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VISUAL CONTEXT MODULATES THE SUBJECTIVE VERTICAL IN NEGLECT: EVIDENCE FOR AN INCREASED ROD-AND-FRAME-EFFECT

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Abstract—Patients with spatial hemi-neglect display systematic deviations of the subjective vertical. The magnitude of such deviations was shown to be modulated by internal factors mediating the perception of verticality, including head-orientation. The present study investigated whether and how spatial orientation deficits are modulated by external, contextual changes in neglect patients. In a classic rod-and-frame task, we analyzed effects of frame orientation on the subjective visual vertical (SVV) in neglect patients, control patients with left- or right-sided brain damage without neglect and healthy participants. We found that neglect patients, but not brain-damaged control patients, generally display a systematic counterclockwise (CCW) tilt in their SVV judgments. Furthermore, all participant groups displayed a typical rod-and-frame effect (RFE), that is, a modulation of the SVV as a function of frame tilt. However, in the control groups, this modulation was only moderate whereas in the neglect group SVV judgments were substantially and systematically modulated by frame orientation: with CCW frame tilts, the spatial bias of neglect patients increased as a function of the magnitude of the tilt whereas with clockwise (CW) frame tilts, the spatial bias was decreased in case of moderate frame tilts and even reversed in case of stronger frame tilts, resulting in a substantial CW spatial bias. This dramatically enhanced RFE might be caused by a pathologically increased influence of contextual cues on the subjective vertical in neglect patients as a consequence of impaired processing of gravitational information. The results indicate a systematic bias of the subjective vertical along with an impairment of spatial orientation constancy which leads to severe perturbations of subjective space as well as an increased reliance on internal and external cues mediating the perception of verticality in neglect.

Key words: neglect, space perception, subjective vertical, RFE (rod-and-frame effect), context.

BRAIN DAMAGE, HEMINEGLECT, AND TILTED SPACE

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 typically fail to detect or respond to stimuli in their contralesional hemispace (Bisiach et al., 1996), show unilateral spatial representational deficits (Bisiach and Luzatti, 1978; Bisiach et al., 1981) and frequently display a reduced use of their contralesional extremities (Laplane and Degos, 1983). Although most neglect models focus on the explanation of impairments in the horizontal plane (Kerkhoff, 2001), numerous studies have demonstrated that other planes are also affected. Impairments in the frontal plane include deficits in the judgment of the subjective visual vertical (SVV) and horizontal (SVH; Howard, 1982; Lenz, 1944), and judgments of oblique line orientations (Benton et al., 1975; De Renzi et al., 1971; Kim et al., 1984). Bender and Jung (1948) found that deviations of the subjective from the true vertical result from frontal or parietal (but not occipital) lobe lesions and that their direction is contralesional, with clockwise (CW) deviations following left- and counterclockwise (CCW) deviations following right-hemisphere injury. In a more recent investigation, Brandt et al. (1994) examined 71 patients with unilateral hemispheric lesions for judgment of the SVV. MRI analyses revealed that the most impaired patients had lesions centering on an area considered as the human homologue of the monkey parieto-insular-vestibular cortex (PIVC; Grüsser et al., 1990).

Interestingly, lesion sites related to deviations of the subjective vertical are neighbouring and overlapping with those known to cause the neglect syndrome, including the insula (Karnath et al., 2004), the temporo-parietal junction (e.g. Vallar and Perani, 1986), posterior parietal (e.g. Mesulam, 1999) and intraparietal cortices (Mort et al., 2003), and the superior temporal gyrus (e.g., Karnath et al., 2001, 2004) at the cortical level as well as the thalamus and basal ganglia (Vallar and Perani, 1986; Karnath et al., 2004) at the subcortical level. For the perceptive/visuo-spatial component of hemineglect especially the right inferior parietal lobule seems to play a critical role (Verdon et al., 2010). Hence, it is not astonishing, that neglect patients present not only with a displacement of an egocentric reference frame to the ipsilesional side of space but also with abnormal visuo-spatial judgments, that is, CCW tilts of axes in the vertical, horizontal, and oblique orientation in the frontal plane (Kerkhoff and Zoelch, 1998). As in the horizontal plane, these deficits in the frontal plane are

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Abbreviations: CCW, counterclockwise; CW, clockwise; RFE, rod-and-frame effect; SVV, subjective visual vertical.

