulus (e.g. right visual hemifield) and its facing direction (e.g. right). The authors argued that the SCR effect is unlikely to explain their results, because subjects were instructed to respond correct rather than to respond as fast as possible. Indeed it was found that median response times did not show a significant interaction between stimulus location and facing direction.

Furthermore, de Lussanet et al. showed that the facing effect still occurs when subjects were requested to discriminate between scrambled and normal point-light figures (4.1 A, B) presented in the visual periphery (e.g. left facing walkers were better discriminated from scrambled stimuli when they were presented in the left visual hemifield). Noteworthy, the effect was present although the facing direction was irrelevant to accomplish the task.

Moreover, de Lussanet et al. demonstrated that the facing effect also occurs for the classical point-light walker, thus, arguing against visual perception-related factors. The facing effect was also still present when only the fore-half of the stimulus was shown (Fig. 4.1 C) but not the backswing of the lower limb, which has been demonstrated to facilitate to discriminate the body orientation (Mather et al., 1992; Troje and Westhoff, 2006). Even when observers saw static point-light walkers with different facing directions – portraying different body configurations but no action – the facing effect remains stable.

By excluding possible influences of response biases and low-level perceptual factors that could explain the facing effect, de Lussanet et al. then hypothesized that the facing effect is a results of observers self-embodiment in the presented stimuli. This hypothesis based on the findings that humans can embody themselves in other through the mirror-neuron system (Rizzolatti and Craighero, 2004). This system, originally discovered in monkey's PMC (Rizzolatti et al., 1996; Gallese et al., 1996), contains neurons that discharge both when individuals act and when they see someone else performing the same action. Specifically, the network of human cortical areas activated by action observation comprises the vPMC, IFG, STS and the IPL. 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).

To test whether or not the facing effect remains a stable effect, even when the body

configurations depicted not walking, subjects saw 'spider-like' crawling or conventional crawling (Figure 4.1 D and E). Indeed de Lussanet et al. demonstrated that recognition rates were highest for crawling figures that faced away from the fixation point compared to those facing towards the fixation dot.

On the basis of these findings I propose that there may be an interhemispheric interaction between the lateralized visual input and the motor representations of the human body if it is seen as a side view in the visual periphery. To this end, each visual periphery may be best represented in contralateral visual areas and each body side is best represented in the contralateral motor and somatosensory cortex. In other words, 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. I will describe in the method section of this chapter a BOLD contrast to test this hypothesis.

4.1.2 Is there a sub-field organization for point-light walkers with different facing directions?

In chapter 3, I showed that the right pSTS/STG possesses a sub-field organization (retinotopy) for peripherally presented stimuli. However, sub-fields can be also emerge from other stimulus properties, e.g. the facing direction. The hypothesis is that objects from the same type (here point-light walkers with different facing directions) are represented in different sub-fields within higher visual areas. The idea for this hypothesis came from cell recordings in monkeys.

Electrophysiological studies in STPa 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) (Oram and Perret, 1994; Oram and Perret, 1996; Jellema et al., 2004). Other neurons in STPa respond to static views of bodies or faces (Perrett et al., 1991; Perrett et al., 1994). Since biological motion perception may be achieved by the analysis of templates (Lange et al., 2006; Lange and Lappe, 2006) or snapshots (Giese, 2004) of human body configuration it is interesting to investigate any functional specialization within pSTS/STG 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; Tsao et al., 2003; Pinsk et al., 2005). 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 features critical 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, 2005b). 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 not only in pSTS/STG but also 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). Therefore, I will investigate in the second part of this chapter the BOLD responses to left and right facing point-light walkers.

4.2 Methods

For the experiment, I examined the same subject group and used the same procedure, experimental design, data acquisition parameters and stimuli (see Fig. 4.1) as described in chapter 3. For the functional data I first verified that the peripherally presented biological motion stimuli compared to baseline and compared to scrambled motion activate the same areas that have been published for centrally presented biological motion. However, in contrast to the statistical comparison of chapter 3 that was:

peripherally presented biological motion versus baseline, I now compared only correctly identified biological motion stimuli to baseline and scrambled motion respectively.

Then I calculated the two main contrasts that is first the contrast for the two oppositely facing stimuli for each visual hemifield: For the left visual hemifield, this was the contrast *facing left* versus *facing right*, and for the right hemifield *facing right* versus *facing left*. The second contrast was the comparison *facing left* versus *baseline* and *facing left* versus *baseline* to investigate the existence of a sub-field organization in higher visual areas.

For contrast one, only clusters larger than 100 anatomical voxels (2.5 functional voxels) and $t > 3.25$ ($p < 0.01$) are reported. For contrast two, I also performed a peak activation analysis on single-subject level in the pSTS/STG and in the fusiform gyrus. The size of the region of interest was defined by anatomical criterions. For example for the fusiform gyrus the occipito-temporal sulcus was used as the lateral and the collateral sulcus was used as the medial border. For the posterior border, I selected the anterior tip of the parietal-occipital sulcus and for the anterior border the anterior end of the occipital-temporal sulcus. I 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 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 to generalize the activation to the population level.

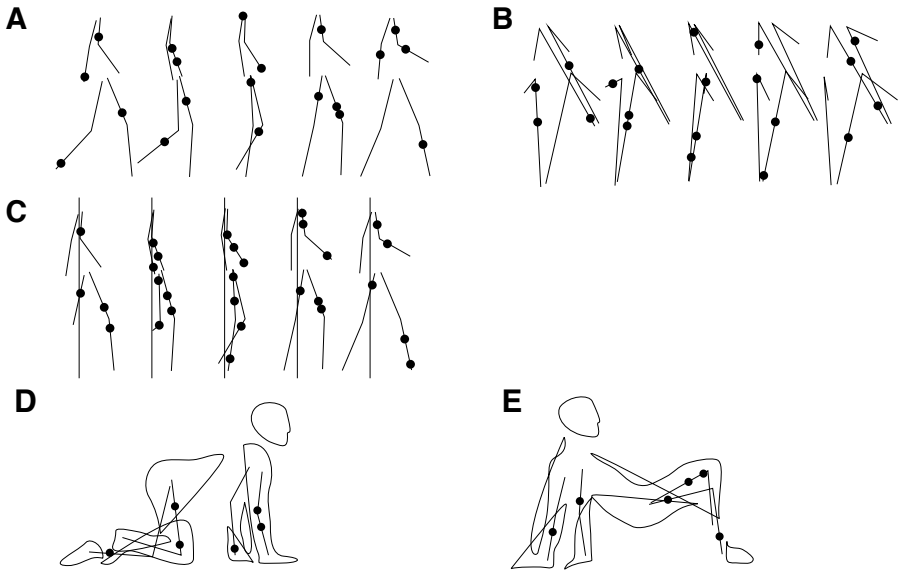

Fig. 4.1: **Schematic illustrations of a subset of the stimuli used in the experiment.** The lines connecting the limb segments were not visible in the experiments. **A** An example out of 9 recorded walking cycles. **B** Scrambled walker's joints received a pseudo-random offset, such that the bounding box remained of the same size, and left and right joints got the same offset. **C** Points in the walkers' back half were invisible. The visible front half was shifted back to be centered at the target position. **D**, **E** The two kinds of recorded crawling movements. In this experiments only the stimuli shown in **A** and **B** were used. Thanks to Marc de Lussanet for providing these stimuli.

4.3 Results

4.3.1 Is there a link between the perception and cortical activation for peripheral biological motion stimuli with different facing directions?

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. 4.2 A). This activity was clearly separated from the region showing the facing effect (cf. circles in Fig. 4.3 E, F). Similar to the results of chapter 3, also correctly identified biological motion (compared to baseline) activated regions of the early visual cortex, regions of dorsal pathway such as the MT complex, and regions of the ventral pathway such as the fusiform gyrus. Additional, significant

activation was found in the Insula, the (inferior) frontal gyrus, premotor cortex, and the posterior parietal cortex. When correctly identified (centrally and peripherally presented) biological motion was contrasted against scrambled controls, a common finding was that the right STS/STG was activated (Fig. 4.2 B). This has been so far only reported for centrally presented biological motion (Vaina et al., 2001; Grossman et al., 2000; Servos et al., 2002). In contrast, the STS/STG region was not differentially activated by outward versus inward facing walkers, suggesting that it cannot account for the facing effect.

Figure 4.3 plots the contrast between left facing and right facing walkers in the left visual hemifield and between right facing and left 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 (MeFG) in the right hemisphere (Fig. 4.3 D: 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 right facing walkers in the right visual hemifields, but the activation difference in the left hemifield did not reach the significance criterion (data not shown).

