Neuropsychologia 48 (2010) 1616–1627

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Effects of lateral head inclination on multimodal spatial orientation judgments in neglect: Evidence for impaired spatial orientation constancy

Johanna Funk[a,*], Kathrin Finke[a], Hermann J. Müller[a], Kathrin S. Utz[b], Georg Kerkhoff[c]

[a] Department of Psychology, General and Experimental Psychology/Neuro-cognitive Psychology, Ludwig Maximilian University, Leopoldstr. 13, D-80802 Munich, Germany
[b] International Research Training Group 1457 "Adaptive Minds", Saarbruecken, Germany
[c] Clinical Neuropsychology Unit and University Ambulance, Saarland University, Saarbruecken, Germany

ARTICLE INFO

Article history:
Received 13 November 2009
Received in revised form 29 January 2010
Accepted 31 January 2010
Available online 6 February 2010

Keywords:
Neglect
Space perception
Subjective vertical
Subjective horizontal
Visual
Tactile
Posture
Gravity

ABSTRACT

Recent research revealed that patients with spatial hemineglect show deficits in the judgment of the subjective vertical and horizontal. Systematic deviations in the subjective axes have been demonstrated in the visual and tactile modality, indicating a supramodal spatial orientation deficit. Further, the magnitude of the bias was shown to be modulated by head- and body-position. The present study investigated the effect of passive lateral head inclination on the subjective visual and tactile vertical and horizontal in neglect patients, control patients with left- or right-sided brain damage without neglect and healthy controls. Subjects performed visual- and tactile-spatial judgments of axis orientations in an upright head orientation and with lateral head inclination 25° in clockwise (CW) or counterclockwise (CCW) direction. Neglect patients displayed a marked variability as well as a systematic tilt in their spatial judgments. In line with a multisensory spatial orientation deficit their subjective vertical and horizontal was tilted CCW in the visual and in the tactile modality, while such a tilt was not evident in any other subject group. Furthermore, lateral head inclination had a differential effect in neglect patients, but not in control subjects. Neglect patients' judgments were modulated in the direction of the head tilt ('A-effect'). That is, a CCW inclination further increased the CCW spatial bias whereas a CW inclination decreased the spatial bias and thus led to approximately normal performance. The increased A-effect might be caused by a pathologically strong attraction of the subjective vertical by an idiotropic vector relying on the actual head orientation, as a consequence of impaired processing of gravitational information in neglect patients.

1. Introduction

Hemispatial neglect is a supramodal neurological disorder characterized by a complex syndrome of sensory, motor and representational deficits (for a review, see Kerkhoff, 2001). Neglect patients fail to detect or respond to stimuli in their contralesional hemispace (Bisiach, Pizzamiglio, Nico, & Antonucci, 1996), show unilateral spatial representational deficits (Bisiach & Luzatti, 1978; Bisiach, Capitani, Luzatti, & Perani, 1981) and frequently display a reduced use of their contralesional extremities (Laplane & Degos, 1983). Most of the current models of neglect focus on the explanation of deficits in the horizontal plane. Such deficits are apparent, for example, as left-sided omissions in visual search, reading, writing and drawing tasks, as deficits in (horizontal) size perception in the contralesional hemispace (Milner & Harvey, 1995; Milner, Harvey, Roberts, & Forster, 1993), as a compression of contralesional hemispace (Gainotti & Tiacci, 1971; Nichelli, Rinaldi, & Cubelli, 1989) or even both hemispaces (Halligan & Marshall, 1991), as rightward deviations in line bisection and in pointing straight ahead, and as a deviation of space representation towards the ipsilesional hemispace (Karnath, 1997). However, numerous studies have demonstrated deficits in visuospatial perception and visuomotor performance that cannot result solely from impairments restricted to the horizontal plane (for a review, see De Renzi, 1982). These include impairments in visual orientation discrimination and position estimation (Tartaglione, Benton, Cocito, Bino, & Favale, 1981; Tartaglione, Cocito, Bino, Pizio, & Favale, 1983; Taylor & Warrington, 1973; Warrington & James, 1967) as well as deficits in the judgment of the subjective visual vertical (SVV) and horizontal (SVH; Howard, 1982; Lenz, 1944), and judgments of oblique line orientations (Benton, Hannay, & Varney, 1975; De Renzi, Faglioni, & Scotti, 1971; Kim, Morrow, Passafiume, & Boller, 1984).

1.1. Brain damage, hemineglect, and tilted space

The relation between brain damage and deviations of the subjective vertical and, thus, spatial judgments in the frontal plane,

* Corresponding author.
E-mail address: Johanna.Funk@psy.lmu.de (J. Funk).

0028-3932/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2010.01.029

was studied extensively by Bender and Jung (1948) already in 1948. The authors found that deviations of the subjective vertical from the true vertical exceeding 2° are indicative of frontal or parietal, but not of occipital lobe lesions. The direction of the deviations was contralesional, with clockwise (CW) deviations following left, and counterclockwise (CCW) deviations following right fronto-parietal lesions. In a more recent large-scale investigation, Brandt, Dieterich, and Danek (1994) tested judgments of the SVV in 71 patients with unilateral hemispheric lesions. MRI analyses revealed that the most impaired patients had lesions centering on the human homologue of the monkey parieto-insular-vestibular cortex (PIVC; Grüsser, Pause, & Schreiter, 1990), and thus closely neighboring and overlapping with those lesions which cause neglect behavior. Hence, it may be mainly the neglect patients who show abnormal SVV judgments in the frontal plane. Accordingly, Kerkhoff and Zoelch (1998) found that 12 out of 13 neglect patients showed deficits in visuospatial judgments of axis orientations in the vertical, horizontal and oblique orientation. The deficits were not an unspecific consequence of brain damage, as patients with left or right hemispheric lesions *without* neglect performed at the level of healthy participants. Furthermore, Yelnik et al. (2002) showed that deviations of the SVV are above all related to the neglect severity, rather than to the lesion size and localization, indicating that SVV tilt is not a consequence of right hemisphere damage per se, but rather of anatomical damage which typically causes spatial neglect, including the gravity system of the right hemisphere. These findings indicate a severe disturbance in the representation of space in the frontal plane in neglect patients which does not seem to constitute an epiphenomenon but one of the core deficits of the neglect syndrome.

De Renzi et al. (1971) found that patients with right posterior lesions are significantly impaired in both the visual and the tactile perception of the horizontal and the vertical axis. Kerkhoff (1999) additionally showed that CCW tilts in the two modalities are correlated with each other and with the neglect severity. Thus, comparably to impairments in the horizontal plane, the deficits in the frontal plane seem to be multimodal (or even supramodal). In a recent study with 80 stroke patients, Pérennou et al. (2008) found that patients with right hemisphere lesions showed CCW visual (in 55% of the subjects), tactile (32.5%) and postural (42%) tilts in the frontal plane. Since especially parietal lesions caused marked visual and tactile tilts in the frontal plane, the authors concluded that the right parietal cortex is crucially involved in the elaboration of an internal supramodal model for verticality perception.

1.2. Effects of posture and head orientation in space on orientation judgments in neglect

Evidence from recent research suggests that deficits in spatial orientation judgments are significantly modulated by gravitational input in neglect patients. These studies modulated the body posture of neglect patients and, as a consequence, also their head orientation in space to investigate the effect of the accompanying modulations of gravitational information on spatial deficits in these patients. Saj, Honoré, Davroux, Coello, and Rousseaux (2005) systematically investigated the effects of body posture on the perception of the visuohaptic subjective vertical in the frontal plane. Posture had no effect on SVV judgments in healthy control subjects. However, in the neglect patients the CCW tilt of SVV judgments was significantly reduced in supine compared to upright posture. In supine posture, the influence of otholitic input on space perception is reduced (Diener & Dichgans, 1988; Howard, 1982). Since in neglect patients graviceptive input from the left and right otholitic system is not processed symmetrically (e.g., Pizzamiglio, Vallar, & Doricchi, 1995), the change of head position in space in supine compared to upright posture and the accompanying modulation of graviceptive input resulted in a reduction of the pathological bias. Positive effects of modulations of graviceptive input in backward-tilted or lying body-position have also been documented for line bisection deviations (Pizzamiglio et al., 1995) and exploration biases (Karnath, Fetter, & Niemeier, 1998) in neglect patients. In a recent study (Funk, Finke, Mueller, Preger, & Kerkhoff, 2010), we investigated effects of posture on the subjective *tactile* vertical (STV) in neglect patients and found that posture affects performance of neglect patients also in the tactile domain (although we found different results than Saj et al., 2005). Apart from whole-body changes, head tilts alone modulate gravitational input and thus also affect spatial orientation judgments in neglect. A further experiment in the Kerkhoff (1999) study showed that the orientation deficit of a neglect patient was significantly aggravated by a CCW tilt of the head by 25°, and significantly reduced by a comparable CW tilt. In a healthy control subject, in accordance with previous evidence (for a review, see Howard, 1986), CW and CCW head tilt slightly deteriorated performance when compared with the upright condition. While these findings indicate that the head-on-trunk orientation (i.e., the angle of inclination) might play an important role in the judgment of spatial orientation in the frontal plane in neglect patients, a more systematic study including a group of patients and controls has not been carried out to date.