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multimodal as they occur in both the visual and tactile modalities (with the deviation in both modalities being correlated with each other and with the neglect severity; Kerkhoff, 1999). Importantly, this multimodal deficit is not an unspecific consequence of brain damage, but seems to be specifically related to spatial neglect, as patients with left- or right-hemispheric lesions *without* neglect perform at the level of healthy control subjects (Kerkhoff, 1999). Furthermore, Yelnik et al. (2002) showed that deviations of the SVV do not primarily depend on the localization and size of the underlying lesion, but are rather related to the severity of spatial neglect. Thus, a severely disturbed representation of space in the frontal plane does not constitute an epiphenomenon, but rather a core deficit of neglect patients.

Opposing this view, there is evidence from a study of Johannsen et al. (2006) who could not find a consistent SVV bias in a group of patients with pusher syndrome and spatial neglect. However, this lack of effect in the pusher neglect patients does not necessarily invalidate the assumption that SVV deviations are a core deficit in spatial neglect since findings from research on the SVV in pusher patients are heterogeneous and there is not yet a consensus whether there is an (ipsiversive) SVV bias (Saj et al., 2005a) or no bias (Karnath et al., 2000; Johannsen et al., 2006) in such patients and how this potential bias interacts with further deficits of the patients. Interestingly, Saj et al. (2005a) found that SVV deviations were clearly clockwise in pusher neglect patients, but anticlockwise in non-pusher neglect patients. Thus, an ipsiversive bias in pusher patients for example might counteract a neglect-induced contraversive bias (note that, in the present study, no pusher patients were included in the sample of neglect patients).

INTERNAL AND EXTERNAL FACTORS MEDIATING BIASES IN SPACE PERCEPTION IN NEGLECT

A better understanding of the factors that mediate different aspects of spatial biases in neglect patients is important for obtaining a clearer picture of the nature and the underlying mechanisms of the deficits and for identifying intervention schemes. Studies on the effectiveness of modulations of internal mediators of spatial deficits have used neck muscle vibration (e.g., Schindler et al., 2002), transcutaneous electroneural stimulation (TENS; Pizzamiglio et al., 1996), postural modulations (Karnath et al., 1998; Pizzamiglio et al., 1995), prism adaptation (e.g., Rossetti et al., 1998; Saevarsson et al., 2009; Vangkilde and Habekost, 2010), and vestibular stimulation (Karnath, 1994); those on modulations of contextual factors have employed optokinetic stimulation (e.g., Mattingley et al., 1994; Kerkhoff, 2000) and cueing (e.g., Butter and Kirsch, 1995; Lin et al., 1996). These studies enabled the development of the most applied neglect-therapies for spatially biased behavior such as, for instance, extinction, the unawareness of contralesional stimuli, or motor neglect.

More recent research has focused on the subjective vertical as a more direct measure of space perception, and examined modulations of internal mediators of verticality perception. As with other aspects of spatial bias, a number of studies have investigated the effectiveness of internal mediators of space perception. Saj et al. (2005b, 2006) demonstrated that the SVV in patients with right-hemispheric lesions (especially neglect patients) was significantly affected by galvanic vestibular stimulation and by postural modulations (in the fore-back dimension). We showed that the subjective tactile vertical (STV), too, was significantly affected by modulations of posture in the fore-back dimension (and therefore head orientation in the sagittal plane; Funk et al., 2010a). Furthermore, we found that *lateral* head tilt (head orientation in the frontal plane) had also a systematic and significant effect on the SVV in neglect patients (Funk et al., 2010b): their CCW bias was further increased by CCW lateral head inclination, while it was substantially reduced by CW inclination. These studies demonstrate that the perception of verticality can be systematically modulated by changes in the setting of internal mediators contributing to the representation of space. However, to our knowledge, no systematic investigation of the effects of *contextual* factors, which are known to critically influence other aspects of spatial behavior (Butter and Kirsch, 1995; Lin et al., 1996; Mattingley et al., 1994; Kerkhoff, 2000), on subjective verticality judgments in neglect has been carried out to date.

