Perception and Understanding of Others' Actions and Brain Connectivity

Marina Pavlova, Alexander N. Sokolov, Niels Birbaumer, and Ingeborg Krägeloh-Mann

Abstract

Perception and Understanding of dispositions and intentions of others through their actions are of immense importance for adaptive daily-life behavior and social communication. Here we ask whether, and, if so, how this ability is impaired in adolescents who were born premature and suffer early periventricular damage, periventricular leukomalada (PVL) that affects brain Connectivity. The visual event arrangement (EA) task was administered to PVL patients and two control groups, premature-born and term-born adolescents without brain abnormalities on a magnetic resonance imaging scan. Performance on the EA task was significantly lower in PVL patients as compared with controls. No difference was found between premature-born participants without lesions and term-born controls. Performance on the EA task was inversely related to the Volumetrie extent of lesions in the parieto-occipital regions of both hemispheres and, in particular, to the right temporal periventricular lesions. Whereas our earlier work reveals that compromised visual processing of biological motion, impairments in visual navigation, and other visual-perceptual disabilities in PVL patients are associated with parieto-ocdpital lesions, difflculties in the visual EA task *solefy are* speciflcally linked to the right temporal periventricular lesions. For the ftrst time, we show that the severity of the right temporal PVL can serve äs a predictor of the ability for perception and understanding of others' actions. We assume that impairments in this ability in PVL patients are caused by disrupted brain Connectivity to the right temporal cortex, a key node of the social brain.

INTRODUCTION

Perception and Understanding of the actions of others are of immense value for a variety of daily-life activities and, in particular, for adaptive social behaviors and nonverbal communication (Grezes, Berthoz, & Passingham, 2006; Dakin & Frith, 2005; Paus, 2005). Research with impoverished point-light displays depicting bodily movements indicates that perceivers reliably and easily infer emotions, desires, intentions, and dispositions expressed by a single person or mutual agents (e.g., Chouchourelou, Toshihiko, Harber, & Shiffrar, 2006; Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Atkinson, Dittrich, Gemmel, & Young, 2004; Heberlein, Adolphs, Tranel, & Damasio, 2004; Pollick, Paterson, Bruderlin, & Sanford, 2001; see also Blake & Shiffrar, 2007). The right temporal lobe, which is of particular importance for visual processing of bodily movements, is also involved in social cognition (Puce & Perrett, 2003; Allison, Puce, & McCarthy, 2000). Visual processing of bodily motion has been suggested to be one stage of a brain network for social perception. It is assumed that the human superior temporal sulcus (STS) is reciprocally connected to the orbito-frontal cortex and the amygdala, and provides the cues necessary for recognition of social properties through actions (Adolphs, 2001, 2003). The neural representations of actual biological motion may also extend to biological movement implied frorn static postures and still photographs of people in action (Lorteije et al., 2006; Kourtzi & Kanwisher, 2000; Senior et al., 2000), and some regions in the temporal cortex are activated in a similar way by dynamic events and by static representation of these events with implied motion (Barraclough, Xiao, Oram, & Perrett, 2006; Jellema & Perrett, 2003a, 2003b).

Structural and functional brain Connectivity is of extreme importance for a proper functioning of the networks involved in perception of social properties through bodily movements and actions (Pavlova, 2005). Examining patients with periventricular leukomalacia (PVL), we showed that Structural brain Connectivity is of particular importance for visual processing of body motion. PVL is characterized by gliosis in the white matter and tissue loss with secondary ventricular dilatation (Figure 1), thereby impinging on the pathways interconnecting subcortical structures with cortical regions. Being a result of necrosis of myelinated fibers around the lateral ventricles in the peritrigonal area (Volpe, 2001), PVL represents a lesion pattern of early origin (third trimester of pregnancy) and relatively high homogeneity in terms of timing, pathogenesis, and topography (Krägeloh-Mann, 2004; Pavlova,