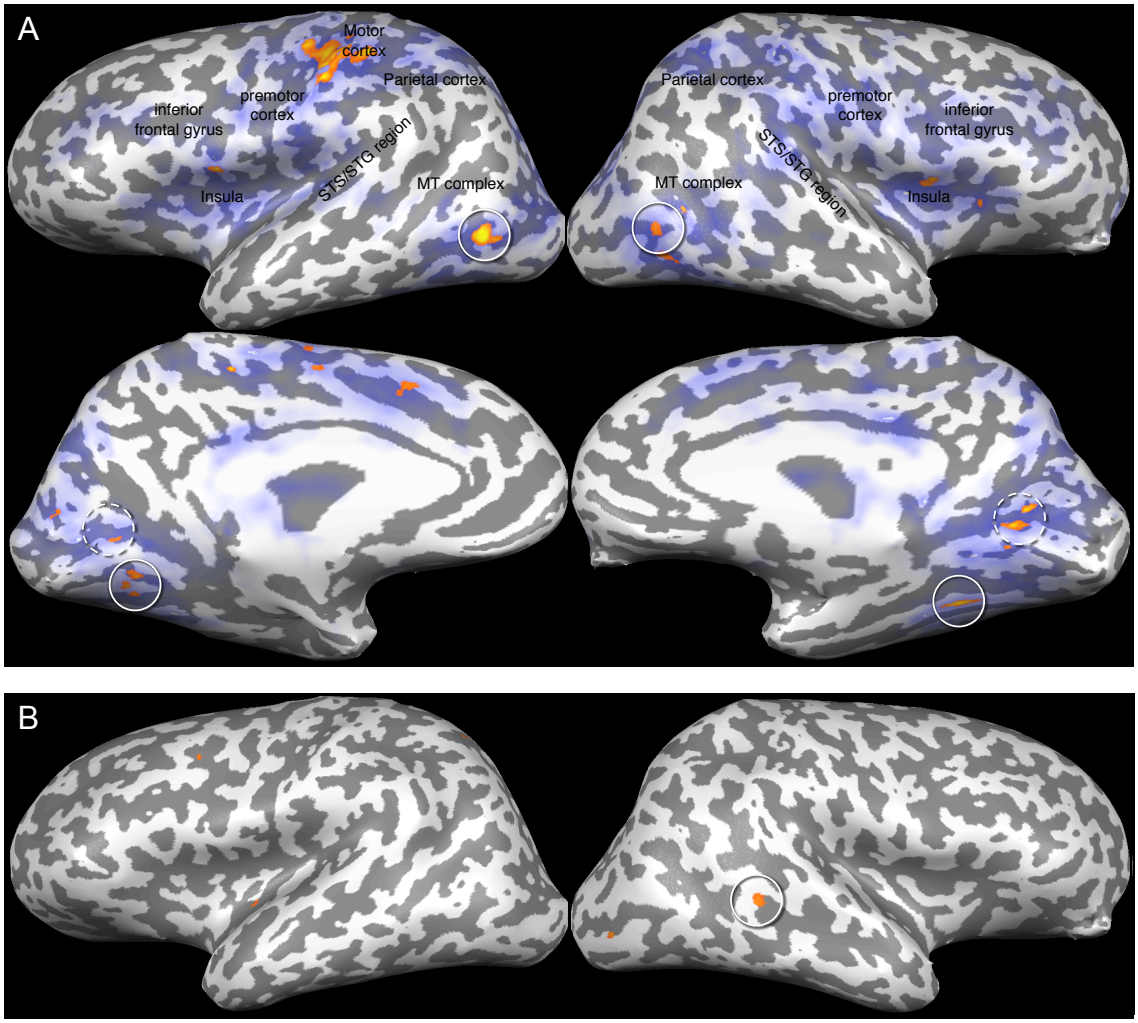

Fig. 4.2: **Illustration of peripheral biological motion activations.** **A** Overview of activation in trials with correctly identified biological motion compared to baseline activity (orange-yellow: $8.0 < t < 15$, transparent blue: $t > 2$). The largest activity is motor and somatosensory activation 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). a, anterior; p, posterior; L, left hemisphere; R, right hemisphere. **B** Activation in trials with correctly identified biological motion compared to the scrambled control conditions ($t > 3.25$: $p < 0.01$). 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).

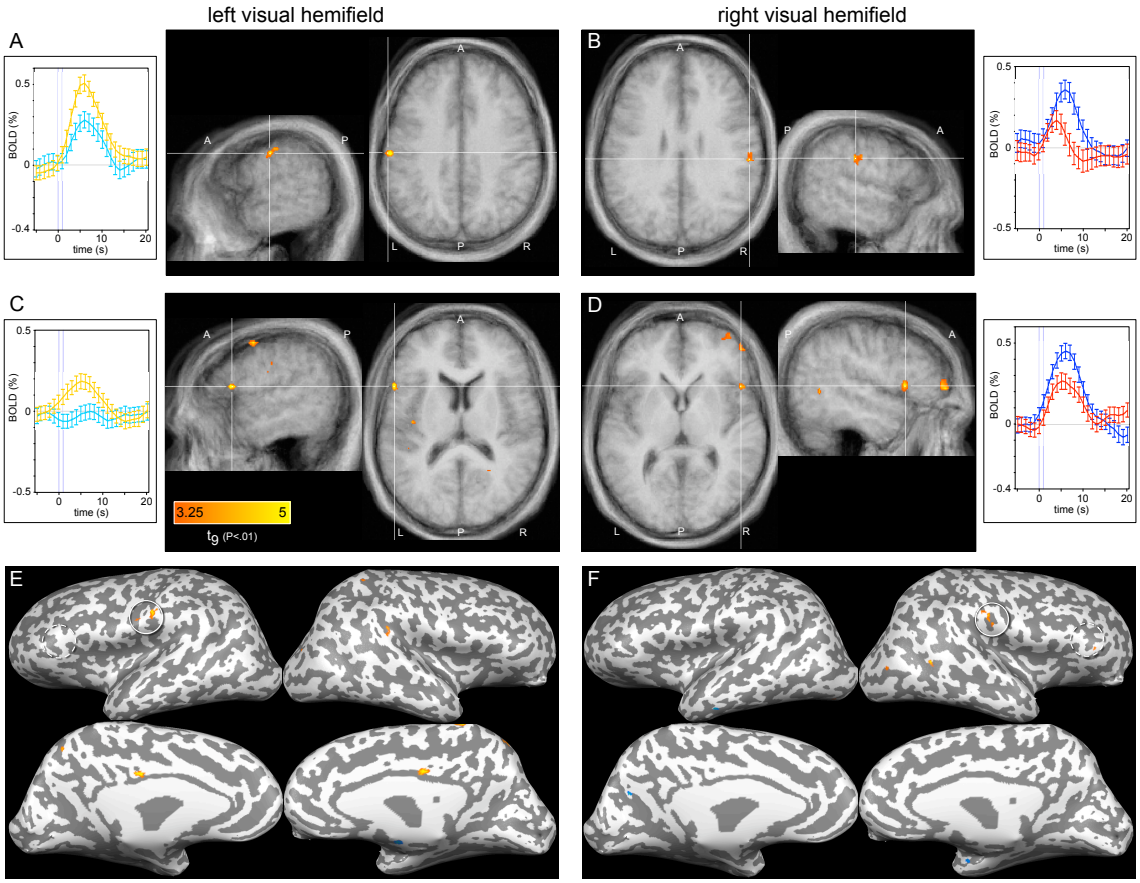

Fig. 4.3: **Illustration of the facing effect.** Statistical activation maps and BOLD responses (% signal change with standard error) for the two sites that show the facing effect ($t > 3.25$: $p < 0.01$, random effect analysis). (A, C): BOLD signal change in the right visual periphery: facing right > facing left (turquoise and yellow BOLD curves). (B, D): BOLD signal change in left visual periphery: facing left > facing right (red and blue BOLD curves). (A): left BA 2 (Brodmann area 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 subjects. (E,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 subjects. Dark and light grey regions represent sulci and gyri, respectively. L, left hemisphere; R, right hemisphere; A, anterior; P, posterior.

4.3.2 Is there a sub-field organization for point-light walkers with different facing directions?

I next analyzed BOLD responses to the two facing directions (left, right) for the peripherally presented stimuli compared to baseline activity. For the fusiform gyrus, Figure 4.4 shows group activity against baseline for left facing (blue) and right facing (yellow) walkers in each hemifield. The left side of Figure 4.4 shows activations from stimuli in the right hemifield; the right side shows activations from stimuli in the left hemifield. The coronal sections (Fig. 4.4 A) show distinct activation clusters for the different facing directions. In the left fusiform gyrus, activation for left facing stimuli was was more lateral (x = –36, y = –56, z = –18) than for right facing stimuli (x = –30, y = –55, z = –18). In the right fusiform gyrus, activation for right facing stimuli was more lateral (x = 29, y = –40, z = –19) than for left facing stimuli (x = 23, y = –44, z = –17). The extent of the activation clusters is shown in Fig. 4.4 B on an inflated brain. In contrast to the fusiform gyrus, pSTS/STG and EBA activations for differently facing point-light walkers mostly overlapped, i.e. did not show a sub-field organization (results not shown).

These results in the fusiform gyrus were corroborated by the single-subject analysis. Figure 4.5 shows activity against baseline for left facing (blue) and right facing (yellow) walkers in each hemifield for the nine subjects. Table 4.1 lists the locations of the peak activations in the fusiform gyrus for each subject. Paired t-tests revealed a significant difference in x-Talairach coordinates, confirming that clusters were different for the two facing directions.