CONTEXT AS A MEDIATOR OF ORIENTATION PERCEPTION/THE ROD-AND-FRAME EFFECT

Visual context is an important mediator of object perception and serves as a frame of reference for the apparent orientation of an object. A classical example of a context effect in the estimation of the subjective vertical is the so-called rod-and-frame effect (RFE; Asch and Witkin, 1948a,b). In rod-and-frame tasks, observers show systematic errors in setting a rod to the vertical position when it is placed inside a tilted frame compared to when it is presented without a frame or with a gravitationally vertical frame (in an otherwise dark environment, i.e., without additional contextual cues). A common interpretation of the RFE is that, in addition to gravity, the tilted frame serves as a frame of reference for the perception of the upright (e.g., Rock, 1990), that is, it acts as a world surrogate determining the apparent visual axes of space. The observers perceive rod orientation with reference to frame orientation and to gravity, so that the resulting rod setting usually is a compromise between the two references. At small degrees of frame tilt (up to 20°), the subjective vertical is typically tilted in the direction of the frame tilt (so-called direct effects), whereas at larger degrees, it can be tilted either in the direction of frame tilt or in the opposite direction (so-called indirect effects), depending on the symmetry axis which is used as a reference (e.g., Beh et al., 1971). The magnitude and direction of rod tilt is furthermore influenced by the size of the frame: large frames typically produce larger rod-setting errors (e.g., Ebenholtz and Callan, 1980) and only direct effects, whereas small frames can produce both direct and indirect effects, depending on the degree of frame tilt (Wenderoth and Beh, 1977). Further research on the mechanisms underlying the RFE revealed a possible role of induced head tilt (Ebenholtz and Benzschawel, 1977; Sigman et al., 1978, 1979) and ocular torsion in the direction of the frame (e.g., Goodenough et al., 1979a). Both effects may be explained in terms of visuo-vestibular interactions. The tilted frame might produce an illusion of self-tilt in the direction opposite to that of the frame. In a compensatory manner, the rod might be set in the direction opposite to that of experienced body tilt and, thus, into the direction of frame tilt (e.g., Goodenough et al., 1979b). However, visuo-vestibular interactions alone cannot explain the variety of effects (i.e., direct and indirect effects) reported in rod-and-frame tasks; rather, purely visual mechanisms seem to be at work, too (e.g., Goodenough et al., 1979b). Therefore, an alternative hypothesis of a dual-process-model has been put forward (for a review, see, e.g. Spinelli et al., 1991), namely: in the case of large frames, RF phenomena are mediated by visuo-vestibular interactions; by contrast, in the case of small frames, purely visual mechanisms would be prominent.

RATIONALE OF THE PRESENT STUDY

The objective of the present study was to investigate whether and how the systematic spatial orientation deficits in neglect patients are modulated by contextual cues. We studied the SVV in patients with right-hemispheric brain damage and left spatial neglect, patients with right- or left-hemispheric brain damage without spatial neglect (further referred to as RBD and LBD controls), and healthy control subjects in a classic rod-and-frame task. In order to systematically analyze effects of frame orientation in the different groups, participants had to vertically adjust a rod in conditions with CW or CCW frame tilts of varying magnitude (5°, 15°, or 45°). Previous research has shown that frame tilts smaller than 20° typically produce direct effects, whereas 45° frame tilts do not cause tilt illusions (probably because the resulting figure is a symmetric diamond, e.g., Beh et al., 1971). Since healthy and also RBD and LBD control subjects can rely on both intact gravitational and contextual references, their rod settings should reflect a compromise between the objective/gravitational vertical and the orientation of the frame. Thus, we expected slight SSV tilts in the direction of frame tilt in case of a 5° or 15° CW or CCW frame tilt and no SVV tilt in case of a 45° frame tilt in these groups. By contrast, in neglect patients, the processing of gravitational information is impaired (Pizzamiglio et al., 1995, 1997). Therefore, they cannot rely on gravitational input to the same extent and have to take into account other (e.g., contextual) information to a greater degree. This should result in an increased RFE in these patients. Since the SVV of neglect patients is already tilted CCW in general, a 5° or 15° CW tilt of the frame should lead to a reduction (or even reversal) of this pathological deviation, depending on the magnitude of the frame tilt. In contrast, a 5° or 15° CCW tilt of the frame should lead to a further increase of the deviation. A vertical (0°) frame might decrease the systematic deviation in neglect patients, as it can be used as a veridical reference for the rod setting. However, a 45° frame might either decrease the systematic error (in case it is subjectively interpreted as a symmetrical diamond) or increase the deviation (if interpreted as a CCW tilted square).