1.3. Which cues are mediating the effects of posture on spatial orientation?

Different reference frames can define a visual orientation in space (for reviews, see, e.g., Howard, 1982; Rock, 1990; Wade, 1992). Most important for the judgment of the subjective main spatial axes are probably the gravitational and the egocentric (head-/body-centered) reference frames. In upright posture, the gravitational and the egocentric vertical are aligned; by contrast, in tilted head-/body-position, the two coordinate systems are decoupled. Therefore, tilts of the head and body can induce displacements in the *subjective* vertical (Luyat, Gentaz, Corté, & Guarrez, 2001; Luyat & Gentaz, 2002) either in the direction of postural inclination (the Aubert, or A-effect) or in the opposite direction (the Müller, or E-effect). It has been suggested that the E-effect occurs at small, and the A-effect at greater angles of tilt (for a review, see Howard, 1986). However, when the tilt is restricted to the head (with stable position of the body), results vary between experiments, that is, E-effects (e.g., Day & Wade, 1969; Wade, 1968), A-effects (e.g., Dichgans, Diener, & Brandt, 1974; Parker, Poston, & Gulledge, 1983) or no general effect (e.g., Dilorenzo & Rock, 1982) were observed. Luyat and Gentaz (2002) argue that "...A- and E-effects demonstrated that tilted subjects have not access to a veridical gravitational reference frame but rather to a subjective gravitational reference frame which is no longer congruent with the physical one. In the visual modality for example, a rod aligned with the physical vertical will be perceived as deviated in the direction opposite of the head or body tilt (A-effect) and, as a result, the subjective vertical, in this case, will be deviated in the direction of the head or body" (p. 1004, first paragraph). In healthy subjects, the subjective vertical is congruent with the physical/objective one in upright posture and, thus, a displacement in either direction would mean a slight decline in performance. By contrast, in neglect patients, the subjective vertical is *not* congruent with the objective one in upright posture (e.g., Kerkhoff & Zoelch, 1998; Kerkhoff, 1999), probably due to asymmetric processing of gravitational input. In such patients, a further CCW displacement of the subjective vertical would represent a further increase in spatial bias, whereas a CW displacement would represent a decrease in spatial bias and thus a trend towards normal performance.

It has been suggested that the effect of head orientation on the perception of space is based on a modulation of gravitational inflow (e.g., changes in vestibular and kinesthetic inputs; Howard, 1982). More specifically, head inclinations reduce the impact of gravitational input (due to reduced sensitivity of the utricles). Since neglect patients process graviceptive information in an asymmetric way (e.g., Pizzamiglio et al., 1995), this gravitational model predicts a reduction of the spatial bias no matter whether the head is tilted CW or CCW. Conversely, in normal subjects, the model would predict a slightly worse performance with head tilt in either direction. Alternatively, Mittelstaedt (1983) suggested that the subjective vertical is the product of a sensory, a gravitational and an idiotropic vector. In this model, the idiotropic vector (i.e., the body- and head-vertical axis) serves as an intrinsic reference frame guiding spatial orientation. Since neglect patients process graviceptive information deficiently, they might rely more on other information, such as the idiotropic vector, than normal subjects. In this case, the model would predict that neglect patients show a tendency to orient verticality judgments towards the head-vertical axis (A-effect). That is, neglect patients would display an even greater CCW tilt of their subjective vertical with a CCW head tilt and a reduction of the CCW bias with CW head tilt. Healthy subjects might display this tendency too, albeit to a significantly lesser degree.

1.4. Rationale of the present study

The present study systematically investigated whether and how spatial orientation deficits are modulated by changes in head orientation in neglect patients. Since head tilt has been shown to modulate gravitational input (e.g., Diener & Dichgans, 1988; Howard, 1982), and furthermore the processing of graviceptive information is known to be deficient in patients with spatial neglect (e.g., Lafosse, Kerckhofs, Troch, Santens, & Vandenbussche, 2004; Pérennou, 2006; Pizzamiglio et al., 1995), we hypothesized that head-on-trunk orientation affects spatial orientation judgments in neglect patients in a different way than in healthy participants and in patients without neglect. Such a differential modulation of performance by head inclination was already demonstrated by Kerkhoff (1999) in a single patient. However, since this pilot study only investigated one single neglect patient and one control subject, it is not clear whether the observed pattern of results is representative for all patients with left spatial neglect or all healthy control subjects and whether the differential modulation of performance as a function of head inclination is characteristic for all patients with right hemisphere damage or exclusively for neglect patients. Therefore, the present, more comprehensive investigation went beyond this demonstration by analyzing visual- and tactile-spatial axis orientation performance in a group study including patients with right hemispheric lesions and left spatial neglect, patients with right or left hemispheric lesions without spatial neglect and healthy control subjects. We predicted that: (1) neglect patients, but not LBD or RBD controls, would display a multimodal orientation deficit with similar impairments in tactile- as in visual-spatial orientation. That is, they were assumed to display a CCW tilt of the subjective vertical and horizontal in both modalities (Kerkhoff, 1999). Furthermore, we predicted that (2) axis orientation performance in neglect patients would be substantially affected by CW and CCW head inclination, whereas in healthy subjects and control patients without neglect, performance was expected to deteriorate only slightly, if at all. More specifically, a replication of Kerkhoff's (1999) original single-case results would become manifest in terms of an increased A-effect in neglect patients leading to a further performance deterioration with CCW and an improvement with CW head tilt. Such a finding would indicate that neglect patients set the subjective vertical in the direction of the idiotropic vector (Mittelstaedt, 1983). Alternatively, neglect patients' performance could generally improve independently of the direction of head tilt. Such a result would support the gravitational inflow model, since it would indicate that with reduced impact of the disturbed graviceptive information neglect patients' spatial bias is ameliorated. In order to test the two alternative models in the present study, two aspects of spatial performance were analyzed: the difference thresholds (half of the range in which the spatial judgments of subjects varied), which is an indicator for the uncertainty and instability of the spatial representation, and the constant errors (mean value of positive and negative deviations) which indicates the magnitude and direction of the spatial bias. The gravitational inflow model would predict a reduced magnitude of the spatial bias, that is, both difference thresholds and constant errors should be reduced with head tilt. The idiotropic vector model assuming an increased A-effect would predict increased constant errors with a CCW head tilt and reduced constant errors with a CW head tilt, but would not predict changes in the difference thresholds.

2. Methods

2.1. Participants

Eight patients with right hemispheric vascular lesions and left spatial neglect documented by clinical tests (see below), eight patients with right hemispheric vascular lesions and eight patients with left hemispheric lesions without spatial neglect in these tests (further referred to as RBD or LBD controls or more generally as control patients) and eight healthy control subjects were tested. Informed consent according to the Declaration of Helsinki II was obtained from all subjects. Table 1 summarizes the demographic and clinical data. The mean age was 49.5 years (range: 38–64) for the neglect patients, 49.6 years (range: 25–62) for the RBD controls, 50.3 years (range: 39–63) for the LBD controls and 51.0 years (range: 32–67 years) for the healthy controls. Age was not significantly different among the four subject groups ($df = 3$, $F = 0.04$, $p > 0.95$, n.s.) and there was no significant difference in the distribution of gender (assessed via the coefficient of contingency; $\Phi = 2.30$, $p > 0.50$, n.s.). The time since lesion or the onset of the illness was similar in the RBD and LBD controls, but slightly longer in the neglect group (neglect group: 8.8 months, RBD controls: 5.1 months; LBD controls: 5.1 months; $df = 2$, $F = 3.77$, $p < 0.05$). Patients were only included in the sample if they had a single, vascular right or left hemispheric lesion and no evidence of a brain stem lesion as revealed by CT/MRI and clinical symptoms. All subjects were right-handed according to their verbal report.

2.2. Neglect tests

All patients underwent a screening for visual neglect including horizontal line bisection of a 20 cm × 1 cm black line presented on white paper, representational drawing of a star, a daisy, a clock, a house and a face, and number cancellation on white paper (size 29.7 cm × 14.7 cm; 10 targets in each hemispace among 100 numbers on the total page). In addition, a 180-word reading test sensitive to neglect and hemianopic reading disturbances (Kerkhoff, Münßinger, Eberle-Strauss, & Stögerer, 1992) was administered. Cutoffs were deviations of more than 5 mm from the true midpoint of a 20 cm line in line bisection, more than one omission in each hemispace in the number cancellation task, and more than two omissions or substitutions of letters or words and/or prolonged reading times (>120 s). Furthermore, omissions or significant distortions of the right half of the copied figures was interpreted as an indicator of hemispatial neglect.

2.3. Visual-spatial tests

Fig. 1A displays the visual-spatial orientation tasks. The subjects were tested using specific software (termed VS; Kerkhoff & Marquardt, 1995) for the measurement of the SVV and SVH. VS is based on the method of limits (Engen, 1971). In the subtests measuring the SVV and SVH, the experimenter successively rotates an oblique white line (18 cm × 1.4 cm) presented on a dark background until the subject indicates that it lies exactly vertically or horizontally. With this method, two psychophysical parameters were calculated: the constant error and the difference threshold. The constant error denotes the difference between the subject's mean estimate (the point of subjective equality) and the objective correct orientation. Hence, the constant error gives information about the central tendency or central error of the subject. The interval of uncertainty indicates the complete range within which the subject considers the displayed line as exactly vertical, horizontal or parallel in the oblique task. From this value the difference threshold is calculated, which is defined as one-half of the interval of uncertainty. Constant errors and difference thresholds were computed by the software as described above. The step-width was 0.5° in all measurements.

2.4. Tactile-spatial tests

The tests for the subjective tactile axes (vertical = STV and horizontal = STH) were performed using a rotatable bar (15 cm long, 12 mm wide) which was mounted on a

Table 1
Summary of clinical and demographic data of the neglect patients and the control patients with left- or right-sided brain damage without neglect.