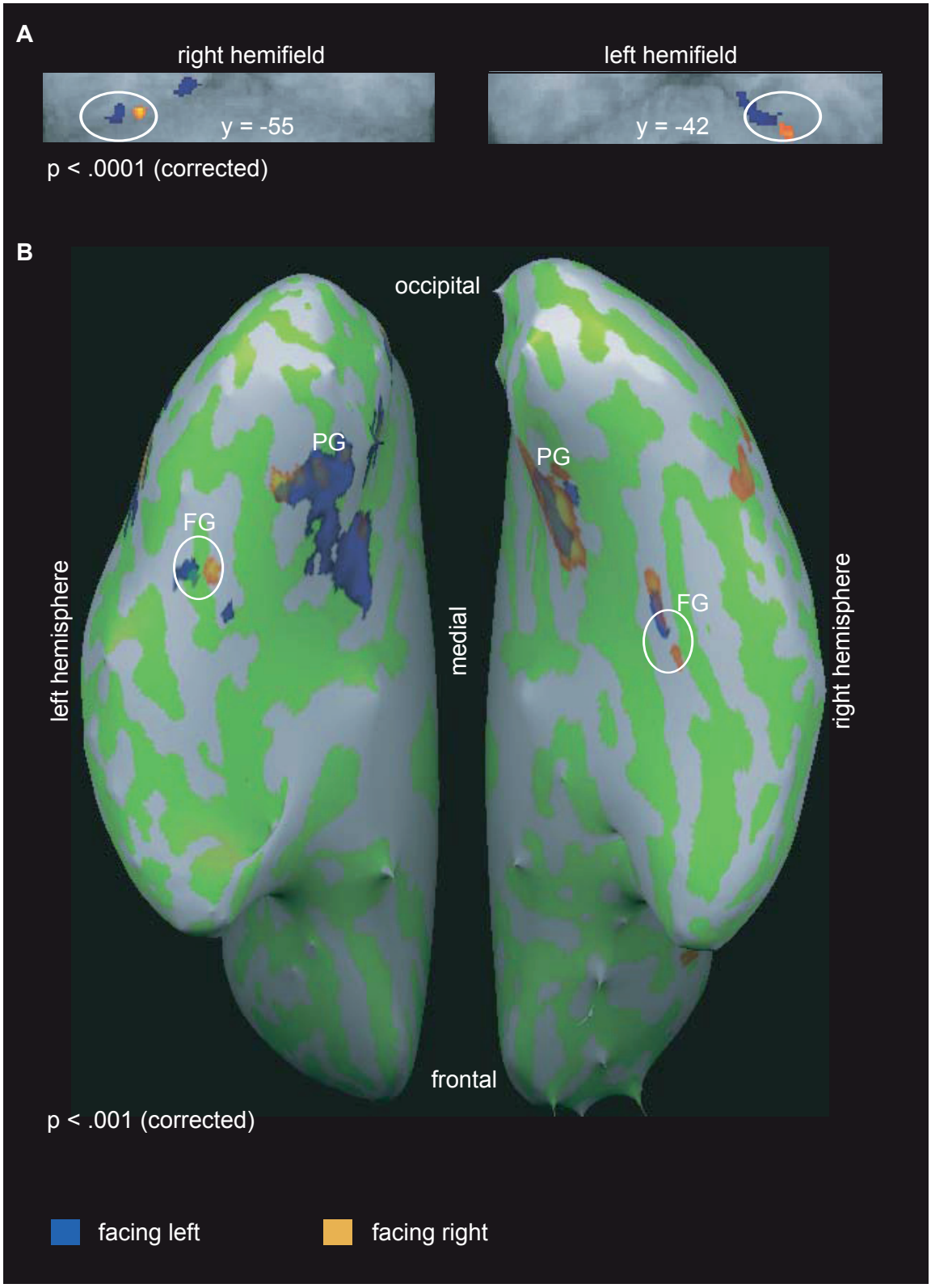

Fig. 4.4: **Group-activity in the fusiform gyrus for contralaterally presented biological motion stimuli with different facing directions.** (A): Activation pattern shown on a coronal slice. The peak activations for left facing stimuli are shown in blue and for right facing stimuli in orange. (B): Group-activity 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. Dark and light grey regions represent sulci and gyri, respectively. Activation clusters for stimuli with different facing-directions were anatomically separated in both hemispheres. PG, parahippocampal gyrus; FG, fusiform gyrus.

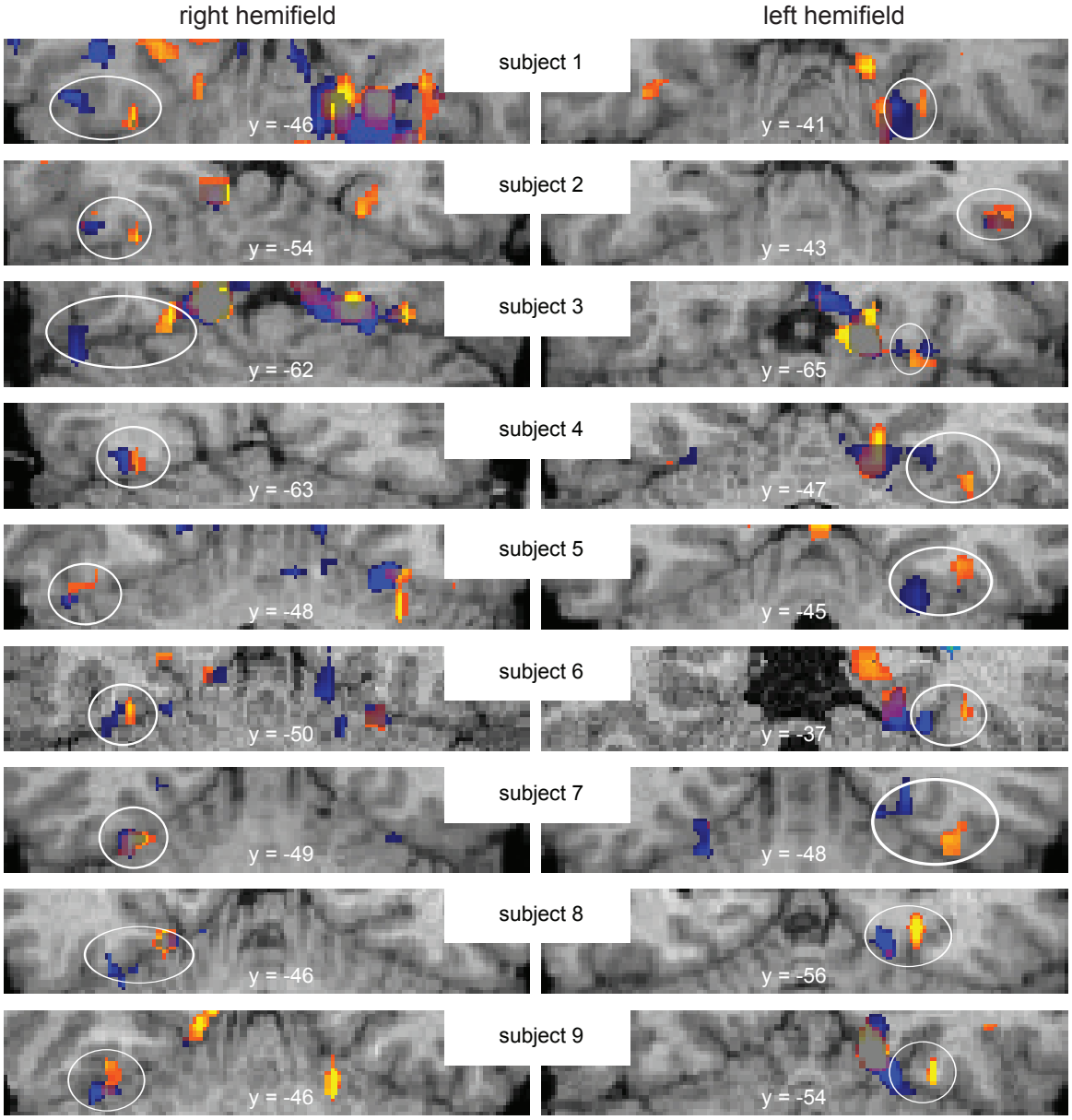

Fig. 4.5: **Single-subject activity in the fusiform gyrus for contralaterally presented biological motion stimuli with different facing directions.** For example, the panels in the left column show activity for stimuli presented in the right visual hemifield. Condition-specific t-values are indicated by the different color bars. The activation peaks (located within the white circles) for left facing stimuli are shown in blue to green and activation peaks for right facing stimuli are shown in orange. t-values are reported at $p < 0.05$ corrected for multiple comparisons (for exceptions see Table 4.1).

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			

Table 4.1: **Talairach coordinates and t-values of the activation peaks in the fusiform gyrus for contralaterally presented biological motion stimuli with facing directions.** t-values are reported at a p-level of < 0.05 corrected for multiple comparisons (* p < 0.01 uncorrected). (A): Activation peaks for stimuli in the right visual hemifield. (B): Activation peaks for stimuli in the left hemisphere. In both the left and in the right visual hemifield the difference for the activation peaks was significant but only for the x-Talairach coordinate.

4.4 Discussion

4.4.1 The human mirror-neuron system and the perception of biological motion

In this fMRI experiment I first replicated the facing effect observed by de Lussanet et al., i.e. that point-light walkers with a facing direction away from the fixation point were better recognized than those facing towards the fixation point.

This result may be surprising from an ecological view (e.g. for a hunter), because

here I would expect the opposite effect that is that objects facing towards the fixation point should be recognized better. I think however that this result can be explained by a brain asymmetry in self-embodiment of the human mirror-neuron system.

I found two areas of the mirror-neuron system, Brodmann area 2 (BA 2) and BA 44, that showed stronger activation for walkers facing away from the fixation point than for walkers facing towards the fixation point. This does not mean that only these two areas are activated by the observation a human walker. For example, Grossman et al. (2004) demonstrated that the activation strength in the STS and the fusiform gyrus for point-light walkers was coupled with the level of training to see such stimuli, which clearly points out that there can be a link between perceptual performance and the BOLD activation strength. Rather, I will discuss the results of the interaction between right-left facing stimuli and right-left visual hemifield presentation.

I think that the following explanation could account for my observation. The human body is processed in extrastriate visual areas, the pSTS and in the fusiform gyrus (Grossman and Blake, 2001; Vaina et al., 2001; Peelen and Downing, 2005b; Peelen et al., 2006). The functional properties of the somatosensory and the premotor cortex allows humans to embody themselves to the observed actions of others (Rizzolatti and Craighero, 2004). Based on the knowledge that the motor and the visual system are engaged in the perceptual process of the human body, and given that both systems are functionally lateralized, perception of peripheral biological motion may be enhanced if both representations are manifested in the same brain hemisphere. This is the case when the observed stimulus faced away from the fixation point, because then it matches the side of the own body in the sensori-motor system to the side in which the stimulus is processed first in the visual system (the contralateral hemisphere).

BA 2 is the most caudal part of the somatosensory cortex and processes somatosensory information from the contralateral body-side. Usually BA 2 is activated bilaterally during touch of the skin (Seitz and Binkofski, 2003). First, it is important to note that the part of BA 2 that responded to the facing effect, did not match the contralateral hand region, which was activated by the (right) hand button-press.

Haslinger et al. (2005) showed silent movie-sequences of piano playing and of meaningless hand-movements to pianists and non-pianists. The authors observed increased activity in the left ventral BA 2 region for the pianists observing right-handed piano playing. This demonstrates (1) that the BA 2 is heavily engaged in the recognition process of observed actions and (2) that the observed lateralization is in line with my

findings.

I think that whenever the subjects embody themselves in point-light walkers, then right BA 2 corresponds to the left body side of the visual stimulus and the left BA 2 corresponds to the right body side of the visual stimulus. A right facing walker presents its right body side to the observer. This is consistent with the selectivity of the left BA 2. If I hypothesize that BA 2 is engaged in the recognition process, then this contribution should be strong for visual stimuli that are processed predominantly in the same cortical hemisphere that is for example for stimuli from the right visual hemifield for the left BA 2.

Although the point-light walkers activated also regions of the dorsal BA 2, which correspond to the leg and arm region, however, only when compared to baseline activity. Instead, the differences in activity related to the facing effect were located on the ventral-most part of BA 2, which correspond to the head/face region of the somatosensory homunculus.

I think that the head/face, although not presented in my experiments, is relevant for the task, since facing direction is linked to the orientation of the head. Umilta et al. (2001) demonstrated that mirror neurons responded to invisible actions for which the observer knew the actor must be present. As mentioned, Haslinger et al. (2005) observed ventral BA 2 activity contralateral to the non-seen hand in addition to the more dorsal somatosensory hand area contralateral to the seen hand. Since piano playing is a bi-manual task, these expert players may have automatically generated activity associated to the unseen hand. I suggest that the subjects could have generated activity for the unseen head of the walker.

