Perception and production of biological movement in patients with early periventricular brain lesions

Marina Pavlova, Martin Staudt, Alexander Sokolov, Niels Birbaumer and Ingeborg Krägeloh-Mann

1Department of Paediatric Neurology and Child Development, Children’s Hospital, 2Institute of Medical Psychology and Behavioural Neurobiology, MEG-Ctr, University of Tübingen, 3Institute of Psychology, Braunschweig University of Technology, Braunschweig, Germany and 4Department of Biophysics, University of Trento, Italy

Correspondence to: Marina Pavlova, PhD, Institute of Medical Psychology and Behavioural Neurobiology, University of Tübingen, Gartenstr. 29, D-72074, Tübingen, Germany
E-mail: marina.pavlova@uni-tuebingen.de

Summary
Recent neuroimaging and psychophysical findings suggest that perception and production of human body motion share a common representational network. In the present study, we address the issue of whether early disorders in production of biological movement correspond to impairment in biological motion perception. By using the simultaneous masking paradigm, we examined visual sensitivity to biological motion in adolescents (aged 13–16 years) who were born very preterm (at 27–33 gestational weeks). In a confidence rating procedure, the presence of a point-light walking figure embedded in a moving mask was judged. The participants differed in their locomotion ability, ranging from normal to a complete walking disability exhibiting signs of leg-dominated bilateral spastic cerebral palsy (BS-CP) caused by periventricular leukomalacia (PVL). Irrespective of an ability to produce movement, patients with a similar extent of PVL in the parieto-occipital complex exhibit nearly the same sensitivity to biological motion. Sensitivity correlates negatively with the extent of PVL over the parieto-occipital complex, whereas neither the severity of motor disorder nor the severity of pyramidal tract affection relate significantly to the sensitivity index. The data suggest that perception of biological motion is not substantially affected by an observer’s early restrictions in body movement. Instead, the findings favour the assumption that the common network for perception and production of biological motion might be inherent for the brain. Motor experience per se does not appear to be necessary for the visual analysis of human movement.

Keywords: biological motion; brain structures; visual psychophysics; periventricular lesions; spastic motor disorders

Abbreviations: BS-CP = bilateral spastic cerebral palsy; GA = gestation age; PVL = periventricular leukomalacia; ROC = receiver operating characteristic; A_c = area under ROC curve

Introduction
Recent theoretical reasoning and experimental findings suggest that the process of perception and production of biological movement might share a common representational network (e.g. Prinz, 1992; Parsons and Fox, 1998; Decety and Grèzes, 1999; Rizzolatti et al., 2001; Wheaton et al., 2001). The initial finding of ‘mirror neurons’ in the monkey premotor cortex that fire during both observation and execution of actions (di Pellegrino et al., 1992) has been followed by neuroimaging studies in humans that revealed the similar or widely overlapping topography of brain activation during production and observation of movements (Rizzolatti et al., 1996; Decety et al., 1997; Hari et al., 1998; Nishitani and Hari, 2000). PET demonstrates, for example, that the premotor and inferior parietal cortex are activated selectively only for visual processing of the body movements which conform to the capabilities of the observer, but not for unnatural actions that are impossible to perform (Stevens et al., 2000). Psychophysical data indicate that visual perception of body movement is substantially affected by the biomechanical properties inherent for this movement (Shiffrar and Freyd, 1993; Daems and Verfaillie, 1999; Pavlova and Sokolov, 2000). This agrees well with an assumption that perception of biological movement is constrained by the implicit knowledge of the brain about
the execution of movement (Viviani and Stucchi, 1992; Viviani et al., 1997). Furthermore, it was shown that perception of hand movements [determination of laterality (right/left) of static pictured hands presented at different orientations] not only depends on biomechanical joint constraints, but also is altered in patients in which execution of hand movements is associated with chronic arm pain (Schwoebel et al., 2001; see also Schwoebel et al., 2002).

Yet, it is unclear whether and, if so, how the perception of biological motion is limited by an observer’s experience with his or her own restrictions in production of body movement. This is especially true when motor development has been impaired from the very beginning or extremely early in life.