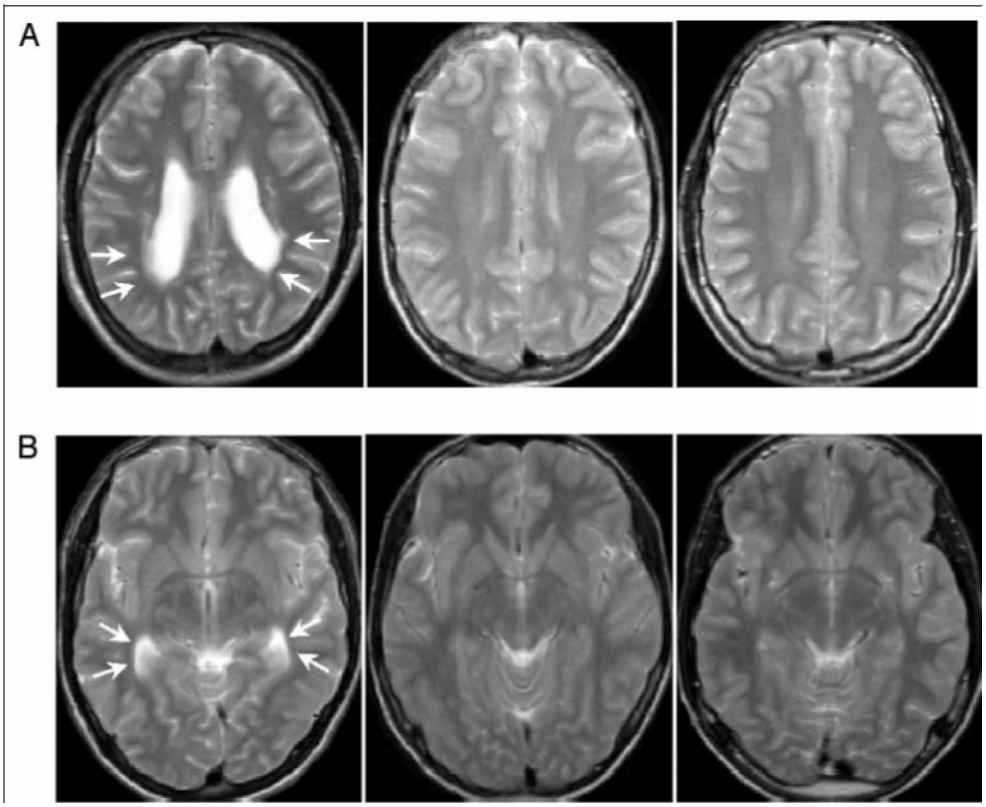

Figure 1. Structural axial T2-weighted MR Images for PVL patients and control participants: (A, first row) z = 32 mm above the bicommissural plane, and (B, second row) at the bicommissural plane level. First column represents images for patient BLE (male, with severe PVL); second column. for a representative control DHE (healthy term-born adolescent, male); third column, for a premature-born control KRO (male) without signs of brain abnormalities. Light arrows point to the signs of parieto-occipital (first row) and temporal (second row) PVL (gliosis in the white matter and secondary ventricular enlargement). For illustrative purposes, we show the MRI of a PVL patient with severe lesions. In this case, Signal changes in the temporal periventricular regions are much more pronounced.

Staudt, Sokolov, Birbaumer, & Krägeloh-Mann, 2003). Our earlier work indicates that biological motion processing is compromised in PVL patients, and this impairment is specifically related to the severity and topography of lesions (Pavlova, Sokolov, Birbaumer, & Krägeloh-Mann, 2006). Early (140-170 msec) evoked RMS (root-mean-square) neuromagnetic cortical activation is weaker in PVL patients than in controls in response to a point-light walking figure over the right parietal lobule (Pavlova, Marconato, et al., 2006). By contrast, the magnetoencephalographic (MEG) response to a control scrambled configuration does not differ between the groups. The modulation of the MEG response is, therefore, stimulus-specific and topographically distinct. Moreover, even mild periventricular lesions modulate the proper functioning of the cortical neuronal assemblies tuned to biological motion by altering their synchronous oscillatory activity over the right temporal lobe (Pavlova, Lutzenberger, Sokolov, Birbaumer, & Krägeloh-Mann, 2007).

In the present work, we address the issue of whether, and, if so, how damage to periventricular brain regions, which contain numerous pathways connecting subcortical structures with the cortex, affects the ability for perception and understanding of others' actions. For this purpose, the visual event arrangement (EA) task was administered to adolescents who were born premature and suffer bilateral periventricular brain damage. For this task, a participant has to organize a set of cards depicting an event in a comic-strip fashion. Similar nonverbal picture tests are failed by autistic children and by adult patients with schizophrenia who are known to have difficulties in perception and nonverbal understanding of the states and intentions of others (e.g., Sarfati, Hardi-Bayle, Besehe, & Widlöcher, 1997; Baron-Cohen, Leslie, & Frith, 1986). It is widely accepted that good performance on such a task requires understanding of the characters' mental states. For successful performance, participants need to grasp the core of the story, which is often based on veridical perception of intentions and dispositions of the characters involved in this particular event. Here we ask (i) how, if at all, performance on the visual EA task is impaired in patients with PVL; and (ii) whether these deficits are specifically related to the topography and extent of periventricular lesions.

METHODS

Participants

Patients were 14 adolescents (aged 13-16 years, 5 girls and 9 boys) born premature between 27 and 33 weeks of gestation with magnetic resonance imaging (MRI) evidence for PVL, which is a form of white matter inJury affecting the regions around the lateral ventricles in the peritrigonal area (Figure 1). Two male patients did not receive neuropsychological examination, and one female patient with PVL was excluded from the data processing because of cortical lesions revealed on her MRI scan. This left the datasets from 11 PVL patients (mean ± *SD* age = 14.55 ± 1.29 years, 4 girls and 7 boys) for

subsequent processing. Eight children who were born premature (4 girls and 4 boys; mean ± *SD* age = 14.5 ± 1.2 years) and eight term-born participants (3 girls and 5 boys; mean ± *SD* age = 14.57 ± 0.78) had MRI scans without any identifiable signs of brain damage or other abnormalities. These children served äs controls. Partic ipants who were born premature were recruited on a voluntary basis from a data pool of the Department of Pediatric Neurology and Child Development, Children's Hospital, University of Tübingen. Term-born controls were recruited äs volunteers from the local Community. All participants had normal or corrected-to-normal vision. Ver bal IQ greater than 85 (HAWIK-III, HAmburg-Wechsler-Intelligenztest für Kinder, 2001; based on the WISC III, adapted to the German population; Tewes, Rossmann, 6 Schallberger, 2001) was an inclusion criterion for all participants. For patients, verbal IQ scores were in the ränge of 101 to 127 (average ± *SD* = 111.09 ± 8.56l), for premature-born controls in the ränge of 103 to 127 (av erage ± *SD* = 112.75 ± 8.972), and for term-born controls in the ränge of 97 to 144 (average ± *SD* = 117.875 ± 14.827). Pairwise comparisons revealed no significant differences in the verbal IQ scores between the groups of participants. We also controlled for oculomotor dysfünctions (such äs nystagmus) that could be observed in pa tients with PVL (e.g., Cioni et al., 1997), and that may affect performance on visual tasks. All participants underwent neurological examination. With respect to locomotion ability, the patients with PVL ranged from normal function through impairment in walking pattern to complete walking disability. More specifically, in 8 of 11 pa tients with PVL, a leg-dominated bilateral spastic cerebral palsy (BS-CP) was diagnosed (for details, see below). All patients attended a mainstream school with the exception of one male patient who attended a special school for motor-disabled children. This patient's score on verbal IQ was within the normal ränge (108). Neither PVL pa tients nor controls had a history of psychiatric disorders including autistic spectrum disorders or attention-deficit hyperactivity disorder. Informed written consent was obtained from the participants and their care-providers in accordance with the requirements of the Ethical Committee of the Faculty of Medicine at the University of Tübingen.