I found that BA 44 is the second area consistent with the facing effect. It has been demonstrated that BA 44 respond to biological motion perception, action recognition and imitation (Rizzolatti and Craighero, 2004; Goldenberg and Karnath, 2006; Binkofski et al., 2000; Saygin et al., 2004). However, it is difficult to say from my results whether the involvement of BA 44 in the facing effect contributes to the generation of the facing effect or whether it reflects the better embodiment for outward facing walkers. Further research is necessary to clarify this issue.

There is recent support for my findings, namely that the mirror-neuron system represents interpersonal body representation in a somatotopic manner (Buccino et al., 2001; Aziz-Zadeh et al., 2006; Sakreida et al., 2005). Additionally, it has been shown that imagined body-actions, during both the imagining and the preparation of move-

ments, are contralaterally organized (Michelon et al., 2006). This lateralization was strongest in the premotor- and somatosenory cortex. The reported coordinates of postcentral activation are comparable to my findings.

Thomas et al. (2006) demonstrated that a visual cue presented on a limb of a person who is sitting opposite the observer, facilitates the response to a sensation on the corresponding limb of the observer. Furthermore, it was demonstrated that the reaction times to the presentation of images of hands 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 (Aziz-Zadeh et al., 2006).

4.4.2 Sub-field organization in higher visual areas

In the second part of this chapter I demonstrated that in the fusiform gyrus, but not in pSTS/STG or EBA, BOLD responses for walkers with different facing directions was anatomically separated in each contralateral hemisphere. The sub-field organization in the fusiform gyrus is consistent with a known clustering of selectivity for other objects (Peelen and Downing, 2005b; Kanwisher et al., 1997; Gauthier et al., 2000). My 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) proposed a template-matching model of biological motion perception which consists of two stages. 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 left- or a right 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 predicted from the model was comparable to the physiological responses of EBA and fusiform gyrus to biological motion. My finding of a sub-field organization for left- and right facing walkers in the fusiform gyrus is consistent with this prediction.

In previous work it has been 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. This

leads to the question whether or not the different sub-fields in the fusiform gyrus in fact represent recognized biological motion vs. not recognized biological motion rather than left- vs. right facing walkers. I 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). Activity was not different in the fusiform gyrus. I 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).

Activation in the fusiform gyrus occurred only for stimuli from the contralateral hemifield. A predominantly contralateral activation in the fusiform gyrus was also found for body parts, i.e. hands, or faces (Shmuelof and Zohary, 2005; Hemond et al., 2007).

In contrast to the fusiform gyrus, I did not observed different sub-fields for facing direction in the pSTG. This does not mean that the human pSTG does not discriminate the facing direction. Instead, this finding could reflect a similarity between humans and monkeys because electrophysiological findings showed that cells that specifically respond to a single orientation are all located within a narrow region (Oram and Perret, 1996; Jellema et al., 2004). Further research may clarify this issue.

4.5 Conclusion

In these experiments I demonstrated that the higher recognition rates for peripherally presented point-light walkers, which faced away from a central fixation point, were linked to increased activity in areas of the human mirror-neuron system. This finding lends support to the view that both somatosensory and motor structures contribute to visual action recognition. Specifically, the findings enrich providing evidence that the representation of other people's body-sides is achieved through an embodiment on the somatosensory map of our (the observer) own body.

Additionally, I have shown that the fusiform gyrus contains a functional sub-field organization of biological motion stimuli with different facing directions. This finding supports the hypothesis that the fusiform gyrus is not only engaged in the processing of faces (Kanwisher et al., 1997), but also heavily engaged in the processing of human

movements. Specifically, my result suggests that the fusiform gyrus could be a neuronal correlate for body-view templates of the human body.

Chapter 5

General Discussion

The question that was investigated in this thesis was how the human brain processes the visual perception of human movements. The motivation for this question is based on the idea that action understanding is only possible, when humans interpret an observed gesture, posture, intention, or movement correctly. Understanding the goals and intentions behind the actions of other individuals is essential for survival and for normal social functioning. The non-invasive brain imaging method fMRI is an excellent tool to enable the study of the neuronal network involved in the processing of human movements, because it allows the examination of whole-brain activations at a high spatial resolution. Specifically, I used fMRI in this thesis to study the BOLD responses to the visual features provided by the biological motion stimulus such as form and motion information (chapter 2). In addition, I studied the influence of the stimulus location on the BOLD responses, in order to discover how the brain responds to peripherally presented human movements (chapter 3). Finally, I examined whether there was an interaction of the visual hemifield and body view in biological motion perception (chapter 4).

In this chapter I will discuss and compare my results to other brain imaging studies, and if necessary, also to non-brain imaging studies.

5.1 The role of visual areas for the perception of biological motion

In my experiments I found activations in areas of the ventral as well as in the dorsal visual pathway. Among early visual areas, I observed activations in higher visual areas

that are the fusiform gyrus, EBA, and pSTS/STG. Activation in one or all of these areas was reported in many fMRI studies of biological motion perception (Beauchamp et al., 2003; Vaina et al., 2001; Grossman and Blake, 2002; Grossman and Blake, 2004; Downing et al., 2001; Servos et al., 2002; Santi et al., 2003; Grèzes et al., 1998; Pelphrey et al., 2005; Ptito et al., 2003; Peuskens et al., 2005; Santi et al., 2003; Saygin et al., 2004). However, their specific contribution relating to human movement perception is not fully understood yet. In this thesis I found that two visual areas show a functional specialization for images of the human body: the fusiform gyrus and the pSTS/STG.

In the fusiform gyrus I observed increased activations for the SFL walker compared to the Cutting walker. Secondly, only in the fusiform gyrus activations were dominantly manifested in the contralateral hemisphere for peripherally presented point-light walkers. Thirdly, I found within the contralateral hemisphere a sub-field organization for point-light walkers. This sub-field organization was evident by distinct activation clusters for point-light walkers with different facing directions. Whereas fusiform gyrus activation to point-light walkers was reported in other fMRI studies (Beauchamp et al., 2003; Vaina et al., 2001; Peelen and Downing, 2005b; Grossman and Blake, 2004; Peuskens et al., 2005; Peelen et al., 2006; Thompson et al., 2005), the other two findings were not reported yet. The contralateral preference indicates that, in addition to early visual areas, higher visual areas are not invariant to the stimulus location, which was also demonstrated recently for body-like stimuli in other fMRI studies (Schmuelof and Zohary, 2005; Hemond et al., 2007).

However, the strongest evidence for a specialization of the fusiform gyrus in the perception of biological motion was the observed sub-field organization. So far, fMRI studies reported that the fusiform gyrus respond to different kind of stimuli-like objects, faces or pictures of the whole-body (Peelen and Downing, 2005b; Peelen et al., 2006; Schwarzlose et al., 2005; Kanwisher et al., 1997; Downing et al., 2001). For example, it was shown that the fusiform gyrus contains a body-selective region, which is anatomically different from the face-selective region. There is no brain-imaging study that investigated whether or not the fusiform gyrus respond to within-object features such as the facing direction. There is only one optical imaging in monkeys that indicates a regional clustering of cells in the ITC for the orientation of face stimuli (Wang et al., 1998). I suggest that the sub-field organization, as observed by the anatomical clustering for point-light walkers with different facing directions, could be the first evidence for a neuronal correlate for body-view specific templates of the human body in

humans.

A recent model of biological motion perception supports this hypothesis. Lange et al. (2006) and Lappe and Lange (2006) demonstrated that using global form information alone may be sufficient for biological motion perception. Specifically, the authors showed that a template-matching model can explain for humans' behavior in different tasks to biological motion perception. Lange and Lappe (2006) demonstrated their model possesses neural plausibility. They developed a dynamical model, which does not treat the templates as static but rather as interacting templates. The authors demonstrated that the model is consistent with a wide range of neurophysiological and psychophysical data. The model consists of two hierarchically organized stages. The first stage in their model 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 (temporal) evolution of the postures over time. The first stage requires template cells that are sensitive to the different postures of the gait cycle, e.g. a for a left- or a right facing walker. The activity of these template cells, containing a library of stored static postures, was used to calculate the percent correct level in a left-right discrimination task. For stage one, they suggested that the EBA and the fusiform gyrus were candidate areas, which are sensitive to the (static) posture of human bodies and point-light animations (Downing et al., 2001; Peelen and Downing, 2005b; Downing et al., 2006b; Peelen et al., 2006). Lange and Lappe showed that the responses of the model and the physiological responses in EBA and the fusiform gyrus showed similar behavior. Specifically, the responses of the model for these two were not statistically different from the BOLD responses found in the experiments of chapter 2. For both, EBA and the fusiform gyrus, responses were higher for the SFL walker as compared to the Cutting walker. Fig. 5.1 shows a comparison of the simulated model stage one to my fMRI results for EBA and the fusiform gyrus (FFA/OFA).

Lange and Lappe (2006) assigned the second stage of their model to the STS, which uses the frames from stage one to analyze their temporal order. I suggest that my results could emphasize the key role of the pSTS/STG for the perception of biological motion for four reasons. First, I found activations in the pSTS/STG for all types of point-light walkers. Secondly, I revealed stronger (although not significant) activations for form-dominant SFL walkers compared to the Cutting walker. In line with this finding, Beauchamp et al. (2003) showed that pSTS activations were stronger for whole-body displays than for point-light walkers or for tool motion. This could indicate

that in contrast to MT, pSTS/STG integrates global form information rather than the local motion signals of the human body. Third, pSTS/STG was the only visual area that showed stronger BOLD responses for peripherally presented biological motion as compared to scrambled controls. So far, this has been only reported for central biological motion (Grossman and Blake, 2002; Grossman and Blake, 2004). Fourth, the retinotopy of the right pSTS/STG could indicate that biological motion involves a specialized neuronal population for the processing of human movements.