The visual system is well tuned to biological motion represented solely by a set of moving dots attached to the main joints of the invisible human body. Adult observers need only very brief exposure (400 ms of stimulus duration) to distinguish point-light displays depicting human locomotion from actions of animated point-light puppets (Johansson, 1976). Perception of gait in point-light stimuli is more accurate than of social and instrumental actions (Dittrich, 1993). The visual sensitivity to point-light locomotion emerges early in perceptual development. By 8–16 weeks of age, infants exhibit a preference for a point-light walking figure over dynamic noise or the same configuration inverted 180° in the image plane (Fox and McDaniel, 1982). Infants at the age of 3–5 months discriminate a point-light walker from similar displays with scrambled spatial relationships between moving dots (Bertenthal et al., 1987) or from a figure without natural relationships of occlusion between moving dots during a gait cycle (Bertenthal et al., 1985). There is also evidence in 5- to 7-month-old infants for visuo-proprioceptive intermodal perception of point-light displays which represent movements of the lower extremities (Schmuckler et al., 2001). By the age of 5 years, children without a history of neurological disorders reach a ceiling level for recognition of point-light configurations depicting human locomotion (Pavlova et al., 2001). The mature visual system of adults robustly tolerates embedding of a point-light walker into a simultaneous moving mask (Cutting et al., 1988; Neri et al., 1998; Pavlova and Sokolov, 2000). Moreover, deficit in higher cognitive functions affects interpretation of point-light displays very little. Adolescents with impairments in high-level symbolic processing need only very brief exposure to recognize actions of point-light walkers (Moore, 2001). Even mentally retarded children with Williams syndrome aged 9–15 years are reported to be able to judge the facing (left- or rightward) of a slightly camouflaged point-light walker (Jordan et al., 2002).

In the present study, within the context of a basic study aimed at assessing visual perceptual deficiencies in adolescents who were born preterm, we ask whether early disorders in ability to produce biological motion relate to impairments in biological motion perception. We are also interested in the relationship between extent and structural topography of subcortical brain damage in these patients and functional visuo-perceptual outcome. By using the simultaneous masking paradigm, we examined visual sensitivity to biological movement in former preterms with periventricular leukomalacia (PVL), a lesion pattern of early origin (early-middle

### Table 1: Characteristics of participants, neurological assessment and structural MRI data

<table>
<thead>
<tr>
<th>Participants with PVL (code)</th>
<th>Age (years)</th>
<th>Gender</th>
<th>GA (weeks)</th>
<th>Birth weight (g)</th>
<th>Motor disorders (score)</th>
<th>Ventricular extent in PT plane (mm)</th>
<th>Volume of PVL (ventricular extent and gliosis, ml)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SHE</td>
<td>16</td>
<td>M</td>
<td>33</td>
<td>1500</td>
<td>0</td>
<td>38</td>
<td>41.5</td>
</tr>
<tr>
<td>MAT</td>
<td>14</td>
<td>M</td>
<td>29</td>
<td>1120</td>
<td>0</td>
<td>39</td>
<td>41.5</td>
</tr>
<tr>
<td>HAK</td>
<td>13</td>
<td>F</td>
<td>33</td>
<td>1250</td>
<td>0</td>
<td>38</td>
<td>41.5</td>
</tr>
<tr>
<td>BMI</td>
<td>15</td>
<td>M</td>
<td>32</td>
<td>2050</td>
<td>0</td>
<td>42.5</td>
<td>42</td>
</tr>
<tr>
<td>AAR</td>
<td>14</td>
<td>M</td>
<td>33</td>
<td>1600</td>
<td>0</td>
<td>41.5</td>
<td>44</td>
</tr>
<tr>
<td>UKE</td>
<td>13</td>
<td>F</td>
<td>28</td>
<td>1240</td>
<td>0</td>
<td>41</td>
<td>42</td>
</tr>
<tr>
<td>BLE</td>
<td>16</td>
<td>M</td>
<td>33</td>
<td>1780</td>
<td>0</td>
<td>50</td>
<td>53</td>
</tr>
<tr>
<td>RUL</td>
<td>15</td>
<td>F</td>
<td>28</td>
<td>1300</td>
<td>0</td>
<td>41.5</td>
<td>44</td>
</tr>
<tr>
<td>TSA</td>
<td>16</td>
<td>F</td>
<td>27</td>
<td>1460</td>
<td>0</td>
<td>38.5</td>
<td>44</td>
</tr>
<tr>
<td>SSA</td>
<td>16</td>
<td>F</td>
<td>33</td>
<td>1380</td>
<td>1</td>
<td>47</td>
<td>57</td>
</tr>
<tr>
<td>SSI</td>
<td>14</td>
<td>M</td>
<td>29</td>
<td>1130</td>
<td>2</td>
<td>55</td>
<td>60.5</td>
</tr>
<tr>
<td>SMA</td>
<td>13</td>
<td>M</td>
<td>29</td>
<td>1280</td>
<td>2</td>
<td>51.5</td>
<td>57</td>
</tr>
<tr>
<td>Mean</td>
<td>15</td>
<td>F</td>
<td>31</td>
<td>1424</td>
<td>2</td>
<td>47.08</td>
<td>43.63</td>
</tr>
<tr>
<td>±SD</td>
<td>1.19</td>
<td></td>
<td>2.32</td>
<td>264</td>
<td></td>
<td>7.59</td>
<td>5.81</td>
</tr>
</tbody>
</table>