Structural MRI and Quantification of Lesion Extent

MRI scans were obtained äs axial dual turbo spin-echo slices [35 axial slices, TR (repetition time) 4800 msec, TE (echo time) 85 msec, 4 mm slice thickness] through a 1.5-T Siemens Vision Scanner (Erlangen, Germany). PVL is characterized by gliosis in the white matter and tissue loss with secondary ventricular dilatation (Krägeloh-Mann et al., 1999). For quantification of the Volumetrie extent of PVL, on each T2-weighted slice the area of the lateral ventricle and any identifiable gliosis in the white matter were manually traced on contiguous axial planes using the MRIcro Software. The resulting volume was divided into anterior (frontal), inferior (temporal) and posterior (parieto-occipital) sections for each hemisphere. The central sulcus served äs a border between the posterior and anterior sections, and the tip of the occipital hörn of the lateral ventricle was taken äs a border between the superior and inferior sections. In order to achieve Standard dimensions and orientation, a linear normalization was performed through SPM99 (Statistical Parametric Mapping, Wellcome Department of Imaging Neuroscience, University College London). The normalized lesion volumes were determined using the MRIcro Software with a 50% threshold for interpolated voxels.

Motor Disorders Assessment

All participants underwent a standardized neurological examination which is described in detail elsewhere (Pavlova et al., 2003). The scores for assessment of spastic motor disorders of lower limbs 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 for unaided walk, 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 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 a 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 of the two scores was taken for fürther processing. For making the outcome of neurological examination suitable for fürther data processing, the severity of motor disability was assessed äs zero if no signs of BS-CP were detected.

In participants with a normal MRI scan, neurological examination did not reveal any signs of motor disability. Among 11 patients with bilateral PVL, three were free from impairment of either lower or upper extremities (score 0), and in eight of them a leg-dominated BS-CP was diagnosed: Lower limbs were more affected than upper limbs. Upper limbs were affected only in three patients: one with a score of l and two with a score of 2. Lower limbs scores were 2 in two patients, and 3 in four patients. Two participants were completely unable to walk autonomously (score 4). In respect to walking ability, therefore, the patients ranged from normal function over impairment in walking to complete inability for autonomous locomotion.

Neuropsychological Examination

HAWIK-III (Tewes et al., 2001) was administered to all participants. This testing procedure is divided into ver-

bal and nonverbal tasks, measuring verbal IQ (VIQ) and Performance IQ (PIQ). These parts are separated into subscales (or factors) which measure a specific ability such äs Verbal Comprehension (VC), Freedom from Distractibility (FD), Perceptual Organization (PO), and Processing Speed (PS). In brief, the VC subscale is based on results from four oral questionnaires revealing common knowledge about objects and physical/social events. The factor FD is based on two tasks, both of which require the ability for concentration and nonvisual attention: (i) arithmetic tasks, and (ii) digit span. The PO subscale is based on four tasks: (i) picture completion or Identification of a missing piece of an object/scene; (ii) EA, for which a participant has to organize a set of cards depicting an event in a comic-strip fashion; (iii) block design, for which a participant has to arrange blocks in a pattern matching a sample; and (iv) object assembly consisting of Jigsaw puzzles. The subscale PS is based on two tasks requiring visual search and attention: (i) symbol search, in which a participant searches in a string of Symbols for one of the two target items; (ii) coding, in which for each digit a participant has to find a paired symbol given äs a sample before.

Visual Event Arrangement Task

The present study is focused on performance on an EA task administered to participants in the course of neuropsychological examination (FIAWIK-III; Tewes et al., 2001). Being a part of HAWIK-III battery based on the WISC III, the EA task is psychometrically standardized, and provides normative scores obtained in a large healthy population. For this task, 14 sets of cards are presented. Almost all sets of cards (13 out of 14) involve human characters, their actions, intentions, and dispositions. The sets of cards differ in their complexity ranging in number of cards from 3 to 6. Each set of cards is presented in a scrambled (false) order, which is the same for all participants. The participant has to rearrange cards into a predetermined sequence depicting an event in a comic-strip fashion, thereby showing understanding of the event represented in the pictures (Figure 2). Two examiners, the principal investigator (MP) and her assistant, tested participants individually. Each participant was required to start immediately once a set of cards was presented. They were also told that each set had a specific time limit for its rearrangement. Both accuracy (correct order of cards in a sequence) and time needed for an EA (äs a specific time limit for each set ranging, according to the event complexity from 45 to 60 sec) are taken into account when assessing performance on the task. For each set, the number of errors corresponds to specific raw scores given in the HAWIK-III Manual (Tewes et al., 2001). For example, for one of the most complex sets (number 13), correct event rearrangement within the first 10 sec yields a score of 5, within 11-15 sec a score of 4, within 16-25 sec a score of 3, within 26-60 sec a score of 2, and beyond 60 sec a score of 0. According to the FfAWIK-III Manual, raw values (sum of scores with a maximum of 64, resulting from summing up the highest possible scores for each sequence, namely, 2 * 2 + 12 * 5) are then transformed into the standardized normative scores ranging from l *(floor performance)* through 10 *(normal performance for this age)* to 19 *(extraordinary or ceiling performance for this age).*