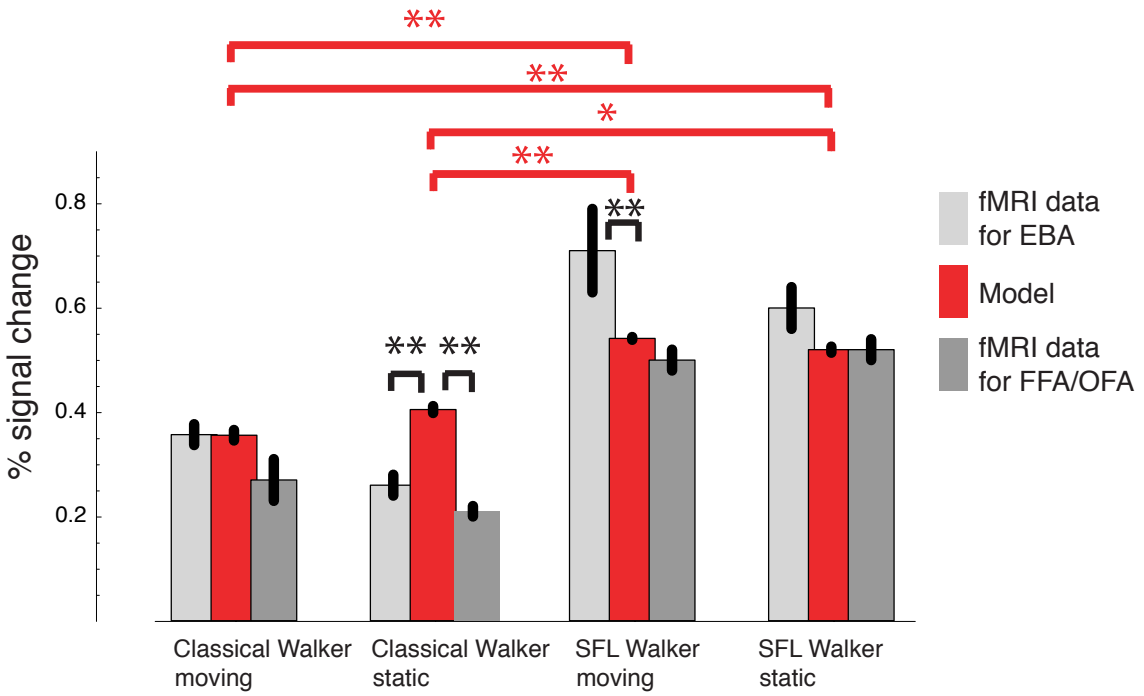

Fig. 5.1: **Illustration of the BOLD and model responses for EBA and the fusiform gyrus (FFA/OFA) for different types of point-light walkers**. Grey bars show BOLD responses for EBA and FFA, red bars 'neuronal' responses from model simulations. Red lines indicates significant differences between model simulations for the four point-light walker types, black lines indicate significant differences between the model simulations and my fMRI results.

As for the fusiform gyrus and pSTS/STG, I found EBA activations for all types of point-light walkers. In addition, I found that the activations were stronger to SFL walkers than to Cutting walkers. I also demonstrated that EBA respond to both types of point-walkers similarly when they were presented as being static or moving. These results indicate that the EBA is sensitive to biological motion stimuli and particularly sensitive to the global form information, but not to (local) motion information. The specificity for the human body-like stimuli has been described in several other brain

imaging studies (Urgesi et al., 2007b; Urgesi et al., 2007a; Peelen et al., 2006; Downing et al., 2001; Downing et al., 2006b; Grossman and Blake, 2004; Peuskens et al., 2005; Santi et al., 2003). For example, Peelen et al. (2006) reported that EBA activations were stronger to point-light walkers than to scrambled motion. In addition, Downing et al. (2006) showed that EBA BOLD responses were strongest for pictures of the whole-body than to the next most effective of the remaining 19 stimulus categories (e.g. faces, spiders, tools) tested.

In contrast to the pSTS/STG, I found no retinotopic organization in the EBA. This could indicate that either the same neuronal population is activated for centrally and peripherally presented point-light walkers or that the spatial resolution of the functional images was not sufficient to reveal a possible retinotopic organization. I also did not found a sub-field organization in EBA. I can only speculate that this region is sensitive to the human form but is – in contrast to the fusiform gyrus – not selective for within-stimulus features such as the body view. New ways of analyzing fMRI data are possible required when interpreting activations –particularly in spatially smoothed group-averaged data or even single-subject functional ROI designs.

For example, Peelen et al. (2006) demonstrated that body-selective regions in the fusiform gyrus (BSR) and the EBA overlap with, but are distinct from, face- and motion-selective regions. First, they used the whole-brain analysis in order to identify gross regions that respond to point-light walkers than to scrambled motion. Secondly, the identified ROIs (EBA, MT, FFA, BSR) and measured the BOLD responses of these individually defines ROIs to the biological motion stimuli. Finally, they performed a series of voxel-by-voxel analyses on the ROIs, with the objective of discovering the relationship between biological motion selectivity and motion, face, and body selectivity in those regions. Peelen et al. first calculated – on an individual subject basis – the biological motion selectivity (expressed by a t value for each voxel). Then, they correlated these t values with t values reflecting the motion and body selectivity in MT and EBA, and body and face selectivity in FFA and BSR. The average correlations were then tested against zero, with subject as the random factor. This so-called multi-voxel pattern analysis revealed the distinction between face-, motion-, and body-selective regions in the EBA and BSR, which was not visible by the conventional ROI analysis. Based on this result, I propose that the multi-voxel pattern analysis could be also used to disentangle, at a fine-grained level, whether or not a pattern of selectivity (e.g. for the facing direction) does exist in the EBA.

Irrespective of the type of the presented point-light walker that means irrespective of whether or not the stimulus contained valid local motion, I found that activations in areas of the dorsal pathway (MT and KO) did not differ. In addition, the comparison of centrally peripherally presented point-light walkers versus scrambled motion revealed pSTS/STG, but not MT or KO activations (chapter 3). An observed non-specificity of motion-processing areas was also found in earlier fMRI studies of biological motion perception (Grossman and Blake, 2002; Beauchamp et al., 2002; Beauchamp et al., 2003). Grossman et al. (2002) found (1) that MT and KO responses were statistically lower compared to the pSTS activation when point-light walkers were compared to scrambled motion and (2) that MT and KO responded to coherent motion or kinetic boundaries, respectively, more strongly than to point-light walkers. In addition, it was shown in several fMRI studies that pictures of tools activate more strongly MT, while pictures of point-light walkers, faces or animals activate more strongly the STS (Chao et al., 1999; Chao and Martin, 2000; Beauchamp et al., 2002; Beauchamp et al., 2003). Beauchamp et al. (2002) demonstrated that MT responded as strongly to point-light displays as to (whole-body) videos, therefore they suggested that motion is the key determinant of response in MT. Also clinical studies support that the STS – but not MT – is specifically activated by biological motion (McLeod et al., 1996; Vaina et al., 1990). Vaina et al. showed that patients with lesions that damage area MT (but sparse the STS) can still decode point-light displays.

The role of the right pSTS/STG for biological motion perception The retinotopic organization of the pSTS/STG was unexpected. In addition, it was also surprising that only the right hemisphere shows this functional specialization. However, right hemispheric dominance was found in several fMRI studies of biological motion (Bonda et al., 1996; Pelphrey et al., 2003; Puce et al., 1998; Grèzes et al., 1998; Grossman et al., 2000; Grossman and Blake, 2001; Grèzes et al., 2001; Peuskens et al., 2005; Beauchamp et al., 2003; Santi et al., 2003; Wheaton et al., 2004; Grossman et al., 2005; Peelen et al., 2006).

Some studies suggested that a right-dominant STS activation could indicate a functional specialization for body-related movements and emotions (Allison et al., 2000; Puce et al., 2003). Allison et al. argued that the right STS becomes activated whenever observers see actions that involve or require interaction with other humans. Therefore, they suggested that STS can be referred to as the perceptual locus of 'social cognition'.

For example, the gaze of another human can give important information relating to the person's intention or emotion. Neurophysiological studies have shown that paying attention to the gaze activates (right) STS while paying attention to other parts of the face does not (Perrett et al., 1992). In addition it has been demonstrated that pSTS is also activated when the stimulus contains information pertaining to emotion. Grezes et al. (2007) demonstrated that dynamic fearful body expressions elicited right pSTS activations when compared to neutral body configurations. I suggest that the right pSTS/STG activation in this thesis can be explained by the concept that was introduced at the beginning of this thesis: "humans are able to quickly interpret the movements, emotions, and intentions of other individuals. Especially, appropriate judgments of different social contexts can be only achieved when the visual system has analyzed and interpreted the depicted action or mood of other individuals".

Two recent studies that used fMRI in monkeys provide evidence for two large clusters of body-selective cells in the STPa with those in the right hemisphere being most strongly activated (Pinsk et al., 2005; Tsao et al., 2003). This result provides a bridge between single-unit recordings in monkeys and fMRI findings in humans by showing that dense clusters of selective individual neurons can underlie selectivity measured at a macroscopic level with fMRI. Although this result indicates that the superior temporal cortex is similarly activated in primates, I suggest that it needs to be established whether or not also monkey's right STPa possesses, for example, a retinotopic organization to support this hypothesis.

5.2 The role of non-visual areas for the perception of biological motion

In my experiments I found activations in areas considered to be part of the human mirror-neuron system (PMC, IFG, PPC, somatosensory cortex areas: BA 2, BA 44). The mirror-neuron system, originally discovered in monkey's PMC (Rizzolatti et al., 1996; Gallese et al., 1996), contains neurons that discharge both when the monkey acts and when it sees other individuals performing the same goal-directed action. Although observers in this thesis viewed no goal-directed actions, activations were still observed in the PMC, but also in the IFG, PPC and somatosensory areas. This result is in line with other fMRI studies of action observation (Saygin et al., 2004; Hasson et al., 2004;

Buccino et al., 2001; Gazzola et al., 2007). However, does it mean that the mirror-neuron system is specifically activated for biological motion? In the following, I will make a differentiation between the activations found in the PMC and activations in somatosensory areas that showed the facing effect.

Recently, Urgesi et al. (2007) used rTMS over the PMC and EBA to study the causal role of these areas in neural underpinnings of visual body processing. In a two-choice matching-to-sample visual discrimination task, participants were instructed to decide which of two upper- or lower-limb images matched a single sample previously presented. The stimuli consisted of static pictures, depicting body parts and were likely to activate EBA (Ruby and Decety, 2001; Downing et al., 2001). However, all pictures also implied actions and were likely to activate the PMC (Rizzolatti and Craighero, 2004). The matching and non-matching stimuli in each pair depicted the same model (hand, arm, leg) performing two different actions (action discrimination task) or the same action performed by two different models (form discrimination task). Importantly, for both tasks the same match-to-sample operation was required. Therefore, any dissociation between the task was likely to emerge from the implicit discrimination of differences in the action or in the morphological details of the models' body parts. When a rTMS pulse was applied over the EBA, participants ability to discriminate body forms was impaired. In contrast, interference with the PMC impaired the ability to discriminate bodily actions. Urgesi et al. suggested that this region may represent the observed action without taking into account the actors' identity. I suggest that this result could explain why I found PMC for both types of point-light walkers (SFL walker, Cutting walker), because they depicted a specific action (apparent walking). The SFL walker contains no local image motion but provides more (global) form information than the Cutting walker. Nevertheless, activations were not significantly different for the two walker types in the PMC or the IFG[1] (chapter 2), which indicates that form information from the human body cannot explain activation in the PMC or IFG.