From the preceding arguments, the following hypotheses were derived: (1) Neglect patients (but not brain-damaged control patients without neglect) generally exhibit a systematic visual-spatial orientation deficit; that is, they generally display a substantial CCW tilt of their SVV. (2) Axis orientation performance is differently modulated by frame orientation in neglect patients compared to control patients and healthy controls: SVV judgments of all participants generally vary in the direction of frame tilt; however, performance of neglect patients is *far more strongly* biased compared to all control groups, since these patients are pathologically biased by contextual cues like frame tilt (as they cannot rely on gravitational information to the same extent as controls).

EXPERIMENTAL PROCEDURES

Participants

Twelve patients with right-hemispheric vascular lesions and left spatial neglect documented by clinical standard neglect tests (see below), twelve control patients with right-hemispheric and twelve control patients with left-hemispheric vascular damage without spatial neglect according to these tests (RBD or LBD controls), and twelve healthy control subjects were tested. Informed consent according to the Declaration of Helsinki II was obtained from all participants. Table 1 summarizes the demographic and clinical data of the patients. The LBD and RBD control patients were selected to match the neglect patient sample as closely as possible regarding demographic and clinical features (age, gender, etiology, time since lesion). The mean age was 51.1 years (SD=6.2, range=43–63) for the neglect patients, 55.6 years (SD=6.0, range=46–65) for the RBD controls, 54.3 years (SD=12.4, range=32–71) for the LBD controls, and 47.2 years (SD=12.7, range=30–67) for the healthy controls. There was no significant difference with regard to age among groups (one-way ANOVA, $df=3$, $F=1.75$, $P>0.15$), nor did the gender distribution differ significantly between groups ($\Phi=0.30$, $P>0.20$). The mean time since the lesion occurred was similar in the patient groups: 5.8 months (SD=3.7, range=2–13) in the neglect group, 5.1 months (SD=2.6, range=1–9) in the RBD group, and 4.7 months (SD=1.8, range=3–9) in the LBD group (one-way ANOVA, $df=2$, $F=0.45$, $P>0.60$). Patients were only included in the sample if they had a single, vascular unilateral lesion and no evidence of a brain stem lesion (as revealed by CT/MRI). “Postural Imbalance” was rated as present in the patients when there was clinical evidence from physiotherapy or occupational therapy of a marked instability in standing and/or sitting upright and a clear preponderance of body orientation towards the ipsilesional side (see, e.g. Pérennou, 2006). None of the neglect patients showed contralesional pushing. All subjects were right-handed according to their verbal report.