M = male; F = female; GA = gestation age; UL = upper limbs; LL = lower limbs; AP = anterior plane; PP = posterior plane; PT = pyramidal tract; Par-occ = parieto-occipital. Eight adolescents (four F/four M) without PVL served as controls. They were aged 13–16 years (14.5 ± 1.2), born premature at 28–33 weeks of gestation (GA 30.63 ± 2.13) with birthweight ranging from 990 to 2280 g (1396 ± 13±16 years (14.5

The visual system is well tuned to biological motion represented solely by a set of moving dots attached to the main joints of the invisible human body. Adult observers need only very brief exposure (400 ms of stimulus duration) to distinguish point-light displays depicting human locomotion from actions of animated point-light puppets (Johansson, 1976). Perception of gait in point-light stimuli is more accurate than of social and instrumental actions (Dittrich, 1993). The visual sensitivity to point-light locomotion emerges early in perceptual development. By 8–16 weeks of age, infants exhibit a preference for a point-light walking figure over dynamic noise or the same configuration inverted 180° in the image plane (Fox and McDaniel, 1982). Infants at the age of 3–5 months discriminate a point-light walker from similar displays with scrambled spatial relationships between moving dots (Bertenthal et al., 1987) or from a figure without natural relationships of occlusion between moving dots during a gait cycle (Bertenthal et al., 1985). There is also evidence in 5- to 7-month-old infants for visuo-proprioceptive intermodal perception of point-light displays which represent movements of the lower extremities (Schmuckler et al., 2001). By the age of 5 years, children without a history of neurological disorders reach a ceiling level for recognition of point-light configurations depicting human locomotion (Pavlova et al., 2001). The mature visual system of adults robustly tolerates embedding of a point-light walker into a simultaneous moving mask (Cutting et al., 1988; Neri et al., 1998; Pavlova and Sokolov, 2000). Moreover, deficit in higher cognitive functions affects interpretation of point-light displays very little. Adolescents with impairments in high-level symbolic processing need only very brief exposure to recognize actions of point-light walkers (Moore, 2001). Even mentally retarded children with Williams syndrome aged 9–15 years are reported to be able to judge the facing (left- or rightward) of a slightly camouflaged point-light walker (Jordan et al., 2002).