RESULTS

Performance on EA Task

On the EA task, performance level of PVL patients was significantly lower than in both control groups [mean

Figure 2. Example of the visual EA task (number 7) administered to participants: (A) the randomized order of cards äs presented to participants, and (B) the correct order of cards to represent an event in a comic-strip fashion.

(SD) scores = 7.273 (4.002), 9.75 (1.581), 10.125 (0.835), for PVL patients, premature-born, and term-born controls, respectively; $t(17) = 2.54$, one-tailed,$p < .02$, pairwise comparison with term-born controls; $t(17) = 2.2$, one-tailed, $p < .04$, comparison with premature-born controls]. As can be seen in Figure 3, the performance scores of 9 out of 11 patients were below the optimal level. There were no significant differences in performance between both control groups, that is, between former preterms without lesions and term-born participants *(t* test, two-tailed, $p = .56$). This indicates that poorer performance in PVL patients is not simply due to the consequences of premature birth by itself.

Visual EA Task and Motor Disability

We explored the possibility that performance on the EA task might be related to motor disorders of either upper or lower extremities. We were interested in these relationships for three decisive reasons. First, our earlier research indicates that some visual-perceptual disabilities, such äs visual navigation, might be strongly related to leg-dominated motor disorders (Pavlova, Sokolov, & Krägeloh-Mann, 2007), whereas others, for example, visual processing of human locomotion, do not exhibit such an association (Pavlova et al., 2003). Second, although most PVL patients involved in the study suffered leg-dominated BS-CP and were almost free from motor

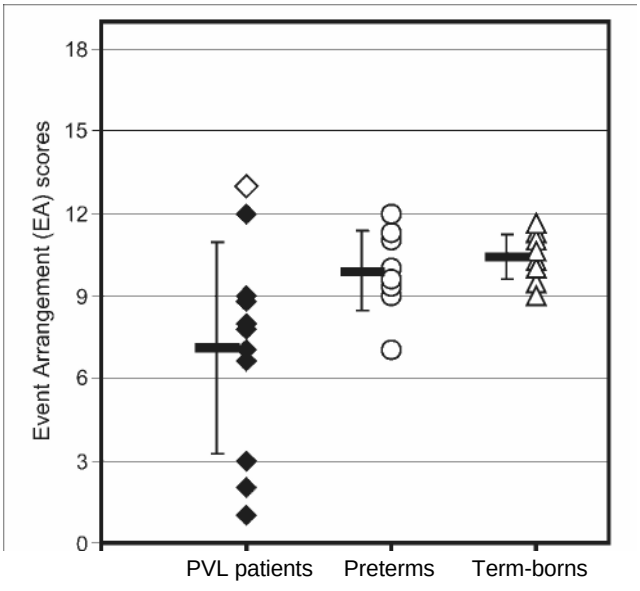

Figure 3- Event arrangement scores in patients with PVL (filled diamonds), and in two control groups: adolescents who were born premature without brain abnormalities on MRI scans (open circles) and healthy term-born controls (open triangles). Maximal score on this task is 18. The open diamond represents data for the patient SMA, who exhibited superior performance on the EA task despite his motor disability. Short horizontal bold lines represent group means, and vertical bars represent ± *SD.*

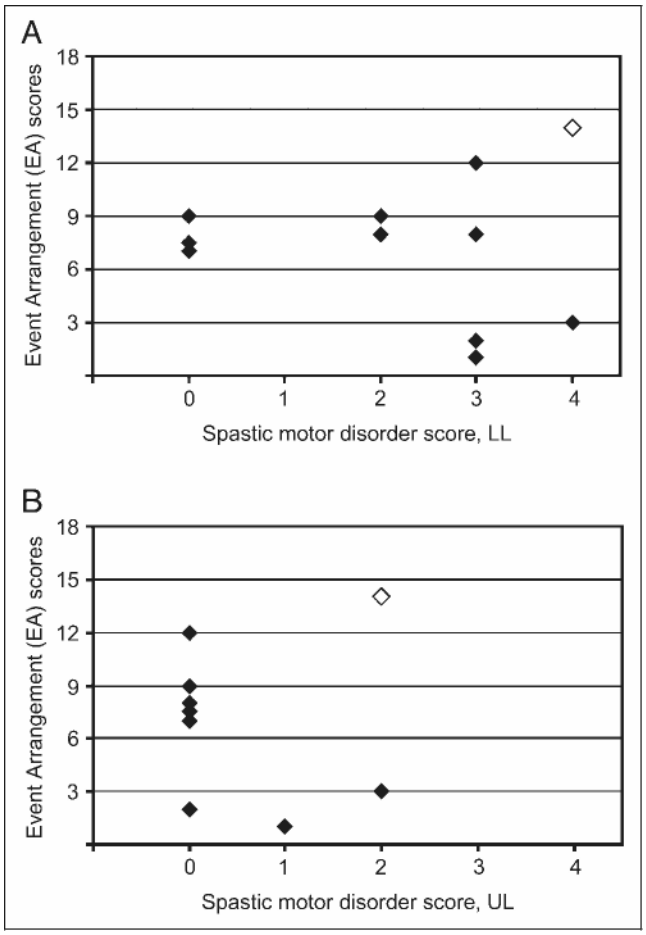

Figure 4. Event arrangement scores plotted against spastic motor disorder scores (A) for lower limbs, LL (Pearson product-moment correlation, $r = —.058$, *ns),* and (B) for upper limbs, UL *(*$r = —.048$, *ns).* The open diamond represents data for the patient SMA, who exhibited superior performance on the EA task despite his motor disability.