Group	Age	Sex	Etiology	Lesion	Months since lesion	Motor deficit	visual field	Neglect dyslexia	Figure copy L/R	Cancell. omissions L/R	Line bisection −/+ (mm)
N+	49	1	R-MCA	P-T	12	Plegia	L-Quan	Yes	−/+	8/3	+22
N+	43	0	R-MCA	P-T	11	Paresis	L-Quan	Yes	−/+	9/4	+15
N+	44	1	R-MCA	P-T	10	Plegia	L-Quan	Yes	−/+	6/4	+9
N+	64	1	R-MCA	P-T	4	Paresis	Normal	Yes	−/+	3/0	+8
N+	59	0	R-PCA	P-Thal	9	Paresis	L-HH	Yes	−/+	5/2	−12
N+	38	0	R-MCA	P-T	9	Paresis	L-Quan	Yes	−/+	7/2	−17
N+	50	1	R-MCA	P-T	13	Plegia	Normal	Yes	−/+	8/5	+12
N+	49	0	R-ICB	BG	2	Paresis	Normal	Yes	−/+	7/1	+33
LBD	41	1	L-MCA	F-P	9	Paresis	Normal	Aphasia	+/+	0/0	−1
LBD	63	1	L-MCA	P-T	4	Paresis	Normal	Aphasia	+/+	0/0	0
LBD	53	1	L-MCA	P-T	5	Paresis	Normal	Aphasia	+/+	0/0	0
LBD	45	0	L-MCA	P-T	8	Paresis	Normal	Aphasia	+/+	0/0	+2
LBD	56	0	L-MCA	F-T	5	Paresis	Normal	Aphasia	+/+	0/0	−3
LBD	56	0	L-PCA	O-T	3	Normal	R-Quan	No	+/+	0/0	+2
LBD	39	0	L-MCA	F	5	Paresis	Normal	Aphasia	+/+	0/0	−2
LBD	49	0	L-MCA	P-T	2	Normal	Normal	Aphasia	+/+	0/0	−2
RBD	50	1	R-MCA	T	5	Paresis	L-Quan	No	+/+	0/0	+1
RBD	48	1	R-ICB	T-P	5	Paresis	Normal	No	+/+	0/0	−1
RBD	46	0	R-MCA	P	9	Paresis	Normal	No	+/+	0/0	+2
RBD	62	0	R-MCA	P-T	9	Plegia	L-HH	No	+/+	1/0	−22
RBD	55	0	R-MCA	P-T	3	Plegia	Normal	No	+/+	0/0	−2
RBD	57	0	R-ICB	BG	5	Paresis	Normal	No	+/+	0/0	−2
RBD	25	0	R-MCA	T	4	Paresis	L-Quan	No	+/+	0/0	+2
RBD	54	0	R-MCA/PCA	P-O	1	Normal	L-HH	No	+/+	0/1	+3

Abbreviations: N+, neglect patient; LBD, left brain-damaged control patient; RBD, right brain-damaged control patient; etiology: MCA/PCA, middle/posterior cerebral artery infarction; ICB, intracerebral bleeding; L/R, left/right; lesion: F, frontal; P, parietal; T, temporal; O, occipital; BG, basal ganglia; Thal, thalamus; visual field: HH, homonymous hemianopia; Quan, homonymous quadrantanopia; neglect screening tests: neglect dyslexia: 180 word reading test; cutoff: max 2 errors; yes/no: neglect dyslexia present/absent; aphasia: reading not tested due to aphasia (documented by the Aachener Aphasie Test); figure copy: − = omissions or distortions; + = normal performance; cancellation: number of omissions per hemispace, cutoff: max 1 per hemispace; horizontal line bisection: deviation from true midline in mm to left (−) or right side (+).

plate and could be rotated in 1°-steps along the frontal plane (see Fig. 1B). The plate (50 cm × 50 cm) was mounted vertically in front of the patient. A scale, concealed from the subject, was drawn on the plate to record the orientation measurements (0° = right horizontal, 90° = vertical, 180° = left horizontal). Participants' task was to adjust the metal rod to their STV and STH. Healthy controls used their right, dominant hand and brain-damaged patients used their ipsilesional hand. Subjects were not allowed to touch the outer surface of the test plate, so as to eliminate any horizontal and vertical reference cues. Before each testing session, the apparatus was calibrated to the gravitational vertical. As for the visual axes, constant errors and difference thresholds were calculated for the STV and STH.

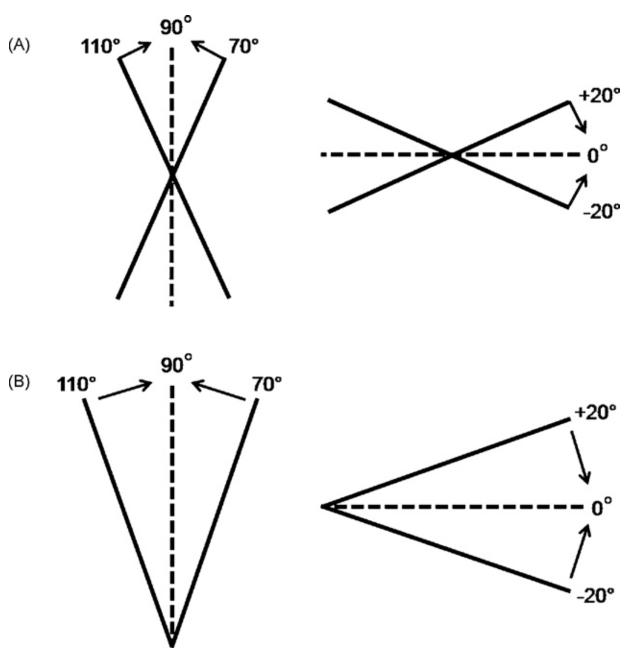

Fig. 1. Experimental setup in the spatial orientation tasks for the visual (A) and tactile (B) modality. Subjects were presented with a line on a computer screen (visual condition) or a metal rod (tactile condition) which they had to adjust to their subjective vertical or horizontal. The tests were performed in total darkness (visual condition) or with the subject blindfolded (tactile condition).

2.5. Testing conditions

Visual-spatial measurements were taken in total darkness with the chassis of the PC-monitor covered by an oval-shaped mask to eliminate any visual reference cues. Subjects were tested at a distance of 0.5 m from the monitor, with corrected-to-normal vision where necessary. The tactile-spatial tests were performed at the same distance with subjects blindfolded before starting the practice trials. Visual- and tactile-spatial tests were administered under three experimental conditions: with the subjects' heads upright (0° head tilt), or with the heads tilted 25° CW or CCW. The trunk remained vertical in all conditions and head position in the pitch-plane (fore-back-dimension) was always stabilized by a head-and-chin-rest (see below). Lateral head inclination was achieved by positioning the subjects' heads in a tiltable head-and-chin-rest (tiltable in the frontal plane) which was fixed to an experimental table (see Fig. 2). Ten trials were presented for each spatial orientation and modality. The sequence of the tests (i.e., spatial orientation and modality) was counterbalanced to avoid systematic practice effects. In all conditions, starting position was 20° away from the vertical/horizontal axis. The direction (CW, CCW) of the initial tilt was balanced throughout all tests to reduce effects of rotation direction. Prior to the completion of valid trials, subjects were familiarized with the experimental setup in each condition and performed five practice trials.

2.6. Statistics

For constant errors and difference thresholds, repeated-measures ANOVAs (with subject group and head orientation as factors) were performed to analyze spatial performance separately for the SVV and SVH and the STV and STH. In the case of significant main effects or interactions, subsequent post hoc comparisons were calculated: post hoc Scheffé tests were used to compare performance between subject groups; one-way ANOVAs and contrasts (where necessary) were used to compare performance between head orientation conditions within one subject group. To further investigate the general direction of tilt, that is, systematic deviations from zero in the constant errors, one-sample *t*-tests were calculated for each subject group. The alpha-level was chosen as $p < 0.05$ for all analyses.

3. Results

3.1. Neglect tests

The data of each patient in the neglect tests are summarized in Table 1. All neglect patients showed impaired copying perfor-

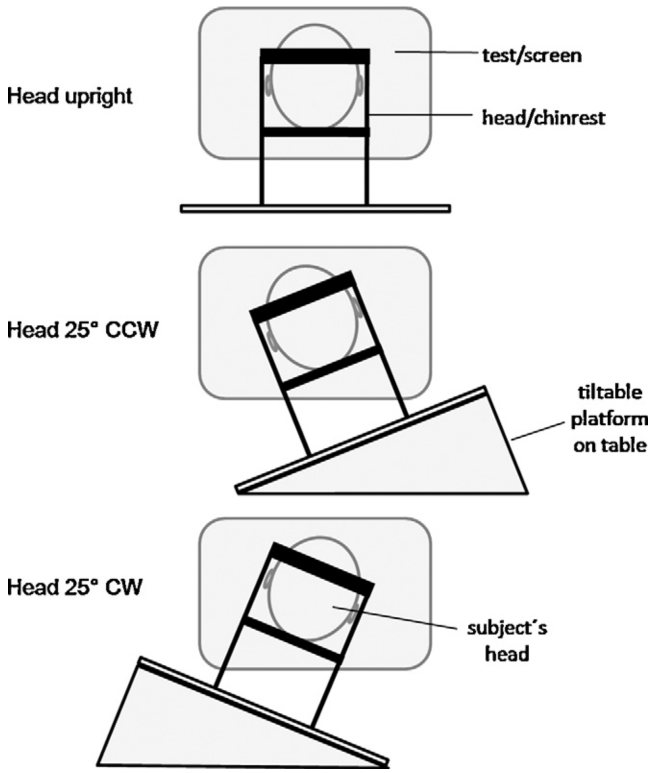

Fig. 2. Experimental setup in the visual- and tactile-spatial tests in three head orientation conditions: with the subject's head upright (0° head tilt), or with the head tilted 25° CW or CCW; head position was modulated and stabilized by a tiltable head-and-chin-rest; the head-and-chin-rest was attached to the experimental table (upright head condition) or to a wedge-shaped block on the table (CW or CCW head orientation condition).

mance, with the typical omissions and/or distortions of the left side of the drawings, as well as impaired reading performance indicating neglect dyslexia. They also showed the characteristic pattern of omissions in the number cancellation task, with significantly more omissions in the left compared to the right hemispace [mean omissions: 6.6 in the left and 2.6 in the right hemispace; $t(7) = 8.00$, $p < 0.01$]. Furthermore, six out of eight patients showed the typical rightward deviation in horizontal line bisection; two patients (both with left-sided visual field defects) showed leftward deviations (mean deviation: 8.8 mm to the right). Left and right brain-damaged control patients did not show impaired drawing or neglect dyslexia (the latter not measured in aphasic LBDs). They also showed intact performance in the number cancellation task (LBD mean: 0 omissions in left and right hemispace; RBD mean: 0.1 omissions in both left and right hemispace) and only nonsystematic, mostly slight, deviations in line bisection performance (LBD mean: 0.5 mm to the left; RBD mean: 2.4 mm to the left).