In the present study, within the context of a basic study aimed at assessing visual perceptual deficiencies in adolescents who were born preterm, we ask whether early disorders in ability to produce biological motion relate to impairments in biological motion perception. We are also interested in the relationship between extent and structural topography of subcortical brain damage in these patients and functional visuo-perceptual outcome. By using the simultaneous masking paradigm, we examined visual sensitivity to biological movement in former preterms with periventricular leukomalacia (PVL), a lesion pattern of early origin (early-middle
third trimester of pregnancy) and high homogeneity in terms of structural topography (Krägeloh-Mann et al., 1999). This lesion pattern may be considered a proper model for addressing the issue of how topography and extent of subcortical brain impairments of similar timing relate to functional abnormalities. Former preterms with periventricular lesions often exhibit signs of motor disorders in a form of leg-dominated bilateral spastic cerebral palsy (BS-CP) (Krägeloh-Mann et al., 1993; de Vries, 1996). The participants in the present study differed in their locomotion ability, ranging from normal to a complete walking disability.

**Material and methods**

**Participants**

Participants were adolescents (n = 21, aged 13–16 years) born very prematurely at gestation age (GA) 27–33 weeks. They were recruited on a voluntary basis from a data pool of the Department of Paediatric Neurology and Child Development, Children’s Hospital, University of Tübingen. Most of them are follow-ups at this Department. Thirteen participants (seven male and six female) exhibited signs of bilateral PVL on MRI scans. (One female participant was excluded from subsequent data processing because of cortical lesions revealed on her MRI scan.) In nine of them, PVL has caused leg-dominated BS-CP. Eight participants (four male and four female) had MRI scans without any identifiable signs of brain lesions or other abnormalities, and served as controls. All participants had normal or corrected-to-normal vision, and verbal IQ >85 (HAWIK-III based on the WISC III, adapted to the German population). All of them attended a mainstream school, with the exception of one male patient with PVL who attended a special school for motor-disabled children. The participant information is summarized in Table 1. The study was conducted with informed written consent obtained from the participants and their care providers. It complied with the requirements of the Declaration of Helsinki, and was approved by the local ethics committee (Ethik-Kommission der Medizinischen Fakultät der Universität Tübingen).

**Motor disorders assessment**

All participants underwent a standardized neurological examination. BS-CP was diagnosed if the following signs were present: abnormal pattern of posture or movement (e.g. hip adduction or internal rotation with equines of the feet or its secondary malposition), increased tone and pathological reflexes (flexor hypertonicity or increased tendon reflexes). Motor disorders of the upper and lower extremities were assessed separately and scored on 4-point scales (adapted from Krägeloh-Mann et al., 1993; Staudt et al., 2000). For lower limbs, one of the major components of spasticity is restriction of forefoot dorsal extension that leads to a characteristic abnormal walking pattern. The scores for assessment of spastic motor disorders were: 1, near to normal walking pattern, able to walk on heels; 2, moderately abnormal walking pattern, walking on heels only with intermittent forefoot-ground contact; 3, severely abnormal walking pattern, restricted ability to walk unaided, marked slowing down of locomotion speed, inability to lift forefoot from the ground when trying to walk on heels; 4, complete inability to walk unaided. For the upper limbs, a separate scale was used: 1, sequential finger opposition not markedly impaired; 2, marked slowing down of/incomplete sequential finger opposition; 3, inability to move single finger, preserved grasp function; 4, complete inability to grasp. If one of the upper or lower extremities was more affected than the other, the greater score was taken. To make the outcome of neurological examination suitable for further data processing, the severity of motor disability was assessed as zero (score 0) if no signs of BS-CP were detected.