disorders of the upper limbs (only in 3 out of 11 patients, mild functional motor disorders were observed), rearrangement of cards in the EA task requires, to some extent, proper functioning of the upper extremities. Third, recent work suggests that production and perception and understanding of intentions through human actions are closely linked to each other (e.g., Molnar-Szakacs, Kaplan, Greenfield, & lacoboni, 2006; Fogassi et al., 2005; lacoboni et al., 2005). In other words, actions that are difficult or impossible to perform might also be associated with deficient visual perception and understanding. We did not find, however, any relationship between performance on the EA task and the severity of leg-dominated BS-CP *(*$r = —.058$, *ns;* Figure 4A) or of functional motor disorders of upper extremities *(*$r = —.042$, *ns;* Figure 4B). The lack of the relationship between the EA task and motor disability in our sample of PVL patients is illustrated by the case of patient SMA, who exhibited superior performance on the EA task, although he is suffering from severe leg-dominated BS-CP (score 4; Figures 3 and 4A), resulting in a complete

inability for independent locomotion, äs well äs a mild motor disorder of the upper limbs (score 2; Figure 4B).

Visual EA Task and PVL Topography and Extent

In PVL patients, performance on the EA task correlated negatively with the Volumetrie extent of lesions over the parieto-occipital complex (Pearson product-moment correlation, r = —.684, p < .03). Overall, the performance level dropped with an increase of the lesion extent over both hemispheres (Figure 5C, E), but for the right hemisphere, this relationship was stronger *(r* = —.745, p < .01, for the right hemisphere vs. r = —.635, p < .05, for the left hemisphere). Neither the right nor the left hemispheric Volumetrie lesion extent in the