3.2. *Visual- and tactile-spatial orientation judgments*

Fig. 3A and B shows the visual- and tactile-spatial orientation judgments in neglect patients and control subjects as a function of head orientation. The lines within the circles display the mean subjective vertical and horizontal of individual patients and control subjects. While the normal subjects and also the RBD and LBD controls show only marginal deviations of their visual and tactile subjective vertical and horizontal, neglect patients display a marked and systematic CCW tilt. As can be seen, the severity of the tilt is heterogeneous in the group of neglect patients, while judgments of controls are very accurate. Furthermore, the neglect patients' judgments are substantially modulated by head orientation, whereas healthy controls and LBD and RBD control patients show only minor and nonsystematic effects of head orientation.

3.3. *General direction of tilt in upright posture*

To assess the systematic direction of tilt in the 'normal' orientation condition, one-sample *t*-tests were calculated for the constant errors of each group in all spatial orientation tests (SVV, SVH, STV and STH) in the upright head orientation condition. Constant errors of healthy, LBD and RBD controls did not differ significantly from zero (all $p > 0.10$; n.s.). By contrast, those of neglect patients were significantly larger than zero for all spatial tests (all $p < 0.05$), indicating a significant CCW deviation from the optimum orientation. This CCW tilt was shown by all eight neglect patients in the visual-spatial as well as in the tactile-spatial orientation task. That is, under normal conditions neglect patients displayed reliable, substantial and systematic CCW tilts of the visual- and tactile-spatial axes.

3.4. *Relation between visual- and tactile-spatial orientation*

The spatial bias in the tactile and visual orientation tests (i.e., the positive constant errors) were compared in repeated-measures ANOVAs with the factors 'group' and 'modality' for the vertical and horizontal axes in the upright head orientation condition. The ANOVA for the subjective vertical revealed a significant effect of group ($df = 3$, $F = 37.02$, $p < 0.01$) and an effect of modality for the vertical axis ($df = 1$, $F = 4.79$, $p < 0.05$), but no interaction of modality with group ($df = 3$, $F = 2.29$, $p = 0.10$, n.s.). Also for the subjective horizontal, a significant effect of group was found ($df = 3$, $F = 58.33$, $p < 0.01$), a significant effect of modality ($df = 1$, $F = 4.29$, $p < 0.05$), but no interaction of group and modality ($df = 3$, $F = 0.48$, $p > 0.65$). For both the vertical and the horizontal, constant errors were generally greater in the tactile condition than in the visual condition. However, as there was no interaction between 'group' and 'modality', the relative pattern of results was equivalent in both modalities.

3.5. *Effects of head orientation on spatial orientation judgments*

Table 2 summarizes the mean constant errors and difference thresholds and the statistical results for each subject group in the visual and tactile subjective vertical and horizontal across the three different head orientation conditions.

3.5.1. *Constant errors*

Visual vertical and horizontal

Fig. 4 displays the mean constant errors of the SVV and SVH for all subject groups. Constant errors were substantially larger in neglect patients compared to all control groups. Furthermore, as can be seen, constant errors were drastically modulated by passive head inclination in neglect patients, that is, they were aggravated by a CCW and reduced by a CW inclination, whereas constant errors varied only marginally in the control groups.

For the SVV, the repeated-measures ANOVA (with the factors subject group and head orientation) revealed significant effects of group ($df = 3$, $F = 78.57$, $p < 0.01$) and head orientation ($df = 2$, $F = 12.59$, $p < 0.01$), and a significant interaction of group and head orientation ($df = 6$, $F = 10.83$, $p < 0.01$). Neglect patients generally displayed significantly larger constant errors compared to all control groups (all $p < 0.01$), whereas healthy, RBD and LBD controls were comparable to each other (all $p > 0.45$, n.s.). One-way ANOVAs revealed that head orientation significantly affected performance in neglect patients ($df = 2$, $F = 16.67$, $p < 0.01$) and in RBD controls ($df = 2$, $F = 9.75$, $p < 0.01$), but not in LBD and healthy controls (both $p > 0.15$, n.s.). In neglect patients, a CCW head tilt aggravated

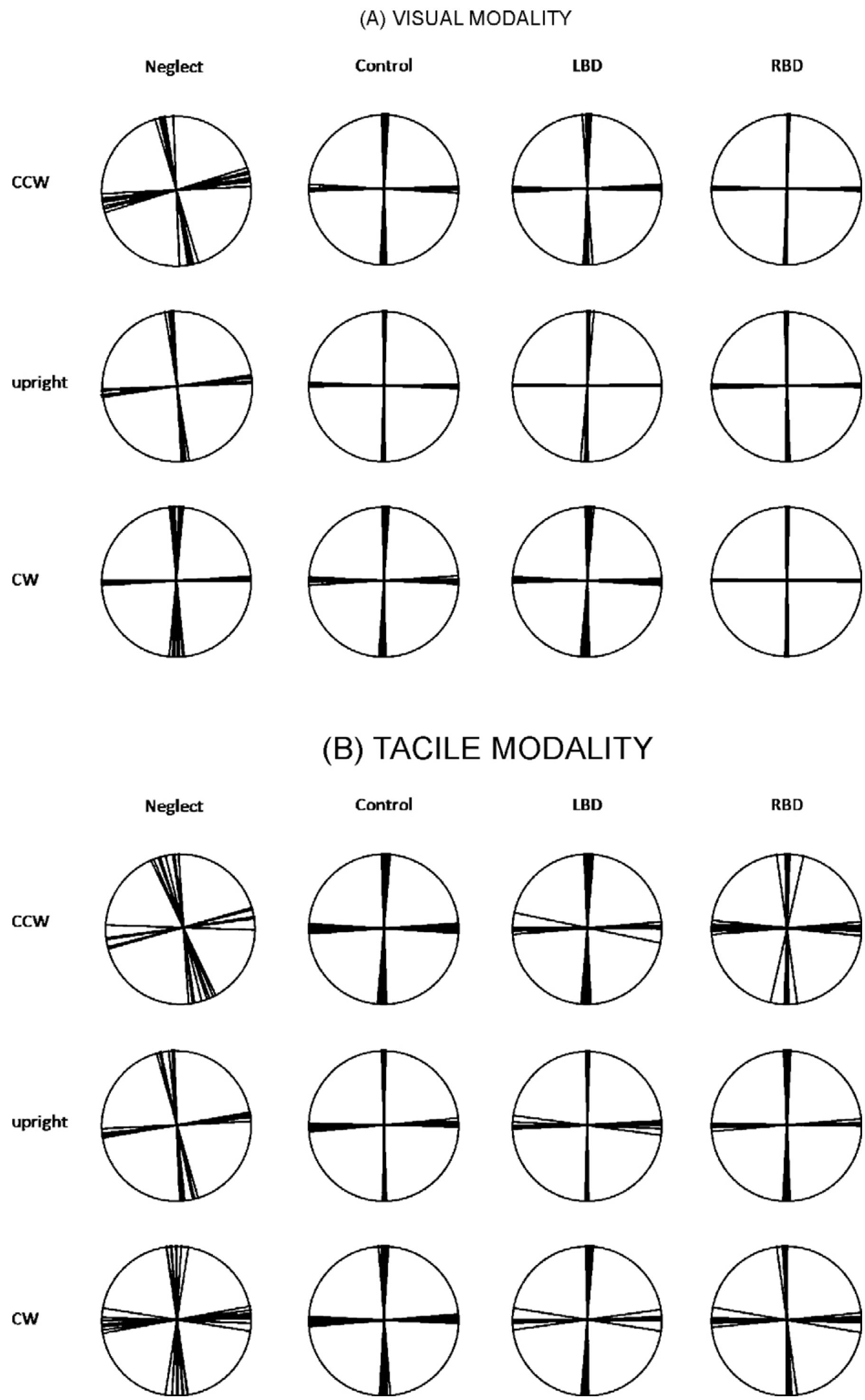

Fig. 3. Mean performance of neglect patients, LBD and RBD control patients and healthy controls in the visual-spatial (A) and tactile-spatial (B) orientation task for the three head orientation conditions; CCW, head inclination 25 ° CCW; upright, vertical head position; CW, head inclination 25 ° CW; the lines within the circles display the mean SVV and SVH of individual patients and control subjects.

the deficit significantly compared with an upright head orientation ($p < 0.01$) and, thus, further increased the pathological bias, whereas a CW head tilt improved performance significantly compared to an upright head orientation ($p < 0.05$), that is, it reduced the bias. In the RBD controls, a CCW head tilt impaired visual-spatial orientation judgments significantly compared with an upright head orientation ($p < 0.01$), while the upright and CW head orientations did not differ significantly from each other ($p > 0.10$, n.s.).