Neglect tests

All patients underwent a screening for visual neglect on white paper (size 29.7×14.7 cm), including representational drawing (of a star, a daisy, a clock, a house, and a face), horizontal line bisection of a 20×1 cm black line, and number cancellation (10 targets in each hemispace among 100 numbers on the total page). In addition, a reading test with 180 words sensitive to neglect and

Table 1. Summary of clinical and demographic data of neglect patients, LBD and RBD control patients without neglect

Group	Age	Sex	Etiology	Lesion	Months since lesion	Motor deficit	Postural deficit	Aphasia	Visual field	Neglect dyslexia (errors)	Figure copy L/R	Cancell. omissions L/R	Line bisection −/+ mm
N+	49	1	R-MCA	P, T	12	Plegia	Pl	NT	L-Quan	12	−/+	8/3	+22
N+	44	1	R-MCA	P, T	10	Paresis	Pl	NT	L-Quan	8	−/+	6/4	+9
N+	43	1	R-MCA	P	5	Plegia	Pl	NT	Normal	7	−/+	8/3	+7
N+	50	1	R-MCA	P, T	13	Plegia	Pl	NT	Normal	8	−/+	8/5	+12
N+	48	1	R-MCA	P	5	Paresis	Pl	NT	L-Quan	5	−/+	5/2	+7
N+	48	1	R-TU	P	4	Paresis	Pl	NT	L-HH	5	−/+	5/1	−6
N+	52	0	R-ICB	T	3	Normal	No	NT	Normal	6	−/+	5/2	+10
N+	56	0	R-MCA	P, T	2	Plegia	Pl	NT	L-Quan	11	−/+	10/3	+17
N+	63	0	R-MCA	P, T	4	Plegia	Pl	NT	Normal	12	−/+	7/2	+13
N+	52	0	R-MCA	P, T	3	Paresis	Pl	NT	L-Quan	10	−/+	5/2	+12
N+	47	0	R-MCA	P, T	4	Plegia	Pl	NT	L-HH	37	−/+	10/5	+29
N+	61	0	R-MCA	P	4	Plegia	Pl	NT	Normal	6	−/+	4/0	+7
LBD	41	1	L-MCA	F, P	9	Paresis	No	Broca	Normal	NT	+/+	0/0	−1
LBD	63	1	L-MCA	F, P	4	Paresis	No	Broca	Normal	NT	+/+	0/0	+7
LBD	56	0	L-MCA	F, T	5	Paresis	No	Amnestic	Normal	NT	+/+	0/0	−3
LBD	56	0	L-PCA	O, T	3	Normal	No	Normal	R-Quan	0	+/+	0/0	+2
LBD	64	0	L-PCA	O	3	Normal	No	Normal	Normal	1	+/+	0/0	+3
LBD	70	0	L-ICB	BG	4	Plegia	No	Broca	Normal	NT	+/+	1/0	−2
LBD	59	0	L-MCA	P, T	7	Plegia	No	Residual	R-Quan	NT	+/+	1/0	+2
LBD	38	0	L-MCA	T, P	5	Paresis	No	Residual	R-HH	NT	+/+	0/0	+5
LBD	49	1	L-MCA	T	5	Normal	No	Residual	R-Quan	NT	+/+	0/0	+4
LBD	71	1	L-TU	T, BG	3	Paresis	No	Residual	Normal	NT	+/+	0/0	0
LBD	53	0	L-TU	T	4	Normal	No	Normal	R-Quan	0	+/+	0/0	+2
LBD	32	1	L-ICB	T	4	Normal	No	NT	Normal	0	+/+	0/1	+2
RBD	46	0	R-MCA	P	9	Normal	No	NT	Normal	11	+/+	0/0	+2
RBD	59	0	R-ICB	T, BG	4	Paresis	No	NT	NT	1	+/+	0/1	−3
RBD	62	0	R-MCA	P, T	9	Plegia	No	NT	L-HH	0	+/+	0/0	−22
RBD	54	0	R-MCA	P, O	1	Normal	No	NT	L-HH	0	+/+	0/1	+3
RBD	55	0	R-MCA	P, T	3	Plegia	No	NT	Normal	1	+/+	0/0	−2
RBD	58	0	R-ICB	BG	4	Paresis	No	NT	Normal	0	+/+	0/0	+5
RBD	49	0	R-ICB	BG	5	Paresis	No	NT	Normal	0	+/+	0/0	+2
RBD	65	0	R-PCA	O	9	Normal	No	NT	L-HH	6	+/+	0/0	−25
RBD	59	1	R-TU	T	3	Paresis	No	NT	Normal	1	+/+	1/0	0
RBD	60	0	R-MCA	T	5	Paresis	No	NT	Normal	0	+/+	0/0	+2
RBD	53	1	R-MCA	F, BG	4	Plegia	No	NT	Normal	1	+/+	1/0	+4
RBD	47	1	R-MCA	T, F	5	Paresis	No	NT	Normal	2	+/+	1/1	+3