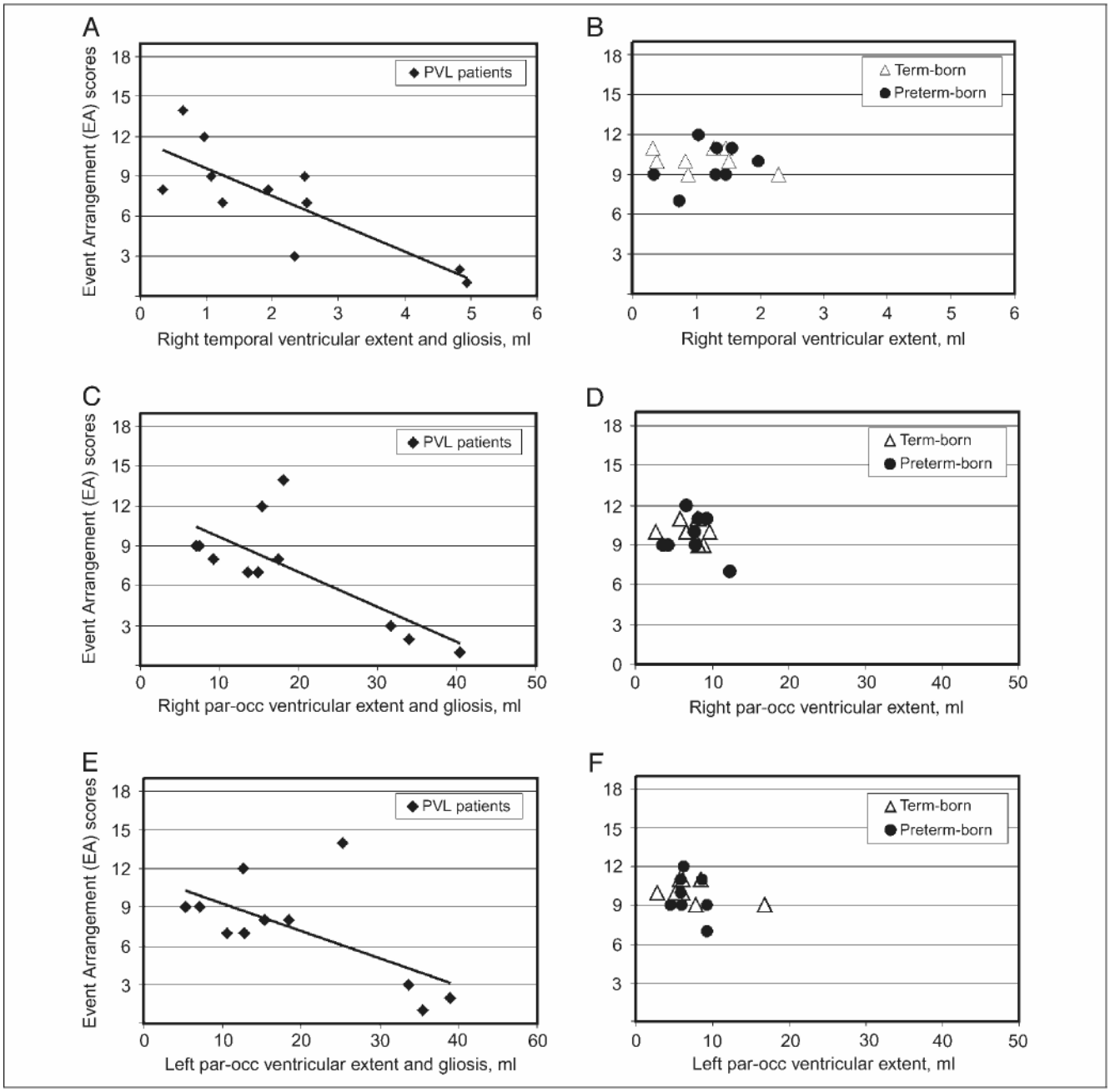

Figure 5. Event arrangement scores plotted against (A) Volumetrie extent of PVL (ventricular extent plus gliosis) in the right temporal regions in patients (Pearson product-moment correlation, r = — .815, p < .01), (B) Volumetrie lateral ventricular extent in the right temporal region in term-born (open triangles; r = —.319, *ns)* and preterm-born controls (fllled circles, r = .377, *ns),* (C) Volumetrie extent of PVL in the right parieto-occipital regions in patients *(r* = —.745,p < .01), (D) Volumetrie lateral ventricular extent in the right parieto-occipital regions in term-born (open triangles; r = —.172, *ns)* and preterm-born controls (fllled circles, r = —.229, *ns),* (E) Volumetrie extent of PVL in the left parieto-occipital regions in patients *(r* = —.635, p < .05), and (F) Volumetrie lateral ventricular extent in the left parieto-occipital region in term-born (open triangles; r = —.486, *ns)* and preterm-born controls (filled circles; r = —.327, *ns).*

frontal periventricular regions was linked to performance on the EA task.

Notably, the strongest correlation was found between performance on the EA task and the Volumetrie extent of PVL in the right temporal region *(r* = —.815,*p* < .01; Figure 5A), whereas the extent of lesions in the left temporal region was not significantly related to the ability for establishing event progression in the EA task *(r* = —.307, *ns).* In both control groups, no link was found between performance on the EA task and the right temporal ventricular extent *(r* = .377, *r* = —.319, *ns,* for premature-born and term-born controls, respectively; Figure 5B). Neither the Volumetrie ventricular extent in the right parieto-occipital regions *(r* = —.229, *r* = —.172, *ns,* for premature-born and term-born controls, respectively), nor the left parieto-occipital ventricular extent *(r* = —.327, *r* = —.486, *ns,* for premature and term-born controls, respectively) was related substantially to performance on the EA task (Figure 5D, F).

In earlier work (Pavlova, Sokolov, et al., 2006), we reported a strong negative link between the extent of bilateral parieto-occipital PVL and performance on the task requiring visual processing of point-light displays representing human locomotion. We also established the inverse relationship between the extent of bilateral parieto-occipital PVL and the scores on IQ factors perceptual organization and processing speed (Pavlova et al., 2005). The negative relationship occurred between the visual navigation ability in PVL patients and the Volumetrie extent of the parietal and frontal lesions in the right hemisphere (Pavlova, Sokolov, et al., 2007). The strong negative link to the extent of the right temporal PVL found in the present study is specific for performance on the EA task, äs it did not occur for other visual-perceptual tasks (i.e., picture completion, block design, object assembly, symbol search, and coding) administered in the course of neuropsychological examination, for visual navigation ability, for performance IQ, and for visual detection of camouflaged human locomotion.

We further submitted the data to a stepwise multiple regression analysis, with the dependent variable "performance on the EA task" and three independent variables, namely, right temporal PVL, right parieto-occipital PVL, and left parieto-occipital PVL. The Volumetrie extent of the right temporal PVL was entered first, and explained a significant percentage of the variance (63%) in performance on the visual EA task *[F(l,* 9) = 17.85, *p* < .002]. The extent of right parieto-occipital PVL was entered second, but did not explain any further significant proportion of the criterion variance. The third variable (extent of left parieto-occipital PVL) was entered third, and also did not explain any further significant proportion of the criterion variance. Therefore, the extent of right temporal PVL could be considered the best predictor of disability on the EA task.

Visual EA Task, IQ Factors, and Visual Perceptual Abilities

As indicated earlier, normal verbal IQ was an inclusion criterion, and groups of participants did not differ from each other in respect to verbal IQ (see Methods). No linkage was found between performance of PVL patients on the EA task and the scores on VTQ *(r* = .352, *ns)* äs well äs with both factors constituting VIQ, namely, the verbal comprehension *(r* = .227, *ns)* and freedom from distractibility *(r* = .421, *ns).* By contrast, compromised performance on the EA task in PVL patients is positively correlated with PIQ *(r* = .797, *p* < .01) äs well äs with both factors constituting PIQ, namely, perceptual organization *(r* = *.814, p* < .01) and processing speed *(r* = *.816, p* < .01).