For the SVH, significant effects of group ($df = 3$, $F = 46.78$, $p < 0.01$), and of head orientation ($df = 2$, $F = 16.21$, $p < 0.01$), and a significant group-by-head orientation interaction ($df = 6$, $F = 10.55$, $p < 0.01$) were found. Neglect patients generally displayed significantly larger constant errors compared to all control groups (all $p < 0.01$), whereas healthy, RBD and LBD controls did not differ from each other (all $p > 0.90$, n.s.). Separate one-way ANOVAs for the different groups revealed that head orientation significantly affected performance in the neglect patients ($df = 2$, $F = 16.88$, $p < 0.01$), but

Table 2
Summary of the mean constant errors and difference thresholds and the statistical results (contrasts in post hoc one-way ANOVAs) for each subject group in the visual and tactile subjective vertical and horizontal across the three different head orientation conditions.

Parameter	Group	Test	CCW 25°	Versus	Upright	Versus	CW 25°
Constant errors	N+	SVV	10.8	** (>)	5.5	* (>)	0.3
		SVH	9.6	** (>)	6.0	** (>)	1.7
		STV	15.0	** (>)	8.6	* (>)	1.6
		STH	8.5	ns	7.2	* (>)	2.5
	Control	SVV	−0.7	ns	−0.4	ns	−1.6
		SVH	0	ns	−0.4	ns	−0.5
		STV	−0.8	ns	0.2	ns	0.8
		STH	−0.5	ns	0.7	ns	0.9
	RBD	SVV	−1.1	** (<)	0.5	ns	−0.2
		SVH	0	ns	0.4	ns	−0.1
		STV	−0.5	ns	−0.1	ns	1.7
		STH	−1.0	ns	1.2	ns	−0.3
	LBD	SVV	−0.5	ns	−1.5	ns	−1.3
		SVH	0.6	ns	0	ns	−0.2
		STV	−0.9	ns	−0.3	ns	−1.3
		STH	−0.4	ns	−0.1	ns	0.2
Difference thresholds	N+	SVV	5.0	ns	3.5	ns	4.1
		SVH	4.1	** (>)	2.7	ns	2.1
		STV	7.6	ns	8.2	ns	8.6
		STH	6.4	ns	7.1	ns	5.4
	Control	SVV	1.6	ns	1.1	ns	1.5
		SVH	1.1	ns	0.9	ns	1.3
		STV	2.9	ns	2.9	ns	3.1
		STH	3.2	ns	2.5	ns	3.6
	RBD	SVV	2.5	ns	1.9	ns	2.1
		SVH	1.8	ns	1.4	ns	1.6
		STV	4.6	ns	3.6	ns	4.7
		STH	4.4	ns	3.9	ns	3.7
	LBD	SVV	2.4	ns	1.4	ns	2.3
		SVH	2.2	ns	1.0	ns	1.8
		STV	3.2	ns	2.5	ns	4.6
		STH	3.0	ns	2.8	ns	3.2

Abbreviations: CCW 25°, head tilted 25° CCW; upright, upright head orientation; CW 25°, head tilted 25° CW; N+, neglect patients; control, healthy control subjects; RBD, right brain-damaged control subjects; LBD, left brain-damaged control subjects; SVV, subjective visual vertical; SVH, subjective visual horizontal; STV, subjective tactile vertical; STH, subjective tactile horizontal. ns: nonsignificant.

* $p < 0.05$.

** $p < 0.001$.

not in the other groups (all $p > 0.40$, n.s.). In neglect patients, a CCW head tilt aggravated the deficit significantly compared with an upright head orientation ($p < 0.01$) and, thus, further increased the pathological bias, whereas a CW head tilt improved performance significantly compared to an upright head orientation ($p < 0.01$), that is, it reduced the bias.

Tactile vertical and horizontal

Fig. 5 displays the average constant errors of the STV and STH for all subject groups. As can be seen, constant errors are substantially larger in neglect patients compared to all other groups. Furthermore, constant errors are drastically modulated by lateral head inclination in neglect patients, that is, they are aggravated by a CCW and reduced by a CW head inclination, whereas constant errors vary only marginally in the healthy controls and the control patients without neglect.

For the STV, significant effects of group ($df = 3$, $F = 13.82$, $p < 0.01$) and head orientation ($df = 2$, $F = 5.67$, $p < 0.01$) and a group × head orientation interaction ($df = 6$, $F = 12.26$, $p < 0.01$) were

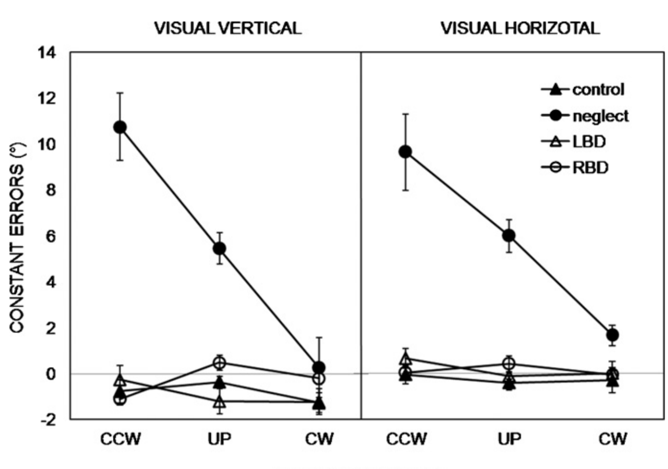

Fig. 4. Constant errors (means and standard errors) in the visual-spatial orientation task for the three head orientation conditions (CCW, head tilted 25° CCW; UP, upright head orientation; CW, head tilted 25° CW) in neglect patients, healthy control subjects, left brain-damaged control subjects (LBD) and right brain-damaged control subjects (RBD); positive constant errors indicate CCW rotations, negative constant errors CW rotations.

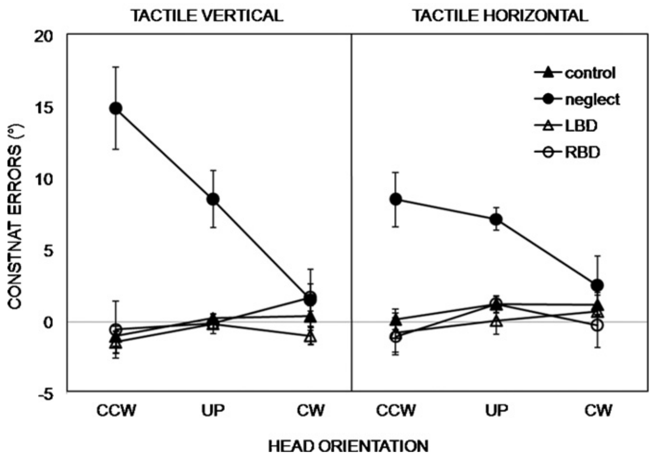

Fig. 5. Constant errors (means and standard errors) in the tactile-spatial orientation task for the three head orientation conditions (CCW, head tilted 25° CCW; UP, upright head orientation; CW, head tilted 25° CW) in neglect patients, healthy control subjects, left brain-damaged control subjects (LBD) and right brain-damaged control subjects (RBD); positive constant errors indicate CCW rotations, negative constant errors indicate CW rotations.

found. Neglect patients generally displayed significantly larger constant errors compared to all control groups (all $p < 0.01$), whereas those of the control groups were comparable to each other (all $p > 0.90$, n.s.). One-way ANOVAs revealed that in neglect patients, head orientation significantly affected constant errors ($df = 2$, $F = 16.68$, $p < 0.01$): a CCW head tilt aggravated the deficit significantly compared with an upright head orientation ($p < 0.01$) and, thus, further increased the pathological bias, whereas a CW head tilt improved performance significantly compared to an upright head orientation ($p < 0.05$), that is, it reduced the bias. In the different control groups, constant errors did not differ significantly among head orientation conditions (all $p > 0.20$, n.s.).

For the STH, the main effect of group ($df = 3$, $F = 6.70$, $p < 0.01$), head orientation ($df = 2$, $F = 3.41$, $p < 0.05$) and the group-by-head orientation interaction was significant ($df = 6$, $F = 5.44$, $p < 0.01$). Neglect patients generally displayed significantly larger constant errors compared to healthy controls and RBD and LBD controls (all $p < 0.05$), whereas the other groups did not differ significantly from each other (all $p > 0.90$, n.s.). One-way ANOVAs revealed that in the neglect patients, head orientation significantly affected performance ($df = 2$, $F = 9.22$, $p < 0.01$): a CW head tilt improved performance significantly compared to an upright head orientation ($p < 0.05$) and, thus, reduced the pathological bias. There was no significant aggravation of performance with CCW head tilt compared with an upright head orientation ($p > 0.30$), but compared with a CW head tilt ($p < 0.01$). In healthy, LBD and RBD controls, constant errors did not differ significantly among head orientation conditions (all $p > 0.08$, n.s.).

To summarize, constant errors were consistently increased in neglect patients compared to healthy and brain-damaged control subjects. Furthermore, CCW head inclination (by 25°) consistently aggravated the axis orientation deficit in the neglect patients and, thus, increased the pathological bias, whereas CW head orientation improved it relative to upright head orientation, that is, it reduced the bias. In the healthy and brain-damaged control subjects, head orientation in few cases had an effect on the constant errors as well. However, the direction of the constant errors did not covary with the direction of head tilt as in the neglect patients.