Hence, I claim that the activations in the PMC – and possibly also the activation in the IFG and PCC – reflect selectivity to actions but not a selectivity for the global form of the human body. This hypothesis is supported by a recent fMRI study (Gazzola et al., 2007). In this study, subjects viewed different actions performed by humans or artificial agents. Gazzola et al. found increased BOLD responses in three areas of

[1]With the exception of the static Cutting walker in IFG

the human mirror-neuron system, i.e. the dPMC vPMC and PPC, for both robotic and human movements. These responses were strongest for complex activations, i.e. removing a tea bag from a cup of tea, as compared to simple actions (simple grasping) or non-goal directed hand movements. Interestingly, the activations for the different actions were similar for both agents (robot, human). Gazzola et al. suggested that the mirror-neuron system contributes to the understanding of a wide range of actions, and that the goal of the action might be more important for the activations rather than the way in which the action is performed.

In contrast to the activation in the IFG, PMC or PPC reported in this thesis, I found activations for different body-views only in the somatosensory areas BA 2 and BA44 ('facing effect'). An interesting open question is why other regions of the mirror-neuron system did not show specific responses to the facing effect. One reason might be that the lateralization effects in the PMC and the somatosensory cortex are small (Michelon et al., 2006). In addition, mirror-neuron responses are weaker for filmed actions than for real actions (Jarvelainen et al., 2001). Another reason why I did not find specific activations in other regions of the mirror-neuron system could be that we used an unusual task. Mirror-neuron activity was usually investigated in tasks with respect to the goal such as the goal to grasp or manipulate an object (Rizzolatti and Craighero, 2004). In my task the performed action (apparent walking) did not represent any particular goal. Instead, the observers' task was related to understanding the presented body configuration and hence was more related to the somatosensory than to the motor representation of the action.

de Lussanet et al. showed in psychophysical experiments that the facing effect remains stable even when the point-light walkers were presented as being static. This strongly suggest that the facing effect is a results of observers self-embodiment in the presented stimuli (different configurations of the human body), and thus is not produced by the portrayed action, i.e. apparent walking to the left or right. They also showed that the facing effect is not limited to human walking, because the facing effect was also observed when the stimuli depicted as crawling point-light stimuli.

I suggest that three experiments could clarify whether or not the responses in BA 2 and BA 44 are specifically related to understanding human body configurations. In one experiment static versions of peripherally presented point-light walkers with different facing directions are presented. Here it would be interesting to see whether or not the facing effect remains stable (stronger BOLD responses in BA 2 and BA 44 for outward

facing stimuli), but also whether or not the effect is quantitatively about the same size (expressed by the t value of the contrast outward facing vs. inward facing stimuli). In the PMC it was shown that BOLD responses to static images of body parts were reduced (Gazzola et al., 2007). In the second experiment, crawling point-light stimuli with different facing directions could be compared. As for experiment one, it would be interesting to know whether or not the facing effect is still present and if so is the quantitative size of the effect in a similar range to that of the walking condition. The latter would indicate whether or not perception (= embodiment) of more complex body configurations – such as crawling – correlates with the strength of the BOLD signal.

In the third experiment, subjects would view incoherent moving point-light walkers. For example, in one condition the upper body-part is facing to the right, whereas the lower body-part is facing to the left. In the other condition, the stimuli depict the opposite. Although the body parts of the stimuli of both conditions are facing in different directions, the facing effect should disappear, because the stimuli do not provide a real body configuration.

5.3 Is there a mechanism for human movement perception?

Do the fMRI results of this thesis allow the conclusion that there is a specific mechanism for human movement perception? I suggest the following: Biological motion perception activates several early and higher visual areas. Some of these areas respond to motion cues provided by the point-light walker (MT), whereas others respond more to the (global) form information (EBA, fusiform gyrus), or to both (pSTG/STG). In this particular neuronal network, however, only activation of the fusiform gyrus and pSTS/STG are specific for the recognition of human movements (chapters 2-4). The increase for form-dominant stimuli and functional organization of the fusiform gyrus for point-light walkers could indicate that perception of biological motion involved specifically the ventral visual pathway. In addition, the unspecific responses in motion-sensitive areas for the different types of point-light walkers argue against a specific involvement of the dorsal visual pathway for biological motion perception (chapter 2). The retinotopic organization of the pSTS/STG for biological motion stimuli could suggest that irrespective of the stimulus location, the integration of global form information

(static body templates) over time can be used to derive the global motion direction of the stimulus. Therefore, I suggest that human movement perception is based on a motion-from-structure mechanism, rather than on a structure-from motion mechanism. Although there are no fMRI studies proposing such a mechanism, the results from the model from Lange and Lappe (2006), but also psychophysical (Bertenthal and Pinto, 1994; Shiffrar et al., 1997; Cutting et al., 1988) and clinical studies (Vaina et al., 1990; Zihl et al., 1983) support the existence of a motion-from-structure mechanism.

In addition, my results suggest that there could be a second mechanism that promotes biological motion perception. This mechanism integrates signals from specific areas of the mirror-neuron system. The proposed mechanism is rather simple. Each time an individual sees an action (here human walking) done by another individual, neurons that represent that action are activated in the observer's PMC and sometimes also IFG and PPC. This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Thus, the mirror-neuron system transforms visual information into knowledge. However, it has been demonstrated that the PMC is not only activated by biological motion but also for other (goal-related) actions. This means that this area is involved but is not specific for biological motion perception. I rather claim that specifically somatosensory areas (BA 2 and BA 44) heavily involved in the understanding of human body configurations. According to this hypothesis, the activations in somatosensory areas are related to the somatosensory rather than to the motor representation of the action. Thus, the activation in somatosensory areas could explain the observed facing effect. The possibility of a self-embodiment into an observed action does allow humans to translate the action into the vocabulary of their own actions. This in fact, is a necessary prerequisite to interpret the emotional status of other individuals or the intention of an action, such as walking.

Chapter 6

Summary and conclusions

6.1 Summary

One of the most important functions of vision is to provide information about the identities, actions, and intentions of other individuals. Even when the observed actions are complex and presented in various social contexts, humans are able to recognize and to react to these actions quickly, often even without being aware of the complexity of the observed action.

Neurophysiological studies in monkeys and neuroimaging (e.g. fMRI) research in humans into how the human brain accomplishes this task suggest that human body movements are represented in a large neuronal network, which involves visual and non-visual areas.

A major focus in neuroimaging research on human movement processing has been carried out with specific biological motion stimuli that are point-light walkers. These displays consist of only a few dots that are, for example, placed on the major joints of an otherwise invisible body and which move in a way that is characteristic of human movements. Although the form and the motion information related to the human body are reduced to these few point-lights, observers can perceive the depicted actions. However, it is still not fully understood how form and motion information contribute to the neuronal processing of biological motion.

The interpretation of neuroimaging studies using point-light walkers has largely focused on a region in the posterior part of the superior temporal cortex (pSTS/STG), because it is known that this region integrates form and motion information over time and is activated in response to movements that are biologically plausible. But human

movements consistently activate also (non-visual) areas that belong to the so-called human mirror-neuron system, which is characterized by neurons that respond similarly during the observation and the execution of the (same) action. To date, the role of activations to human movement patterns in visual as well as non-visual areas remains unexplained.

So far, all neuroimaging studies have focused on the investigation of foveally presented biological motion stimuli. In contrast to the processing of foveal stimuli, processing of peripheral visual stimuli is more lateralized, because of the few callosal connections. Despite these few connections, perception of peripheral biological motion is nevertheless possible when the stimuli were not embedded in noise. However, it is still unknown which cerebral network is activated by peripheral biological motion.

In the experiments of this thesis, I varied the properties of the point-light walker such as the amount of form- and motion signals, the stimulus location and the stimulus facing direction, in order to investigate whether these variations influenced the BOLD responses and the behavioral responses to biological motion. In this final chapter, I will summarize the results from chapters 2-4 of this thesis, which is then followed by a general conclusion.

6.1.1 The role of form and motion information in biological motion perception

In chapter 2, I used two different types of point-light walkers to investigate, whether the BOLD responses are influenced by the provided form and motion signals of the stimuli. In one stimulus type, the dots were presented in each frame of the animation at specific joint locations, thus, the stimulus contained (global) form and valid local motion signals (Cutting walker). The other type of point-light walkers lacked local motion signals and provided only (global) form information, because the dots jumped in each frame of the animation to a random position between the joints (SFL walker). The results of the chapter were:

- Irrespective of the type of the presented point-light walker observers could discriminate the biological motion stimuli from scrambled motion at a performance level of at least 80%.
- A similar performance level was observed when static versions of point-light walkers were presented.

- The activations in areas known to be involved in form-processing – the fusiform gyrus and the EBA – were statistically stronger for SFL walkers than for Cutting walkers, irrespective of whether the stimuli were presented as being static or moving.

- Unlike areas of the ventral stream, activations were not statistically different for the two types of point-walkers in areas of the dorsal pathway (MT and KO).

- BOLD responses could be observed in regions of the human mirror neuron system such as the IFG and PMC, irrespective of the type of point-light walker.

- Single-subject analysis revealed that the BOLD responses in the investigated brain regions showed only a small intersubject-variability. This result was observed for both types of point-light walkers.

6.1.2 The perception of peripheral biological motion

In chapter 3, I compared the behavioral responses and the neuronal activations for central and peripheral presentations of point-light walkers. The results of the chapter were:

- Peripherally presented point-light walkers were perceived similarly compared to those centrally presented, but only when they faced away from the central fixation dot. That is, point-light walkers that faced to the left were better detected than point-light walkers that faced to the right, when presented in the left visual hemifield. In contrast, point-light walkers in the right visual hemifield were more readily detected when they faced to the right.