**Structural MRI and quantification of lesion extent**

Structural MRIs were obtained from all participants as axial dual turbo spin-echo slices [35 axial slices, TR (repetition time) 4800 ms, TE (echo time) 85 ms, 4 mm slice thickness] and as T1-weighted three-dimensional data sets [MPRAGE, 128 sagittal slices, TR = 9.7 ms, TE = 4 ms, flip angle 8°, TI (inversion time) 300 ms, 1.5 mm slice thickness] through a 1.5 T Siemens Vision scanner (Erlangen, Germany). For quantification of the extent of PVL, on each T2-weighted slice the area of the lateral ventricle and any identifiable gliosis in the white matter were traced manually on contiguous axial planes using the MRICro software (available at: http://www.psychology.nottingham.ac.uk/staff/crl/mricro.html). The resulting volume was divided into an anterior (frontal), inferior (temporal) and posterior (parieto-occipital) section for each hemisphere. The central sulcus served as a border between the posterior and anterior sections (Yousey et al., 1997), and the tip of the occipital horn of the lateral ventricle was taken as a border between the superior and inferior section. In order to achieve standard dimensions and orientation, a linear normalization was performed through SPM99 (Statistical Parametric Mapping, Welcome Department of Cognitive Neurology, University College London). The normalized lesion volumes were determined in the MRICro software with 50% threshold for interpolated voxels.

For the assessment of the pyramidal tract affection, MRI reconstruction over the corticospinal tract was performed (Staudt et al., 2000). By using the triplanar tools of SPM99, semicoronal planes were reconstructed for each extremity from the three-dimensional data sets along the course of the corticospinal tract from the precentral gyrus to the internal capsule. For the upper limbs, an anterior plane including the hand knob of the precentral gyrus and the anterior third of the posterior limb of the internal capsule was examined, and for the lower limbs, a posterior plane including the uppermost
portion of the central sulcus and the middle third of the posterior limb of the internal capsule. The lateral extent of lateral ventricle in the respective portion of the pyramidal tract (in mm) was used as a measure of pyramidal tract affection (Staudt et al., 2002). This measurement was performed by and averaged among two independent experts blind with respect to patient information. For further data processing, a sum of values of pyramidal tract affection for both right and left (either upper or lower) limbs was used (see Table 1).

Experimental design

Stimuli

Participants were presented with biological motion stimuli of two types. One type represented a point-light walker embedded in a 44-dot simultaneous mask (Fig. 1). The other type of stimulus was a 55-dot mask. A point-light walking figure consisted of 11 dots attached to the head and the main joints (ankles, knee, shoulder, etc.) of an invisible human body. It was seen moving facing right, in a sagittal view, with no net translation. A gait cycle was accomplished in 40 frames with frame duration of 36 ms. This resulted in a walking speed of ~42 complete cycles per min that corresponded to the normal walking speed that ranges from 30 to 70 cycles per min (Inman et al., 1981). A walker subtended a visual angle of 4.0° in height and 2.8° in width at the most extended point of a gait cycle. Forty-four moving dots that corresponded to spatially scrambled points on the joints of a walker were added as a mask. The number of moving dots in the mask was chosen as a result of the previous study conducted in healthy 14-year-old full-term children (Pavlova et al., 2000). With a 66-dot mask, usually used for camouflaging a point-light walker (see, for example, Pavlova and Sokolov, 2000), the sensitivity in full-terms was significantly lower than in adults. With a 44-dot mask (under stimulus duration of 1 s), the sensitivity in full-terms approached the ceiling level. In a display, moving dots were distributed within a region of ~5.0° in height by 6.8° in width. Stimuli were generated using a variant of Cutting’s algorithms (Cutting, 1978).

Task and procedure

Participants were tested individually. None had previous experience with point-light biological motion stimuli. An observer sat at a distance of 57 cm from the screen. His or her head was fixed in a head-and-chin rest. On each trial, by using a confidence-rating procedure, participants judged the presence of a walker. A 5-point equal spaced scale was used (1, confident of the presence of a walker from 100 to 80%; 2, from 80 to 60%; 3, from 60 to 40%; 4, from 40 to 20%; and 5, from 20 to 0%). The stimulus-known-exactly (SKE) detection task (a task in which observers know which target they have to look for) was administered to the participants: each of three experimental runs (32 stimuli in a run \times 3 runs = total 96 stimuli) was preceded by a 10 s exposure to the non-camouflaged walking figure. Each run contained an equal number of stimuli with and without the walking figure; the order of stimulus presentations was randomized. The stimulus duration was 1 s. To avoid time pressure during performance
of the task, participants were asked to determine an appearance of each trial by pressing a button on a keyboard. No feedback was given regarding the subject’s performance.