3.5.2. Difference thresholds

Visual vertical and horizontal

Fig. 6 displays the average difference thresholds of the SVV and SVH separately for each subject group. As can be seen, the certainty of the judgments was decreased in neglect patients compared to the other subject groups, as indicated by generally larger difference thresholds. For the SVV, the repeated-measures ANOVA with the factors subject group and head orientation revealed a significant group effect ($df = 3$, $F = 20.05$, $p < 0.01$), a significant effect of head orientation ($df = 2$, $F = 5.15$, $p < 0.01$), but no significant interaction ($df = 6$, $F = 0.42$, $p > 0.85$, n.s.). Neglect patients generally displayed significantly larger difference thresholds compared to all other groups (all $p < 0.01$), whereas the control groups did not differ significantly from each other (all $p > 0.20$, n.s.). Across subjects, difference thresholds were larger when the head was tilted CW or CCW compared with an upright head orientation (both $p < 0.05$). For the SVH, a significant group effect was found ($df = 3$, $F = 13.80$, $p < 0.01$), a significant effect of head orientation ($df = 2$, $F = 11.32$, $p < 0.01$), and a significant group × head orientation interaction ($df = 6$, $F = 4.13$, $p < 0.01$). Neglect patients generally exhibited significantly larger difference thresholds compared to all other groups (all $p < 0.01$), whereas the control groups again did not differ significantly from each other (all $p > 0.30$, n.s.). One-way ANOVAs revealed that in the neglect patients, head orientation significantly affected performance ($df = 2$, $F = 11.02$, $p < 0.01$): a CCW head tilt increased difference thresholds significantly compared with a CW head tilt or an upright head orientation (both $p < 0.01$), whereas thresholds did

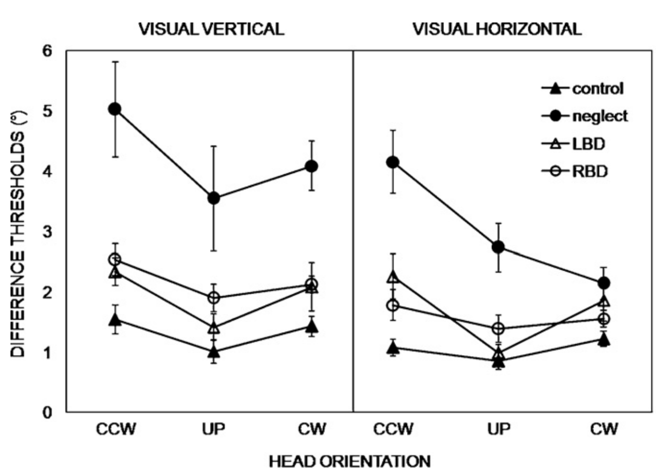

Fig. 6. Difference thresholds (means and standard errors) in the visual-spatial orientation task for the three head orientation conditions (CCW, head tilted 25° CCW; UP, upright head orientation; CW, head tilted 25° CW) in neglect patients, healthy control subjects, left brain-damaged control subjects (LBD) and right brain-damaged control subjects (RBD).

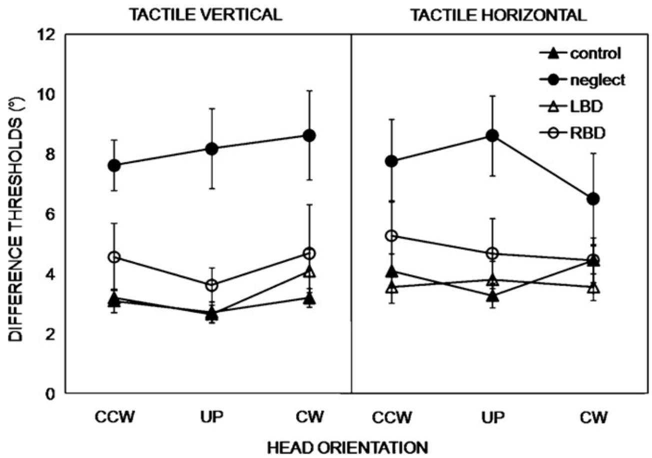

Fig. 7. Difference thresholds (means and standard errors) in the tactile-spatial orientation task for the three head orientation conditions (CCW, head tilted 25° CCW; UP, upright head orientation; CW, head tilted 25° CW) in neglect patients, healthy control subjects, left brain-damaged control subjects (LBD) and right brain-damaged control subjects (RBD).

not differ significantly between CW and upright head orientations ($p > 0.20$, n.s.). In the control groups, difference thresholds did not differ significantly among the three head orientation conditions (all $p > 0.05$, n.s.).

Tactile vertical and horizontal

Fig. 7 displays the difference thresholds of the STV and STH for all groups. As can be seen, those of neglect patients were generally increased compared to the control groups. For the STV, a significant effect of group ($df = 3$, $F = 11.36$, $p < 0.01$), but no effect of head orientation ($df = 2$, $F = 1.67$, $p > 0.15$, n.s.) and no significant group × head orientation interaction ($df = 6$, $F = 0.45$, $p > 0.80$, n.s.) was found. Neglect patients displayed significantly larger difference thresholds compared to all control groups (all $p < 0.01$), whereas those of the different controls were comparable to each other (all $p > 0.60$, n.s.). For the STH, a significant group effect ($df = 3$, $F = 6.19$, $p < 0.01$), but no effect of head orientation ($df = 2$, $F = 0.25$, $p > 0.75$) or a group × orientation interaction was obtained ($df = 6$, $F = 1.23$, $p > 0.30$). Neglect patients exhibited significantly larger difference thresholds compared to healthy and LBD controls (all $p < 0.05$), but not to RBD controls ($p > 0.10$); the different control groups did not differ significantly from each other (all $p > 0.75$, n.s.).

To summarize, difference thresholds were consistently increased in neglect patients compared to healthy controls and brain-damaged control subjects. However, head inclination did not consistently modulate this parameter of uncertainty in the neglect patients in any way other than in healthy or brain-damaged controls.

4. Discussion

The rationale of the present study was to investigate whether and how multimodal spatial orientation deficits are modulated by head orientation, more specifically, by *lateral* head inclination. Visual- and tactile-spatial axis orientation performance was analyzed in patients with right hemispheric lesions and left spatial neglect, left and right brain-damaged control patients without neglect and healthy control subjects. In order to show that neglect patients display a multimodal orientation deficit, we tested whether they show analogous, direction-specific impairments in tactile-spatial orientation as in visual-spatial orientation. Furthermore, we assessed whether axis orientation performance deficits are modulated by variations in gravitational and somatosensory input differently in neglect patients compared to brain-damaged and healthy controls.

4.1. Evidence for a supramodal orientation deficit in neglect

In accordance with our prior hypothesis of a multimodal or even supramodal spatial orientation deficit (Kerkhoff, 1999), the neglect patients investigated in the present study showed systematic and analogous tilts of the subjective *visual* and *tactile* vertical and horizontal. The spatial conformity of deviations in the frontal plane in both modalities indicates a disturbed central representation of gravity after parieto-temporal lesions (Brandt et al., 1994). Recently, Pérennou et al. (2008) showed that the most marked visual and tactile tilts in the frontal plane were associated with right parietal lesions, suggesting that an internal model of verticality is elaborated in right parietal cortex. The assumption of the parietal cortex as the anatomical substrate of a supramodal spatial reference frame is further supported by findings indicating the existence of multimodal (e.g., Duhamel, Colby, & Goldberg, 1998; Graziano & Gross, 1995) and 'axis-orientation-selective' (Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997) neurons in the parietal cortex. Based on single-cell recordings in the monkey parietal cortex, Sakata et al. (1997) identified neurons in the lateral bank of the caudal intraparietal sulcus which are relevant for the coding of axis orientation in three-dimensional space. Since bimodal neurons have been described in the monkey parietal areas (Duhamel et al., 1998; Graziano & Gross, 1995), these neurons might also be activated by the touch of objects with similar spatial orientations. Damage to such multimodal and orientation-selective neurons might be responsible for the deficits in the perception and representation of the principal spatial axes (that become manifest in identical tilts in different modalities). Moreover, cells in the posterior parietal cortex have been reported to contribute to the representation of space by integrating multimodal afferent and reafferent information (Andersen, Essick, & Siegel, 1985). Parietal areas 7a and LIP (lateral intraparietal) have been shown to receive visual signals and eye-position signals (Andersen & Mountcastle, 1983; Andersen et al., 1985), as well as efference copies of motor signals, vestibular signals and neck proprioceptive signals (e.g., Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Brotchie, Andersen, Snyder, & Goodman, 1995; Snyder, Batista, & Andersen, 1997) to account for head orientation and head movements in space. Damage to the right posterior parietal cortex might therefore lead to a systematic error in the integration of information – as for example somatosensory (head-position) and graviceptive (vestibular) input – in neglect patients. This is in line with the view that systematic tilts of the coordinate systems can be caused by damage to various parts of a complex system underlying the representation of space, including lesions of the central vestibular pathways (brain stem, thalamus, or vestibular cortex), as well as sensory pathways and (right) parietal lesions (as suggested, e.g., by Brandt et al., 1994). The neglect patients examined in the present study had lesions of structures that are involved in the representation of space, including the parietal or temporoparietal cortex and in two cases also the thalamus and the basal ganglia.

4.2. Differential effects of head tilt on spatial performance

Head orientation significantly and consistently affected the perceptual tilts in the visual and spatial orientation tests only in neglect patients. CCW passive head tilt resulted in a significant aggravation of the spatial bias, that is, in further increased CCW deviations of orientation judgments, whereas CW passive head tilt led to a reduction of the CCW tilt and thus a trend towards normal performance. Our data suggest a significant influence of the head-vertical axis in determining the perceptual vertical and horizontal. This influence seems to be much greater in the neglect patients compared to healthy and brain-damaged controls who displayed only small and inconsistent effects.