- The activation patterns for both centrally and peripherally presented point-light walkers showed not only a large overlap in early and higher visual areas, but also in areas outside the ventral and dorsal visual pathways.

- However, the activations for peripherally presented point-light walkers were found dominantly in the contralateral hemisphere in early visual areas, and in the fusiform gyrus, whereas more bilateral activations were found for centrally presented point-light walkers.

- BOLD responses in the pSTS/STG region were independent of the stimulus location only visible in the right hemisphere
- Centrally and peripherally presented biological motion evoked stronger right pSTS/STG activations when compared to centrally and peripherally presented scrambled motion.
- The activation locations within the right pSTS/STG depended on the stimulus location, that means they were organized retinotopically, as revealed by single-subject analysis.

6.1.3 The perception of peripheral biological motion with different body views

In chapter 4, I examined the BOLD responses for peripherally presented point-light walkers with different facing directions. The results of the chapter can be summarized as:

- A comparison of the BOLD responses for point-light walkers with different facing directions revealed contralateral activation in two areas of the human mirror-neuron system (BA 2 and BA 44) when the stimuli faced away from the fixation dots. That means activations were stronger in these areas when the stimulus was presented in the right visual hemifield with a facing direction to the right rather than with a left facing direction.
- These results show that human movement perception not only activates motor areas but also somatosensory areas of the human mirror-neuron system.
- The contralateral fusiform gyrus contains a functional sub-field organization for peripherally presented point-light walkers with different facing directions as revealed by group and single subject analysis.

6.2 General Conclusions

A widely accepted theory of the perception of point-light displays of biological motion is that (global) form information is not sufficient to explain its perception. Rather, local motion signals might explain the perception. In this thesis, I demonstrated that

subjects were able to recognize biological motion stimuli irrespective of the amount of local motion signals in the stimulus (SFL or Cutting walker). In addition, I found stronger activation in form-processing areas – the fusiform gyrus and the EBA – for SFL walkers compared to Cutting walkers. In contrast to ventral stream areas, I found no statistical differences in the activations of motion-processing areas, such as MT and KO, when both point-light walkers types were compared. These results strongly argue against the theory mentioned above.

Further, I demonstrated that perception of peripherally presented point-light walkers was possible and that the brain activations for both centrally and peripherally presented point-light walkers largely overlapped. For peripheral biological motion stimuli, I showed that the fusiform gyrus possesses not only a preference for contralaterally presented point-light walkers but that this region also contains a sub-field organization for different body views. The functional clustering for the human body suggest that also for the perception of peripheral biological motion the ventral visual pathway is heavily engaged.

I concluded that not only the fusiform gyrus is specifically engaged in central as well as in peripheral biological motion perception but also the pSTS/STG. In this area I found not only activation for different types of point-light walkers but also a functional specialization, i.e. a retinotopy. Although the latter findings contradict the general theory that higher visual areas possess a retinotopic organization, recent fMRI studies provide evidence for such an organization relating to complex body-like visual stimuli. The retinotopy in the pSTS/STG in this thesis was found exclusively in the right hemisphere. This could be explained by the well-known lateralization of biological motion processing in humans. Also recent fMRI studies in monkeys demonstrated that the right STS was activated by (central) biological motion, which could indicate that this lateralization is a common specialization in some primates.

In summary, the observed activations in visual areas in this thesis suggest that biological motion perception is based on a motion-from-form mechanism rather than on a form-from-motion mechanism, because for both central and peripheral biological motion different functional specializations (e.g. sub-field organization) were found in the ventral but not in the dorsal visual pathway. According to this hypothesis, the static body templates (= global form) are neuronally coded in the form-processing areas such as the fusiform gyrus. The integration of the temporal order of the static body templates could then take place in the pSTS/STG, and allows the perception of

different (human) walking directions.

As a result, this thesis also revealed that biological motion processing and perception did not only activate visual areas but also non-visual areas, such as areas of the mirror-neuron system. This involved areas of the motor cortex (e.g. PMC) and also areas of the somatosensory cortex (BA 2 and BA 44). The latter showed an interaction with the visual hemifield and the body view ('facing effect'), i.e. these areas were more strongly activated when peripherally presented stimuli faced away from a central fixation dot. I suggest that this indicates that the detection of the body view could not be explained by a pure visual mechanism, because there should be neither a visual preference for a particular body configuration (facing right or left) nor a preference for a visual hemifield.

Based on this result, I hypothesize that a second mechanism is used for human movement perception. On the one hand, this mechanism involves motor areas (i.e the PMC) of the human-mirror neuron system. Whenever an observer sees an action – such as human walking – this automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Additionally, this mechanism integrates signals from somatosensory areas of the mirror-neuron system and from visual areas. This process allows humans to embody themselves into different body views of an observed action. Specifically, somatosensory areas are activated to understand different human body configurations. The possibility of a self-embodiment into observed actions allows humans to translate the action into the vocabulary of their own actions. This mechanism can therefore be used to interpret the intention of an observed action, or to understand the emotion of other individuals, and thus to plan appropriate behavioral responses.

6.3 Zusammenfassung

Eine wichtige Fähigkeit des menschlichen Gehirns ist die Wahrnehmung der Identitäten, der Handlungen und der Intentionen anderer Lebewesen. Obwohl die Betrachtung einer spezifischen Aktion äußerst komplex sein und einen unterschiedlichen sozialen Kontext darstellen kann, sind Menschen zumeist in der Lage die dargestellte Aktion schnell und unbewusst zu interpretieren und auf diese zu reagieren.

Sowohl neurophysiologische Studien beim Affen sowie bildgebende Verfahren (z.B.

funktionelle Magnetresonanztomografie, fMRT) beim Menschen haben versucht die Frage zu beantworten, welche neuronalen Verarbeitungsprozesse an der Wahrnehmung von menschlichen Bewegungs- bzw. Handlungsmustern beteiligt sind. In den meisten dieser Studien wurden Aktivierungen in einem neuronalen Netzwerk gefunden, welches sowohl visuelle als auch nicht-visuelle Areale umfasst.

Ein Forschungsschwerpunkt in der menschlichen Bewegungsanalyse wurde auf die neuronalen Verarbeitungsprozesse sogenannter biologischer Bewegung gelegt. In den meisten Studien wurde dazu die Wahrnehmung von Lichtpunkt-Läufern untersucht. Lichtpunkt-Läufer bestehen nur aus wenigen Lichtpunkten, die z.B. an den Hauptgelenkpositionen angebracht sind und deren Bewegungen ein für Menschen charakteristisches Gangmuster darstellen. Trotz der reduzierten Form- und Bewegungsinformation können Betrachter die dargestellte Aktion erkennen. Dennoch konnte noch nicht eindeutig erklärt werden, wie Bewegungs- und Forminformationen zum neuronalen Verarbeitungsprozess biologischer Bewegung beitragen.

Die Interpretation bildgebender Studien mit Lichtpunkt-Läufern konzentrierte sich häufig auf eine Region im posterioren superioren temporalen Kortex (pSTS/STG), da bekannt ist, dass diese Region Form- und Bewegungsinformation zeitlich integriert und auf biologisch-plausible Objekte reagiert. Allerdings wurde in zahlreichen Studien gezeigt, dass die Beobachtung von Lichtpunkt-Läufern auch zu Aktivierungen von (nicht-visuellen) Arealen führt, die zum sogenannten Spiegelneuronensystem gehören. Dieses System reagiert gleichermaßen auf eine beobachtete wie auf eine selbstdurchgeführte (der Beobachtung identischen) Handlung. Trotz detaillierter Untersuchungen der visuellen und nicht-visuellen Areale ist es bisher noch nicht gelungen, deren spezifische Rolle im Verarbeitungsprozess menschlicher Bewegungen eindeutig zu bestimmen.

Bisher wurde in bildgebenden Studien lediglich untersucht wie foveal präsentierte biologische Bewegung neuronal verarbeitet wird. Im Gegensatz zur Verarbeitung fovealer Reize ist die Verarbeitung peripherer Reize stärker lateralisiert, da es weniger zwischenhemisphärische (callosale) Verbindungen gibt. Dennoch konnte gezeigt werden, dass Probanden auch peripher präsentierte Lichtpunkt-Läufer erkennen können, solange diese nicht in einer Maske von Rauschpunkten präsentiert werden. Für diesen psychophysischen Befund wurde bisher aber noch keine physiologische Erklärung angeboten.

In den Experimenten dieser Arbeit habe ich verschiedene Eigenschaften des Lichtpunkt-Läufers, wie den Anteil von Form- und Bewegungsinformation, den Stimulus-

präsentationsort und die Stimulusorientierung variiert. Dadurch habe ich versucht herauszufinden, ob diese Variationen einen Einfluss auf die mittels fMRT gemessene Hirnaktivität bzw. auf die Wahrnehmung biologischer Bewegung haben. In diesem Kapitel werde ich erst die Ergebnisse der Kapitel 2-4 dieser Arbeit zusammenfassen und dann das Kapitel mit einigen Schlussfolgerungen abschließen.

6.3.1 Die Rolle von Form- und Bewegungsinformation für die Wahrneh-mung biologischer Bewegung

In Kapitel 2 habe ich zwei verschiedene Arten von Lichtpunkt-Läufern verwendet um zu untersuchen, ob das Vorhandensein von Bewegungs- bzw. Forminformation einen Einfluss auf das BOLD Signal hatte. Einer der Lichtpunkt-Läufer war dadurch gekennzeichnet, dass die Lichtpunkte während der Präsentation permanent auf den Gelenkpositionen gezeigt wurden, so dass dieser – neben der (globalen) Forminformation – auch lokale Bewegungssignale enthielt (Cutting Läufer). Im Gegensatz dazu wurden beim anderen Lichtpunkt-Läufer die Lichtpunkte in jedem Einzelbild an einer anderen Stelle präsentiert, so dass dieser Lichtpunkt-Läufer keine lokalen Bewegungssignale enthielt (SFL Läufer). Die Resultate dieses Kapitels waren:

- Unabhängig von der Art des präsentierten Lichtpunkt-Läufers konnten Versuchspersonen diesen von Lichtpunkt-Reizen unterscheiden (Erkennungsrate $> 80\%$), deren Punkte identische lokale Bewegungsvektoren trugen, aber keine menschlichen Bewegungsmuster darstellten.

- Die Unterscheidungsrate war ähnlich hoch wenn statische Lichtpunkt-Läufer präsentiert wurden.