Abbreviations: LBD, left brain-damaged control patient; N+, neglect patient; RBD, right brain-damaged control patient. Etiology: ICB, intracerebral bleeding; L/R, left/right; MCA/PCA, middle/posterior cerebral artery infarction; TU, tumor. Lesion: BG, basal ganglia; F, frontal; O, occipital; P, parietal; T, temporal. Postural deficit: No, no postural imbalance; Pl, postural imbalance. Aphasia: NT, reading not tested due to aphasia (documented by the Aachener Aphasie Test). Visual field: HH, homonymous hemianopia; Quan, homonymous quadrantanopia. Figure copy: −=omissions or distortions; +=normal performance. Cancellation: number of omissions per hemispace. Line bisection: deviation from true midline in mm to left (−) or right side (+).

hemianopic reading disturbances (Kerkhoff et al., 1992) was administered. Omissions or significant distortions of the left half of the copied figures were interpreted as an indicator of neglect. Cut-offs in the further tests 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).

Visual-spatial RFE tests

Fig. 1 displays the different conditions of the visual spatial rod-and-frame tasks. The computerized “visual-spatial perception” program (VS; Kerkhoff and Marquardt, 1995) was used for the measurement of the SVV. VS is based on the method of limits (Engen, 1971). In the measurement of the SVV, the experimenter manipulates the orientation of an oblique white line (18 cm×1.4 mm) presented on a dark background in a stepwise manner until the subject indicates that it is oriented exactly vertically and then further until the subject indicates that it is no longer vertical. Based on this procedure, the psychophysical parameter “constant error” can be calculated which denotes the difference between a participant’s mean estimate (the SVV) and the true vertical and, thus, provides information about the central tendency or central error of the subject. The task was carried out either with a 20 cm×20 cm yellow frame, presented in various orientations around the white line, or without a frame. There were seven different frame conditions: (1) no frame, (2) 0° frame, (3) −5° frame, (4) +5° frame, (5) −15° frame, (6) +15° frame, and (7) 45° frame (see Fig. 1). Constant errors were computed directly by the software (as described above) for each subject in each frame condition. The step-width was 0.5° in all measurements.

Visual-spatial measurements were taken in total darkness with the chassis of the PC-monitor, that is, the borders of the screen, covered by an oval-shaped mask to eliminate or at least

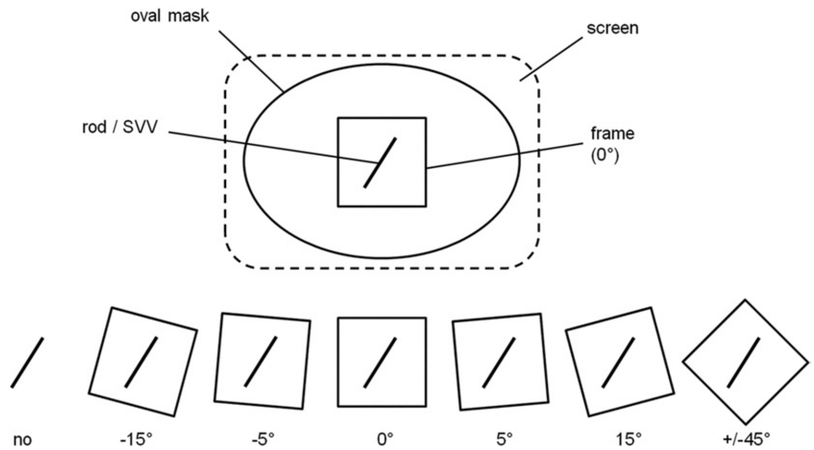

Fig. 1. Experimental setup in the visual-spatial rod-and-frame task for the different frame orientation conditions (no frame, −15°, −5°, 0°, +5°, +15° and ±45°). Participants viewed only the rod and frame, the borders of the screen (dashed line) were hidden behind an oval-shaped mask to eliminate vertical/horizontal reference cues.