From previous research on the effects of head orientation on the perception of space, two influential models have emerged which assume that such effects reflect gravitational inflow (e.g., changes in vestibular and kinesthetic inputs—Howard, 1982) and/or the importance of the body- and head-vertical axis as an intrinsic reference in guiding spatial orientation (Mittelstaedt, 1983). According to the gravitational inflow model, effects of head tilt on the subjective vertical are at least partly based on a decrease in otolith sensitivity when the head is inclined, which leads to a reduced impact of graviceptive input on the perception of space. This view is supported by studies demonstrating effects of upright versus supine head orientation on space perception in neglect patients (Pizzamiglio et al., 1995; Saj et al., 2005; Saj, Honoré, Bernati, Richard, & Rousseaux, 2008). The present study investigated spatial performance as a function of *lateral* head inclination (i.e., head orientation was varied in the *frontal* plane). Unlike previous studies, our data reveal a systematic modulation pattern, that is, the direction of head orientation is critical for the direction of the modulation: a CCW head tilt modulated performance in the opposite direction to a CW head tilt. This systematic, orientation direction-specific pattern of results in neglect patients cannot be explained by a general reduction of the impact of gravitational input with head inclination, since a head tilt in either direction should lead to a reduced sensitivity of the utricles and, thus, an ameliorated spatial bias according to the gravitational inflow hypothesis (Howard, 1982). If neglect patients would rely mainly on gravitational information as a reference for their spatial judgments, the present pattern of results could result only if the asymmetry in the processing of gravitational information would be increased or reduced depending on the direction of head orientation; that is, if head inclination in the direction of the spatial bias (i.e., a CCW tilt of the head) would lead to a further increased asymmetry in the processing of gravitational input, while head inclination in the opposite direction (i.e., a CW head tilt) would lead to reduced asymmetry in the gravity vector. However, the present results rather favor the conclusion that neglect patients use different information as a reference for their spatial judgments. Neglect patients seem to rely mainly on their idiotropic vector, or more specifically, their head-vertical axis. They display a tendency to orient verticality judgments towards their head *z*-axis, leading them to set their subjective vertical towards this axis in the conditions where the head is tilted (A-effect). Since the trunk always remained vertical in the present experiment, the orientation-specific effect is attributable to head orientation alone. This is in line with findings by Kerkhoff and Schindler (1997) indicating that variations in head orientation independently affect spatial performance in neglect patients.

Another, but similar, model which has been suggested by Luyat et al. (2001) and Luyat and Gentaz (2002), assumes that spatial orientations are mapped in a *subjective* gravitational reference frame. The authors argue that tilted subjects do not have access to a 'veridical' gravitational reference frame, but rather to a subjective reference frame which is not congruent with the physical one. However, in healthy subjects, the *subjective* gravitational reference frame is at least congruent with the physical one in upright posture. Also, even in tilted posture, healthy subjects can still use gravitational information to counteract the attraction of the subjective vertical by the idiotropic vector. Accordingly, the healthy subjects investigated in the present study displayed only minor and nonsystematic effects of head tilt on spatial performance. Their difference thresholds were numerically slightly larger with lateral head tilt compared to upright head orientation, while there was no such effect on the constant errors. By contrast, in neglect patients, the *subjective* gravitational reference frame is *not* congruent with the physical one in upright posture. Furthermore, they cannot rely on gravitational information (as it is biased) to counteract the attraction of the subjective vertical by the idiotropic vector. Therefore, neglect patients display an increased A-effect, that is, in the case of head tilt their subjective vertical is attracted by the idiotropic vector to a much greater degree compared to healthy subjects or control patients without neglect. This means that the direction of tilt, which is mirrored by the constant errors, varies as a function of head orientation condition.

Our finding of an abnormally large A-effect in patients with neglect is in line with previous studies showing similar results in patients with impaired or absent vestibular function (e.g., Bronstein, Yardley, Moore, & Cleeves, 1996) and support the view that this particular tilt-mediated effect is somatosensory in origin (Yardley, 1990). Somatosensory information about the orientation of the head and body in space contributes to the idiotropic vector. Since neglect patients display impaired processing of vestibular information and, thus, cannot rely on a gravitational reference frame, they have to rely on somatosensory information to a greater degree than healthy subjects.

4.3. Clinical consequences of impaired spatial orientation constancy in neglect

The present findings, showing a strong influence of head inclination in the frontal plane induced by head inclination of $\pm 25^{\circ}$, combined with previous findings, showing a significant modulation of spatial orientation performance in the lateral plane (*z*-plane, Kerkhoff & Schindler, 1997) and a modulation of spatial orientation in supine versus upright body-position (Funk et al., 2010; Saj et al., 2005), imply a loss of *spatial orientation constancy* in patients with neglect. In other words, perception of the subjective vertical or horizontal in the visual and tactile modality changes dramatically with every change in head- or body-position in neglect patients, but not so in control patients or healthy subjects. This loss of spatial orientation constancy is multimodal and, arguably, related to the poor postural and mobility capacities characteristic for neglect patients (Lafosse et al., 2007; Pérennou, 2006; Pérennou et al., 2008). Neglect patients frequently show a very typical group of symptoms mirroring postural deficits in the frontal plane characterized by a postural imbalance caused by lateropulsion or 'pushing' behavior (Karnath, Ferber, & Dichgans, 2000), and head-/eye-position deficits in the horizontal plane characterized by marked deviations of spontaneous eye and head orientation towards the right (Fruhmann-Berger & Karnath, 2005). Such deviations in posture, eye and head position may be understood as a pathological adjustment of the patients' 'default position', which is shifted to a new (more rightward in the frontal as well as in the horizontal plane) origin in patients with spatial neglect.

Our present results suggest that different head-positions in the frontal plane (CW or CCW head tilts) have a strong effect on visual and tactile judgments of the subjective vertical and horizontal in patients with neglect but not without neglect. Although we did not measure spontaneous head-positioning in our study, passive manipulation of head-position significantly affected verticality judgments in neglect. As it is very likely that neglect patients will change their head position spontaneously in their daily life, for instance during transfers to bed, standing, sitting or walking, these changes in head position will inevitably also affect their judgments of verticality. We assume that the right-sided shift in spontaneous head- and eye-position described by Fruhmann-Berger and Karnath (2005) and the typical postural deficits in the frontal plane (Karnath et al., 2000; Lafosse et al., 2007; Pérennou et al., 2008; Pérennou, 2006) together with the pattern of results found in our study demonstrate that neglect patients show postural (including head- and eye-position) deficits in all spatial planes, which in turn affect the processing of spatial information in all spatial planes. The result of this may be an inaccurate and very instable spatial orientation – due to the pathological bias and enhanced variability of verticality judgments on the one hand and changes in verticality perception as a result of changes in head position on the other – hence an impairment in spatial orientation constancy.

5. Conclusion

In conclusion, the results of the present study can be taken as evidence for a supramodal spatial orientation deficit and a loss of spatial orientation constancy in neglect patients. In upright posture, spatial orientations are systematically tilted CCW in both the tactile and the visual modality. Spatial orientation judgments are furthermore systematically modulated by lateral head inclination in neglect patients and this modulation is specific for spatial neglect and not due to unilateral brain damage in general. CCW tilts of the head result in a further increase in spatial bias, whereas CW tilts of the head lead to a decrease in CCW spatial bias and thus a trend towards normal performance. This pattern of results corresponds to an increased A-effect, which can be explained by a stronger attraction of the subjective vertical by the idiotropic vector, due to impaired processing of gravitational information.

Acknowledgements

This work was supported by a Deutsche Forschungsgemeinschaft (DFG) grant to Peter Bublak, Kathrin Finke, and Georg Kerkhoff (project FOR 480, BU 1327/2-1) and to Georg Kerkhoff (IRTG 1457 “Adaptive minds”).

References

Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). The encoding of spatial location by posterior parietal neurones. *Science*, *230*, 456–458.

Andersen, R. A., & Mountcastle, V. B. (1983). The influence of the angle of gaze upon the excitability of the light sensitive neurons of the posterior parietal cortex. *Journal of Neuroscience*, *3*, 532–548.

Bender, M., & Jung, R. (1948). Abweichungen der subjektiven optischen Vertikalen und Horizontalen bei Gesunden und Hirnverletzten. *European Archives of Psychiatry and Clinical Neuroscience*, *181*, 193–212.

Benton, A., Hannay, H. J., & Varney, N. R. (1975). Visual perception of line direction in patients with unilateral brain disease. *Neurology*, *25*, 907–910.

Bisiach, E., Capitani, E., Luzatti, C., & Perani, D. (1981). Brain and conscious representation of outside reality. *Neuropsychologia*, *19*, 543–551.

Bisiach, E., & Luzatti, C. (1978). Unilateral neglect of representational space. *Cortex*, *14*, 129–133.

Bisiach, E., Pizzamiglio, L., Nico, D., & Antonucci, G. (1996). Beyond unilateral neglect. *Brain*, *119*, 851–857.

Brandt, Th., Dieterich, M., & Danek, A. (1994). Vestibular cortex lesions affect the perception of verticality. *Annals of Neurology*, *35*, 403–412.

Bremmer, F., Klam, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2002). Visual–vestibular interactive responses in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, *16*, 1569–1586.

Bronstein, A. M., Yardley, L., Moore, A. P., & Cleeves, L. (1996). Visually and posturally mediated tilt illusions in Parkinson’s disease and in labyrinthine defective subjects. *Neurology*, *47*, 651–656.

Brotchie, P. R., Andersen, R. A., Snyder, L. H., & Goodman, S. J. (1995). Head position signals used by parietal neurones to encode locations of visual stimuli. *Nature*, *375*, 232–235.