A strong positive link occurred between performance on the EA task and two out of three visual-perceptual tasks constituting the factor perceptual organization, namely, with block design test *(r* = *.685, p* < .01) and object assembly *(r* = *.652, p* < .01). Performance of PVL patients on both of these tasks is also negatively correlated with the Volumetrie extent of parieto-occipital lesions in the right hemisphere *(r* = —.626, *p* < .05, block design, and *r* = —.799, *p* < .01, object assembly). In addition, the strong positive linkage occurred between performance on the EA test and on a symbol search task, one of the two tasks constituting the processing speed factor *(r* = .839, *p* < .01). Performance on the symbol search task was also inversely related to the extent of the right parieto-occipital lesions *(r* = —.692,*p* < .02). As expected from the HAWIK-III Manual (Tewes et al., 2001), in both control groups, a strong positive correlation was found between performance on the EA task and the perceptual organization factor *(r* = .824, *r* = .797, *p* < .02, for preterms without PVL and for term-born adolescents, respectively). For both control groups, no significant link was found between performance on EA tasks and other visual-perceptual tasks administered in the course of neuropsychological examination.

Notably, in PVL patients, performance on the EA task was also positively linked to the visual sensitivity to biological motion *(r* = *.742,p* < .01). Biological motion processing was inversely related to the parieto-occipital lesions in both hemispheres, but more strongly to the right hemispheric lesions (Pavlova, Sokolov, et al., 2006; Pavlova et al., 2003).

It is important to stress that although performance on EA task is also inversely related to the Volumetrie extent of parieto-occipital lesions bilaterally, *the EA task solely has a specific negative link with the extent of temporal lesions in the right hemisphere,* and äs shown by the regression analysis (see above), the right temporal PVL could serve the best predictor of difficulties on this task. This underscores the specificity of the impairments in perception and understanding of others' actions in the EA task äs compared to other visual perceptual abilities in PVL patients.

DISCUSSION

Combining Volumetrie analysis of the structural MRI with neuropsychological investigation, we addressed the issue of whether and, if so, how perception and understanding of others' actions is impaired in adolescents who were born premature and who suffer from periventricular brain damage. The main outcome of this work reveals that performance on the visual EA task requiring perception and understanding of states and intentions of others is compromised in PVL patients even if lesions are acquired early in life, are relatively small in size, and the verbal IQ is within the normal ränge. Moreover, the severity of this impairment is specifically related to the topography and extent of PVL: Performance on the visual EA task is inversely related to the Volumetrie extent of damage to the right temporal region and the parieto-occipital lesions in both hemispheres. The lack of differences in performance on the visual EA task between term-born and premature-born controls with normal MRI scan indicates that the factor of brain prematurity alone is irrelevant for normal development of the perception and understanding of the actions of others even if they are depicted in a static comic-strip fashion. These data dovetail with recent findings in children aged 5-6 years who were born premature with low weight, indicating that deficits in motion-defined form recognition relate to the presence of periventricular brain inJury and/or retinopathy of prematurity, that is, *to premature birth complications,* rather than to a history of prematurity per se (Jakobson, Frisk, & Downie, 2006). The findings are also in good agreement with our previous data revealing that the factor of prematurity, by itself, is not critical for visual processing of biological motion (Pavlova, Sokolov, et al., 2006; Pavlova et al., 2003), visual navigation (Pavlova, Sokolov, et al., 2007), äs well äs other visual-perceptual and attentional abilities (Pavlova et al., 2005). Higher-order visual-perceptual and cognitive functions such äs visual navigation ability or attentional ca-pacity depend on intact communication between several areas throughout the brain. Damage to the parietal periventricular regions that contain many interconnecting fibers projecting to the cortex might Interrupt functioning of several cortical-subcortical networks that subserve higher visual perceptual functions (see also Skranes et al., 2007). Periventricular lesions might break, for example, the reciprocal thalamocortical interrelations impinging on posterior thalamocortical fibers (Krägeloh-Mann et al., 1999). Diffusion tensor imaging (DTI) suggests that PVL affects the posterior thalamic radiation (Thomas et al., 2005; Hoon et al., 2002) connecting the pulvinar and the lateral geniculate nucleus (LGN) with the parietal cortex (Behrens et al., 2003). Interruptions of these connections might affect performance on a number of visual perceptual and attentional tasks. In a healthy population, the posterior thalamocortical fibers are much more numerous and widely distributed on the left side of the brain (Thomas et al., 2005), and, therefore, left hemispheric functions might remain relatively intact in patients with bilateral damage to periventricular regions. However, right hemispheric functions might be heavily affected. In earlier work (Pavlova, Sokolov, et al., 2006; Pavlova et al., 2005), we showed that compromised visual processing of point-light displays representing human walking was associated with the severity of parietal periventricular lesions in both hemispheres. We also established the inverse relationship between the extent of bilateral parieto-occipital PVL and the scores on the factors perceptual organization and processing speed constituting performance IQ (Pavlova et al., 2005). Moreover, visual navigation ability in PVL patients also exhibits an inverse relationship to the right parieto-occipital lesions (Pavlova, Sokolov, et al., 2007). Here we report an inverse linkage between the Volumetrie parieto-occipital PVL extent and the scores on visual-perceptual tasks, constituting performance IQ, namely, the block design and object assembly tasks, which are best predictors of the IQ factor perceptual organization (Tewes et al., 2001), and the Symbol search task. One might assume, therefore, that bilateral parieto-occipital lesions *nonspecifically* affect a wide ränge of visual perceptual and attentional functions. We have shown, however, that one of the best predictors of visual impairments in visual navigation and way finding is the Volumetrie extent of periventricular lesions over the right frontal region (Pavlova, Sokolov, et al., 2007). The present study shows that although performance on the visual EA task is negatively correlated with the extent of parieto-occipital PVL in both hemispheres, the best predictor of impairments in the visual EA is the Volumetrie extent of *right temporal* PVL. Depending on their topography and severity, periventricular lesions *specifically* affect distinct neural networks involved in subserving different visual perceptual abilities. This opens a window for the possibility of making early predictions of abnormalities and of subsequent training of specific visual-perceptual skills.