Results

Motor disorders

In all participants without PVL, neurological examination did not reveal any signs of motor disability. Among 12 patients with bilateral PVL, three were free from impairment of either lower or upper extremities (score 0), and in nine of them a leg-dominated BS-CP was diagnosed (Krägeloh-Mann et al., 1993): lower limbs were more affected than upper limbs. The individual scores for motor disorders are represented in Table 1. Upper limbs were affected in three patients: in one of them with score 1 and in two with score 2. In assessment of the lower extremities, one patient exhibited only slight signs of spastic CP with almost intact locomotion functions (score 1). Lower limbs scores were 2 in two, and 3 in four patients. Two participants were completely unable to walk without external support (score 4). With respect to walking ability, the patients, therefore, ranged from normal function through impairment in walking pattern to complete walking disability.

Relationship of visual sensitivity to motor disability

For psychophysical data processing, we pooled individual data from participants either with or without PVL by averaging the frequencies which each observer gave each rating. The jackknife procedure was employed to calculate statistically unbiased parameters of receiver operating characteristic (ROC) curves from pooled rating-method data (Dorfman and Berbaum, 1986). For further analysis, individual values of the jackknife estimation of the area under the ROC curve ($A_z$), a standard measure of sensitivity in signal detection theory (Macmillan and Creelman, 1990), were taken as a sensitivity index.

We tested the hypothesis that if early motor disability is related to impairments in biological motion perception, then the sensitivity to a camouflaged point-light walker would decrease with increases in the severity of motor disorders. In the patients with PVL, no significant relationship between visual sensitivity to a point-light walker and the severity of functional motor disorders of lower extremities was found (Spearman rank–order correlation, $r = -0.31$, ns; see Fig. 2). We were interested mainly in this relationship for two decisive reasons. First, all patients in the present study had leg-dominated motor disorders. Secondly, there is evidence in adult observers indicating that movement of the lower extremities of a point-light walker is essential not only for a variety of recognition tasks (e.g. Kozlowski and Cutting, 1977) but also for performance on the particular task administered here (Pavlova and Sokolov, 2000). Neither the severity of motor impairment of the upper extremities nor the total severity of motor disorder (defined as a sum of scores given for upper and lower limbs together) related substantially to the sensitivity index (Spearman rank–order correlation, $r = -0.25$, $r = -0.35$, ns, respectively). Overall, the data show that patients with impaired motor ability can have a relatively high sensitivity to a point-light walker, while low sensitivity can be found in patients with normal motor outcome.

Relationship of sensitivity to extent of periventricular lesions

The severity of motor impairment for all four extremities correlates with the lateral extent of the periventricular lesions on MRI reconstruction along the course of the pyramidal tract, i.e. with affections of corticospinal projections (Staudt et al., 2000, 2002). We asked, therefore, whether the sensitivity to biological motion is related to the extent of damage along the course of the pyramidal tract. Neither for lower limbs (Pearson product–moment correlation, $r = -0.45$, ns, for both hemispheres together, Fig. 3B) nor for upper limbs ($r = -0.39$, ns) did the severity of pyramidal tract affection correlate significantly with the sensitivity index.

The sensitivity, however, was found to correlate negatively with the volumetric extent of periventricular lesions over the parieto-occipital complex (Pearson product–moment correlation, $r = -0.68$; $P < 0.02$, for both hemispheres together; Fig. 4B). The negative linkage between sensitivity and extent of parieto-occipital lesions was slightly stronger over the right hemisphere than over the left one ($r = -0.69$, $P < 0.02$, versus $r = -0.63$, $P < 0.05$, respectively). No correlation was found between the sensitivity index and the volumetric lesion extent over the frontal ($r = -0.29$, ns, for both hemispheres together, Fig. 4C; $r = -0.19$, $r = -0.33$, ns, for the left and right hemispheres, respectively) or temporal regions ($r = -0.3$, ns, for both hemispheres together, Fig. 4D; $r = -0.13$, $r = -0.35$, ns, for the left and right hemispheres, respectively). This points to the specificity of the relationship between
parieto-occipital lesions and deficiencies in the detection of biological motion in patients with bilateral PVL.