- Die Aktivierung in zwei formverarbeitenden Gehirnregionen – dem fusiformen gyrus und dem extrastriären Körperfeld (EBA) – waren signifikant stärker für SFL Läufer als für den Cutting Läufer. Dies konnte auch beobachtet werden, wenn die Aktivierungen für statische Versionen der beiden Lichtpunkt-Läuferarten verglichen wurden.

- Im Gegensatz zu formverarbeitenden Arealen waren die Aktivitäten für den SFL und den Cutting Läufer in den bewegungsverarbeitenden Arealen (MT und KO) nicht signifikant verschieden.

- Aktivität in Arealen des Spiegelneuronensystems, wie etwa dem inferioren frontalen gyrus oder dem premotorischen Kortex, konnte für beide Lichtpunkt-Läufer beobachtet werden.

- Die Untersuchung der einzelnen Versuchspersonen ergab, dass die BOLD Signalveränderungen in den untersuchten Arealen zwischen den Versuchspersonen gering waren. Dies war unabhängig von der Art des Lichpunkt-Läufers.

6.3.2 Die Wahrnehmung peripher präsentierter biologischer Bewegung

In Kapitel 3 habe ich die Wahrnehmung und die Verarbeitung für zentral und peripher präsentierte Lichtpunkt-Läufer miteinander verglichen. Die Resultate dieses Kapitels waren:

- Peripher präsentierte Lichtpunkt-Läufer konnten überhalb der Zufallsrate erkannt werden – und damit ähnlich gut wie zentral präsentierte Lichtpunkt-Läufer –, aber nur wenn sie vom Fixationspunkt weggerichtet waren. Dies bedeutete, dass Lichtpunkt-Läufer im linken visuellen Halbfeld besser erkannt wurden, wenn sie nach links zeigten. Andererseits wurden Lichtpunkt-Läufer im rechten Halbfeld besser erkannt, wenn sie nach rechts zeigten.

- Für zentral und peripher präsentierte Lichtpunkt-Läufer fanden sich Aktivierungen nicht nur in frühen und höheren visuellen Arealen, aber auch in nicht-visuellen Arealen.

- Ein Unterschied war, dass nur die Aktivierungen für peripher präsentierte Lichtpunkt-Läufer in frühen visuellen Arealen, aber auch im fusiformen gyrus, stärker in der kontralateralen Hemisphäre ausgeprägt waren.

- BOLD Signalveränderungen im pSTS/STG wurden, unabhängig vom Präsentationsort, nur in der rechten Hemisphäre gefunden.

- Im rechten pSTS/STG waren die Aktivierungen für zentral und peripher präsentierte Lichtpunkt-Läufer stärker als für zentrale bzw. peripher präsentierte visuelle Reize, die nicht-menschliche Bewegungsmuster darstellten.

- Eine Einzelversuchspersonenanalyse ergab, dass die Aktivierungsorte innerhalb des rechten pSTS/STG abhängig vom Präsentationsort – also retinotop – organisiert waren.

6.3.3 Die Wahrnehmung peripherer biologischer Bewegung mit unterschiedlichen Körperansichten

In Kapitel 4 habe ich die neuronale Aktivität für periphere Lichtpunkt-Läufer mit unterschiedlichen Körperansichten untersucht. Die Resultate dieses Kapitels können wie folgt zusammengefasst werden:

- Lichtpunkt-Läufer mit unterschiedlichen Körperansichten aktivierten zwei Regionen (BA 2 und BA 44) des Spiegelneuronensystems kontralateral stärker, wenn sie vom Fixationspunkt wegzeigten. Dies bedeutete z.B., dass die Aktivierung für Lichtpunkt-Läufer im rechten visuellen Halbfeld stärker war wenn diese nach rechts zeigten.

- Dieses Resultat zeigt, dass menschliche Bewegungswahrnehmung nicht nur motorische, sondern auch somatosensorische Areale des Spiegelneuronensystems aktiviert.

- Wie eine Gruppen- und Einzelversuchspersonenanalyse ergab, wurden im kontralateralen fusiformen gyrus abhängig von der Körperansicht unterschiedliche Gebiete aktiviert.

6.4 Schlussbemerkungen

Eine weithin akzeptierte Theorie zur Wahrnehmung biologischer Bewegung ist, dass die (globale) Forminformation eines Lichtpunkt-Läufers für seine Erkennung nicht ausreichend ist. Vielmehr wird angenommen, dass die lokale Bewegungsinformation der einzelnen Lichtpunkte benötigt wird, um einen menschlichen Körper und dessen Bewegungsmuster zu erkennen. In dieser Arbeit konnte ich zeigen, dass Versuchspersonen verschiedene Arten von Lichtpunkt-Läufern wahrnehmen konnten, die entweder lokale (Cutting Läufer) oder keine lokalen Bewegungsinformationen (SFL Läufer) enthielten. Ich konnte zudem zeigen, dass die Aktivierung in formverarbeitenden Arealen – dem fusiformen gyrus und EBA – stärker für den SFL Läufer als für Cutting Läufer war.

Im Gegensatz dazu waren die Aktivierungen in bewegungsverarbeitenden Arealen (MT und KO) nicht signifikant unterschiedlich für die beiden Lichtpunkt-Läuferarten. Diese Resultate wiedersprechen demnach der zuvor angesprochenen Theorie.

In dieser Arbeit konnte ich zudem zeigen, dass auch die Wahrnehmung peripherer biologischer Bewegung möglich war und dass die Aktivierungen für peripher und zentral präsentierte Lichtpunkt-Läufer stark überlappten. Ich konnte weiterhin zeigen, dass im kontralateralen fusiformen gyrus unterschiedliche Gebiete für periphere Lichtpunkt-Läufer mit verschiedenen Körperansichten aktiviert wurden. Diese funktionelle Spezialisierung könnte dafür sprechen, dass auch für periphere biologische Bewegung speziell der form-verarbeitende Pfad beteiligt ist.

Weiterhin deutete die funktionelle Spezialisierung in Form einer retinotopen Organisation des pSTS/STG darauf hin, dass nicht nur der fusiforme gyrus, sondern auch der pSTS/STG an der Wahrnehmung zentraler und peripherer biologischer Bewegung beteiligt ist. Obwohl dieser Befund der allgemeinen Theorie wiederspricht, dass höhere visuelle Areale keine retinotope Organisation besitzen, werden meine Resultate dennoch durch jüngste fMRT Studien unterstützt, da dort ebenfalls eine Retinotopie für komplexe (körperähnliche) Reize gefunden wurde. Die Retinotopie in pSTS/STG wurde in dieser Arbeit ausschließlich in der rechten Hemisphäre gefunden. Dies kann jedoch mit der bekannten Lateralisierung für biologische Bewegungsverarbeitung begründet werden. Zusätzlich wurde in zwei jüngst-veröffentlichten fMRT Studien beim Affen gezeigt, dass ebenfalls nur der rechte STS durch (zentrale) biologische Bewegung aktiviert wurde, was darauf hindeuten könnte, dass die Lateralisierung eine gemeinsame Spezialisierung bei einigen Primaten darstellt.

Zusammenfassend könnte die gefundene Aktivierung visueller Areale darauf hindeuten, dass biologische Bewegung auf einen Form-durch-Bewegung- und nicht durch einen Bewegung-durch-Form Mechanismus basiert, da sowohl für zentrale wie auch für periphere biologische Bewegung verschiedene funktionelle Spezialisierungen (z.B. die Organisation im fusiformen gyrus) in formverarbeitenden, aber nicht in rein bewegungsverarbeitenden Arealen gefunden wurden. Nach dieser Hypothese sollten im fusiformen gyrus statische Körperhaltungen (= globale Form) neuronal repräsentiert sein und die zeitliche Integration der einzelnen Körperhaltungen im pSTS/STG ablaufen. Dies ermöglicht dann die Wahrnehmung einer menschlichen Bewegung.

Die Resultate dieser Arbeit zeigten zudem, dass an der Verabeitung biologischer Bewegung auch bestimmte Areale des Speigelneuronensystems beteiligt sind. Dies waren

sowohl motorische (z.B. der premotorische Kortex) aber auch somatosensorische Bereiche (BA 2 and BA 44). Letztere zeigten eine Interaktion mit dem visuellen Halbfeld und der Körperansicht des Lichtpunkt-Läufers ('Orientierungseffekt'), was dadurch gekennzeichnet war, dass diese Areale nur dann stärker aktiviert waren, wenn periphere Lichtpunkt-Läufer vom Fixationspunkt weggerichtet waren. Ich vermute, dass dieses Resultat darauf hindeutet, dass die Erkennung einer bestimmten Körperorientierung nicht auf einem rein-visuellen Mechanismus beruhen kann, da weder eine visuelle Präferenz für eine bestimmte Körperorientierung (links oder rechts) vorhanden sein sollte noch eine Präferenz für ein bestimmtes visuelles Halbfeld.

Basierend auf diesen Ergebnissen vermute ich, dass für die Wahrnehmung biologischer Bewegung ein zweiter Mechanismus benutzt wird. Auf der einen Seite sind an diesem Mechanismus motorische Areale des Spiegelneuronensystems, wie etwa der premotorische Kortex, beteiligt. Wenn Menschen eine Handlung beobachten – wie etwa menschliches Laufen – verursacht dieser Prozess automatisch eine motorische Repräsentation der beobachteten Handlung. Diese Aktivierung ist mit einer Aktivierung vergleichbar, die immer dann entsteht, wenn der Beobachter selbst eine entsprechende Handlung durchführt und deren Ausgang (z.B. Laufen in eine bestimmte Richtung) für den Agierenden bekannt ist. Auf der anderen Seite, werden in diesem Mechanismus Signale von somatosensorischen Arealen des Spiegelneuronensystems und von visuellen Arealen integriert. Dieser Prozess erlaubt es, dass Menschen in der Lage sind sich in bestimmte Körperhaltungen einer beobachteten Handlung 'hineinzuversetzen'.

Die Möglichkeit sich in eine beobachtete Handlung 'hineinzuversetzen', erlaubt es Menschen diese Handlung in das eigene Handlungsvokabular zu übetragen. Dieser Mechanismus kann also dazu benutzt werden die Absichten einer beobachteten Handlung, aber auch den durch die Körperhaltung ausgedrückten Gefühlszustand, richtig zu interpretieren, so dass entsprechende Verhaltensmuster geplant werden können.

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