One of the essential findings of the present study is the inverse relationship between performance on the visual EA task requiring perception and understanding of others' actions and the extent of temporal PVL in the right hemisphere. A wealth of brain imaging and neuropsychological data point to the right temporal lobe äs an important contributor to both visual processing of bodily motion (e.g., Pavlova, Birbaumer, & Sokolov, 2006; Zacks, Swallow, Vettel, & McAvoy, 2006; Grossman, Battelli, & Pascual-Leone, 2005; Morris, Pelphrey, & McCarthy, 2005; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Thompson, Clarke, Stewart, & Puce, 2005; Grossman, Blake, & Kim, 2004; Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004; Vaina & Gross, 2004; Beauchamp, Lee, Haxby, & Martin, 2003; Pelphrey et al., 2003; Grossman & Blake, 2001; Grossman et al., 2000) and perception of intentions and dispositions of others (e.g., Pelphrey, Morris, & McCarthy, 2004; Adolphs, 2003; Puce & Perrett, 2003;

Schultz et al., 2003; Castelli, Happe, Frith, & Frith, 2002; Allison et al., 2000). This region is reciprocally connected to the orbito-frontal cortex and the amygdala (Adolphs, 2003). A nonverbal task similar to that used in the present study has been reported to activate the temporal-parietal junction (TPJ) and temporal lobes in healthy male participants (Völlm et al., 2006; see also Gallagher et al., 2000). We assume that temporal-parietal periventricular lesions disrupt brain Connectivity, äs well äs subcortical-cortical and cortical-cortical connections with the right temporal cortex. These lesions could lead to difficulties in perception and understanding of social properties such äs states, intentions, desires, and dispositions of others through their actions. These data are in a good agreement with the fmdings in autistic patients that have some difficulties in social attribution. Compared with healthy controls, the extrastriate region of these individuals shows reduced functional Connectivity to the STS (Castelli, Frith, Happe, & Frith, 2002). Autistic patients also exhibit structural abnormalities in the right temporal cortex (McAlonan et al., 2005; Walter et al., 2004). Recent DTI in high-functioning autistic children indicates disrupted white matter tracts (äs revealed by reduced fractional anisotropy values) between regions implicated in social cognition, including the STS (Barnea-Goraly et al., 2004). Most intriguing, it is reported that in very-low-birth-weight adolescents, mild social deficits measured by autism spectrum screening questionnaire (ASSG) correlate with reduced fractional anisotropy values in several white matter tracts (Skranes et al., 2007). Very-low-birth-weight adolescents (who are at a high risk of perinatal white matter inJury such äs PVL) presumably exhibit a considerably milder form of social cognition deficits than individuals with autistic spectrum disorders, and these deficits are due to impaired Connectivity in long association fibers. The present fmdings are in accord with this assumption.

One of the limitations of the present findings is that the visual EA task used here, albeit being a well-established tool for neuropsychological assessment, requires reconstruction of events from static frames or cards representing different parts of events. Neural mechanisms of such reconstruction might substantially differ from the visual perception of real or filmed actions and events (e.g., Lorteije et al., 2006). Although the neural representations of actual biological motion in the temporal lobe also extend to biological motion implied from still photographs of people in action (Barraclough et al., 2006; Jellema & Perrett, 2003a, 2003b), impairments on the EA task found in PVL patients do not necessarily suggest that they would exhibit difficulties in perception and understanding of social properties through real or filmed bodily movement. Further clarification of this issue requires special examination.

The nature of the EA task may also account for a lack of connection between perception and understanding of actions and impaired ability for production of movements. Recent work suggests that production of actions and understanding of intentions and dispositions through human actions are intimately tied (e.g., Molnar-Szakacs et al., 2006; Fogassi et al., 2005; lacoboni et al., 2005). Actions difficult or impossible to perform might also yield deficient visual Interpretation and understanding. Taken together with the lack of association between the visual sensitivity to human locomotion and severity of motor disorders, namely, bilateral leg-dominated cerebral palsy, reported in PVL patients earlier (Pavlova et al., 2003), the present findings suggest that understanding and production of human actions are connected in a more complex, indirect way (for further discussion, see also Blake & Shiffrar, 2007).

In summary, the outcome of the present work indicates that perception and understanding of actions of others are compromised in adolescents who were born premature and exhibit signs of periventricular brain damage. This impairment is related to the Volumetrie extent of periventricular lesions in the parieto-occipital regions in both hemispheres, and, most distinctly, to *the right temporal* region. For the first time, we show that the severity of the right temporal PVL can serve äs a predictor of the ability for perception and understanding of others' actions. We assume that impairments in this ability in PVL patients are caused by disrupted brain Connectivity with the right temporal cortex, a key node of the social brain network. The precise nature of neuronal mechanisms underlying the processes of social attribution revealed through human actions and body dynamics remains an open question, which is of immense value for our understanding of social behaviors.

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Reprint requests should be sent to Marina A. Pavlova, Developmental Cognitive and Social Neuroscience Unit, Department of Pediatric Neurology and Child Development, Children's Hospital, University of Tübingen, Hoppe-Seyler-Str. l, D-72076, Tübingen, Germany, or via e-mail: marina.pavlova @uni-tuebingen.de.

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