Figure 5A represents the ROC curves obtained for two of our participants. One of them (BMI, 15 years old, male, 33 weeks GA, Fig. 5B) exhibited complete walking disability, while the other patient (SMA, 13 years old, male, 29 weeks GA, Fig. 5C) had intact locomotion ability (see Table 1). In both of them, a similar extent of parieto-occipital periventricular lesions was found (Fig. 5B and C, lower panels; see also Fig. 4B). As can be seen in Fig. 5A, the ROC curves for the participants are situated close to one another, indicating similar sensitivity to the point-light walker.
serves as a good illustration for the overall outcome of the present study: independently of an ability to produce locomotion, patients with a similar extent of PVL in the parieto-occipital complex exhibit nearly the same sensitivity to biological motion.

ROC analysis shows that sensitivity in preterms without PVL was significantly higher than in preterms with lesions (Student *t* test, one-tailed; *P* < 0.004). As expected, in former preterms without PVL, the sensitivity to the point-light walker was related neither to the volume of the parieto-occipital part of ventricles nor to the lateral extent of ventricle along the course of pyramidal projections to lower extremities (Pearson product–moment correlation; *r* = -0.23, *r* = 0.16, respectively, ns; Figs 3A and 4A).

**Perception of biological motion in patients with early motor disorders**

Although recent findings suggest that perception and production of human movement are intimately linked, there are not yet any conclusive arguments supporting a common neural code between them (e.g. Decety and Grézes, 1999). This study is, to our knowledge, the first to ask whether visual processing of human locomotion is restricted by an observer’s early motor disorder. The data suggest that, at least in the sample of patients with leg-dominated BS-CP, perception of biological motion is not substantially affected by an observer’s early abnormalities in locomotion. To understand the theoretical implications of this finding, it is important to delineate several possible linkages between visual perception and production of movement.

The first line of research concerns biomechanically impossible actions. By now, it is well documented that visual processing of body movements is limited by biomechanical constraints inherent for this movement. For instance, visual priming is markedly suppressed or even does not occur for distorted or impossible dynamic actions (Kourtzi and Shiffrar, 1999; Pavlova and Sokolov, 2000; Verfaillie, 2000). Using the apparent motion paradigm, Shiffrar and
Freyd (1993) have found that observers’ visual impressions of human body movements follow biomechanically plausible (although longer) paths rather than the shorter but impossible paths (e.g. parts of the body arm presented in apparent motion appear to move around the body instead of directly through the body), i.e. biomechanical constraints substantially modulate visual perception. Accordingly, the motor execution areas during performance of the task are activated only for visual processing of the biologically plausible movements (Stevens et al., 2000).

The next stream of research concerns the perception of biomechanically plausible actions that are either beyond the actual capabilities of an individual observer (e.g. ballet) or infrequent in repertoire (e.g. walking on the hands). Although novices and experts differ in their ability to perceive and estimate technically challenging movements such as dance represented in point-light displays (Brownlow et al., 1997), it is unclear whether experts are better because of skilled perceptual or motor abilities, or both together. Recent behavioural findings demonstrate that not only does watching the performance of other people educate action execution (observational learning), but motor learning without involvement of visual modality enhances perceptual judgements (Hecht et al., 2001). One might assume, therefore, that while perceiving technically challenging movements, the brain activity over the motor execution areas should be reduced in novices. In agreement with this, an enhanced brain activity has been observed for the human body stepping forward relative to infrequent stepping backwards (Wheaton et al., 2001; see also related data of Pavlova et al., 2002).

The present work explores visual processing of biomechanically plausible actions that are beyond the capabilities of an observer due to motor disabilities. Although this research perspective is of great clinical relevance, experimental data in this domain are almost absent, with the exception of a few mental imagery functional MRI (fMRI) studies in amputees that show overlapping brain activity during real movements of the intact upper extremity and for imaginary movements of the amputated hand (e.g. Hugdahl et al., 2001; Lotze et al., 2001).