Day, R. H., & Wade, N. J. (1969). Mechanisms involved in visual orientation constancy. *Psychological Bulletin*, *1*, 33–42.

De Renzi, E. (1982). *Disorders of space exploration and cognition*. New York: Wiley.

De Renzi, E., Faglioni, P., & Scotti, G. (1971). Judgment of spatial orientation in patients with focal brain damage. *Journal of Neurology, Neurosurgery and Psychiatry*, *34*, 489–495.

Dichgans, J., Diener, H. C., & Brandt, T. (1974). Optokinetic–graviceptive interaction in different head positions. *Acta Otolaryngologica*, *78*, 213–221.

Diener, H. C., & Dichgans, J. (1988). On the role of vestibular, visual, and somatosensory information for dynamic postural control humans. *Progress in Brain Research*, *76*, 253–262.

Dilorenzo, J. R., & Rock, I. (1982). The rod and frame effect as a function of the righting of the frame. *Journal of Experimental Psychology: Human Perception & Performance*, *8*, 536–546.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1998). Ventral intra-parietal area of the macaque: Congruent visual and somatic response properties. *Journal of Neurophysiology*, *79*, 126–136.

Engen, T. (1971). Psychophysics. I. Discrimination and detection. In J. W. Kling, & L. Riggs (Eds.), *Woodworth & Schlossberg's experimental psychology* (pp. 11–86). London: Methuen & Co.

Fruhmann-Berger, M., & Karnath, H.-O. (2005). Spontaneous eye and hand position in patients with spatial neglect. *Journal of Neurology*, *252*(10), 1194–2000.

Funk, J., Finke, K., Mueller, H. J., Preger, R., & Kerkhoff, G. (2010). Systematic biases in the tactile perception of the subjective vertical in patients with unilateral neglect, and the influence of upright vs. supine posture. *Neuropsychologia*, *48*(1), 298–308.

Gainotti, G., & Tiacci, C. (1971). The relationships between disorders of visual perception and unilateral spatial neglect. *Neuropsychologia*, *9*(4), 451–458.

Graziano, M. S. A., & Gross, C. G. (1995). The representation of extrapersonal space: A possible role for bimodal, visual-tactile neurons. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (pp. 1021–1034). Cambridge, MA: The MIT Press.

Grüsser, O. J., Pause, M., & Schreiter, U. (1990). Vestibular neurones in the parieto-insular cortex of monkeys (macaca fascicularis): Visual and neck receptor responses. *Journal of Physiology*, *430*, 559–583.

Halligan, P. W., & Marshall, J. C. (1991). Spatial compression in visual neglect: A case study. *Cortex*, *27*, 623–629.

Howard, I. P. (1982). *Human visual orientation*. New York: Wiley.

Howard, I. P. (1986). The perception of posture, self motion, and the visual vertical. In K. R. Boff, L. Kaufmann, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (pp. 18.1–18.61). New York: Wiley.

Karnath, H.-O. (1997). Spatial orientation and the representation of space with parietal lobe lesions. *Philosophical Transactions of the Royal Society, London B*, *352*, 1411–1419.

Karnath, H.-O., Ferber, S., & Dichgans, J. (2000). The neural representation of postural control in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(25), 13931–13936.

Karnath, H.-O., Fetter, M., & Niemeier, M. (1998). Disentangling gravitational, environmental, and egocentric reference frames in spatial neglect. *Journal of Cognitive Neuroscience*, *10*, 680–690.

Kerkhoff, G. (1999). Multimodal spatial orientation deficits in left-sided visual neglect. *Neuropsychologia*, *37*, 1387–1405.

Kerkhoff, G. (2001). Spatial hemineglect in humans. *Progress in Neurobiology*, *63*, 1–27.

Kerkhoff, G., & Marquardt, C. (1995). VS—A new computer program for detailed offline analysis of visual-spatial perception. *Journal of Neuroscience Methods*, *63*, 75–84.

Kerkhoff, G., Münßinger, U., Eberle-Strauss, G., & Stögerer, E. (1992). Rehabilitation of hemianopic alexia in patients with postgeniculate visual field disorders. *Neuropsychological Rehabilitation*, *2*, 21–42.

Kerkhoff, G., & Schindler, I. (1997). Head and trunk orientation modulate visual neglect. *NeuroReport*, *8*(12), 2681–2685.

Kerkhoff, G., & Zoelch, C. (1998). Disorders of visuo-spatial orientation in the frontal plane in patients with visual neglect following right or left parietal lesions. *Experimental Brain Research*, *122*, 108–120.

Kim, Y., Morrow, L., Passafiume, D., & Boller, F. (1984). Visuoperceptual and visuomotor abilities an locus of lesion. *Neuropsychologia*, *22*, 177–185.

Lafosse, C., Kerckhofs, E., Troch, M., Santens, P., & Vandenbussche, E. (2004). Graviceptive misperception of the postural vertical after right hemispheric damage. *Neuroreport*, *15*(5), 887–891.

Lafosse, C., Kerckhofs, E., Vereeck, L., Troch, M., Van Hoydonck, G., Moeremans, M., et al. (2007). Postural abnormalities and contraversive pushing following right hemisphere brain damage. *Neuropsychological Rehabilitation*, *17*(3), 374–396.

Laplane, D., & Degos, J. D. (1983). Motor neglect. *Journal of Neurology, Neurosurgery, and Psychiatry*, *46*, 152–158.

Lenz, H. (1944). Raumsinnesstörungen bei Hirnverletzungen. *Deutsche Zeitschrift für Nervenheilkunde*, *157*, 22–64.

Luyat, M., & Gentaz, E. (2002). Body tilt effect on the reproduction of orientations: Studies on the visual oblique effect and subjective orientations. *Journal of Experimental Psychology: Human Perception and Performance*, *28*(4), 1002–1011.

Luyat, M., Gentaz, E., Corté, T., & Guarrez, M. (2001). Reference frames and haptic perception of orientation: Body and head tilt effects on the oblique effect. *Perception & Psychophysics*, *63*, 541–554.

Milner, A. D., & Harvey, M. (1995). Distortion of size perception in visuospatial neglect. *Current Biology*, *5*, 85–89.

Milner, A. D., Harvey, M., Roberts, R. C., & Forster, S. V. (1993). Line bisection errors in visual neglect: Misguided action or size distortion? *Neuropsychologia*, *31*(1), 39–49.

Mittelstaedt, H. (1983). A new solution to the problem of the subjective vertical. *Naturwissenschatften*, *70*, 272–281.

Nichelli, P., Rinaldi, M., & Cubelli, R. (1989). Selective spatial attention and length representation in normal subjects and in patients with unilateral spatial neglect. *Brain and Cognition*, *9*(1), 57–70.

Parker, D. E., Poston, R. L., & Gulledge, W. L. (1983). Spatial orientation: Visual–vestibular–somatic interaction. *Perception & Psychophysics*, *33*, 139–146.

Pérennou, D. (2006). Postural disorders and spatial neglect in stroke patients: A strong association. *Restorative Neurology and Neuroscience*, *24*(4–6), 319–334.

Pérennou, D., Mazibrada, G., Chauvineau, V., Greenwood, R., Rothwell, J., Gresty, M. A., et al. (2008). Lateropulsion, pushing and verticality perception in hemispheric stroke: A causal relationship? *Brain*, *131*, 2401–2413.

Pizzamiglio, L., Vallar, G., & Doricchi, F. (1995). Gravity and hemineglect. *NeuroReport*, *7*, 370–371.

Rock, I. (1990). The frame of reference. In I. Rock (Ed.), *The legacy of Solomon Asch* (pp. 243–268). Hillsdale, NJ: Erlbaum.

Saj, A., Honoré, J., Bernati, T., Richard, C., & Rousseaux, M. (2008). Reducing rightward bias of subjective straight ahead in neglect patients by changes in body orientation. *Journal of Neurology, Neurosurgery, and Psychiatry*, *79*(9), 991–996.

Saj, A., Honoré, J., Davroux, J., Coello, Y., & Rousseaux, M. (2005). Effect of posture on the perception of verticality in neglect patients. *Stroke*, *36*, 2203–2205.

Sakata, H., Taira, M., Kusunoki, M., Murata, A., & Tanaka, Y. (1997). The parietal association cortex in depth perception and visual control of hand action. *Trends in Neuroscience*, *20*, 350–357.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, *386*, 167.

Tartaglione, A., Benton, A. L., Cocito, L., Bino, G., & Favale, E. (1981). Point localisation in patients with unilateral brain damage. *Journal of Neurology*, *44*, 935–941.

Tartaglione, A., Cocito, L., Bino, G., Pizio, N., & Favale, E. (1983). Further evidence for asymmetry of point localization in normals and unilateral brain damaged patients. *Neuropsychologia*, *21*, 407–412.

Taylor, A. M., & Warrington, E. K. (1973). Visual discrimination in patients with localized cerebral lesions. *Cortex*, *9*, 82–84.

Wade, N. J. (1968). Visual orientation during and after lateral head, body, and trunk tilt. *Perception & Psychophysics*, *3*, 215–219.

Wade, N. J. (1992). The representation of orientation in vision. *Australian Journal of Psychology*, *44*, 139–145.

Warrington, E. K., & James, M. (1967). Disorders of visual perception in patients with localised cerebral lesions. *Neuropsychologia*, *5*, 253–266.

Yardley, L. (1990). Contribution of somatosensory information to perception of the visual vertical with body tilt and rotating visual field. *Perception & Psychophysics*, *48*(2), 131–134.

Yelnik, A. P., Lebreton, F. O., Bonan, I. V., Colle, F., Meurin, F. A., Guichard, J. P., et al. (2002). Perception of verticality after recent cerebral hemispheric stroke. *Stroke*, *33*, 2247–2253.