From the common perception–action code view, it seems logical to expect that visual processing of movements should be restricted in motor-disabled patients, especially if a disability is congenital or occurs early in life. Yet a cross-talk between the visual perception and production of human locomotion might represent a special case. Locomotion in the patients of this study has been impaired from the very beginning and, therefore, extends beyond their actual or former capabilities. However, because of the fundamental evolutionary and functional significance of human locomotion, a hard-wired schema for both perception and production of biological movement might be inherent for the brain (see also Bertenthal, 1996; Booth et al., 2002; Shiffrar and Pinto, 2002). The existence of such a schema may account for the lack of a direct connection between global processing of biological motion and individual experience in locomotion production. This outcome agrees well with the intriguing findings obtained from the patient A.Z. with congenitally absent limbs (Brugger et al., 2000). The speeded laterality judgements (right/left) of depicted feet and hands presented at different orientations were not altered in A.Z. as compared with healthy controls. Moreover, as in controls, her perceptual judgements were restricted by the biomechanical constraints.

The motor disorders in the patients of the present study are related to bilateral PVL, a subcortical lesion pattern. If one assumes that the common network for perception and production of movement involves merely high-level cortical representations (e.g., Prinz, 1992), an assumption that also can be drawn from neuroimaging data restricted to the analysis of cortical activity (Decety and Grèzes, 1999), then an ‘implicit cross-talk’ between the perception and production of movement might be intact in these patients. Up until now, however, the role of subcortical structures in modulation of the interplay between perception and production of movement is not well understood and, therefore, we assume that recording of functional brain activity in the patients with PVL would provide evidence that might clarify this issue.

**Visual processing of biological motion and subcortical lesions**

The findings indicate that perception of human locomotion is significantly related to the volumetric extent of bilateral PVL in the parieto-occipital region. Sensitivity drops with the increase in the extent of parieto-occipital lesions, while it does not correlate with the extent of PVL in the frontal or temporal regions. Moreover, ROC analysis reveals that sensitivity in former preterms with PVL is consistently lower than in preterms of the same gestational age without lesions. Overall, the data suggest that processing of biological motion might be markedly modulated already at the subcortical level.

While subcortical processing routines that subserve biological motion perception are largely unknown, the cortical mechanisms underlying biological motion processing currently are being explored extensively by neuroimaging techniques. fMRI indicates that a gradient of activation is present in the posterior parieto-occipital sulcus, the lingual gyrus at the cuneus border and over the intraparietal cortex (Grossman et al., 2000; Grèzes et al., 2001; Grossman and Blake, 2001, 2002; Vaina et al., 2001; Servos et al., 2002). PET shows that the parietotemporal junction, basal temporal regions (fusiform gyrus and temporal poles adjacent to the amygdala) and extrastriate cortex are involved in the perception of actions represented in point-light displays (Bondi et al., 1996; Castelli et al., 2000). The peaks of early oscillatory magnetoencephalographic (MEG) responses (25 Hz) to a point-light walker occur consecutively over the left occipital...
(80 ms), parietal (130 ms) and right temporal (150 ms) lobes (Pavlova et al., 1999). The enhancements of activity, however, are completely absent in response to a ‘scrambled’ walker consisting of the same number of moving dots whose spatial positions are rearranged randomly on the screen. Furthermore, the peaks of activity are topographically restricted to the occipital areas in response to an unrecognizable point-light walker presented upside down in the image plane. To investigate whether and, if so, how subcortical lesions in patients with and without motor disorders affect the time course and topographical dynamics of functional brain activity we currently are bridging the gap between visual psychophysics and the recording of MEG activity.

Acknowledgements
We wish to thank Ella Maslova, an honoured artist of the Russian Federation, for creating an outline image of the point-light walker and the participants and their family members for their kind cooperation. Anja Höpfner, Franziska Hösl and Selina Böhnm assisted in data collection. This work was supported by the University of Tübingen Medical School (fortüne-Program 716 and 979).

References