strongly reduce any visual reference cues (apart from the frame). Subjects were tested at a distance of 0.5 m from a monitor with spectacle corrections where necessary. Head position was stabilized by means of a head-and-chin rest. There were 10 trials in each frame condition. Frame conditions were blocked and the sequence of blocks was counterbalanced to control for practice effects. In all conditions, starting position was 20° away from the vertical axis. The direction (CW, CCW) of the initial tilt was counterbalanced to control for effects of rotation direction. Prior to the completion of the different conditions, subjects were familiarized with the experimental setup and performed five practice trials.

Statistics

Performance of the four participant groups in the baseline condition (i.e., the "no frame" condition) was compared in a one-way ANOVA with post-hoc Scheffé tests. Furthermore, to analyze systematic deviations of the SVV from zero (the value representing the true vertical) in the baseline condition, one-sample *t*-tests were calculated for each participant group. To analyze the effect of context on spatial performance, a mixed-design ANOVA with the factors participant group (between-subjects factor with four levels: neglect patients, LBD, RBD, and healthy controls) and frame condition (within-subjects factor with six levels: −15°, −5°, 0°, +5°, +15°, ±45°) was performed for the constant errors. In case of significant main effects or interactions, subsequent post hoc comparisons were calculated: post-hoc Scheffé tests were used to compare performance between participant groups; one-way ANOVAs and contrasts (comparing each frame condition with the 0° frame condition) were used to compare performance in the different frame conditions within one subject group. Additionally, *t*-tests were used to compare performance between participant groups within the same frame orientation condition. The alpha-level was chosen as $P<0.05$ for all analyses, corrected for multiple comparisons.

RESULTS

Neglect tests

The data of each patient in the neglect tests are given in Table 1. Neglect patients showed the characteristic pattern of asymmetrical deficits. All neglect patients showed impaired copying performance, with the typical omissions and/or distortions of the left side of the drawings. Furthermore, neglect patients displayed impaired line bisection performance: 11 out of 12 patients showed the typical rightward deviation in horizontal line bisection (mean deviation: 11.6 mm to the right, SD=8.7). They also showed the typical pattern of omissions in the number cancellation task, with significantly more omissions in the left compared to the right hemispace [mean omissions: 6.8 in the left (SD=2.1) and 2.7 in the right hemispace (SD=1.5); $t(11)=10.26$, $P<0.01$] as well as impaired reading performance indicating neglect dyslexia. LBD and RBD control patients did not show such asymmetrical deficits. Rather, they showed intact drawing performance, only nonsystematic and nonsignificant deviations in line bisection performance (LBD mean: 1.8 mm to the right, SD=2.9; RBD mean: 2.6 mm to the left, SD=10.1) and intact number cancellation performance [LBD mean: 0.2 omissions in left (SD=0.4) and 0.1 in right hemispace (SD=0.3); RBD mean: 0.3 omissions in left (SD=0.5) and 0.3 in right hemispace (SD=0.5)]. Reading performance (not measured in eight aphasic LBDs) was not impaired in non-aphasic LBD controls, but in two out of 12 RBD controls (one had hemianopic alexia due to a left-sided homonymous hemianopia).

Visual-spatial orientation judgments

Fig. 2 displays the visual-spatial orientation judgments of neglect patients and healthy, RBD, and LBD controls as a function of frame condition. The lines within the circles represent the mean SVVs of the individual participants. While the healthy subjects, as well as the RBD and LBD controls, show generally only minor deviations of their SSV from the true vertical, SVV judgments of neglect patients display a marked and systematic CCW tilt in the baseline condition and are furthermore substantially and systematically modulated by frame orientation. Table 2 summarizes the mean constant errors for the six different frame orientations in all subject groups.

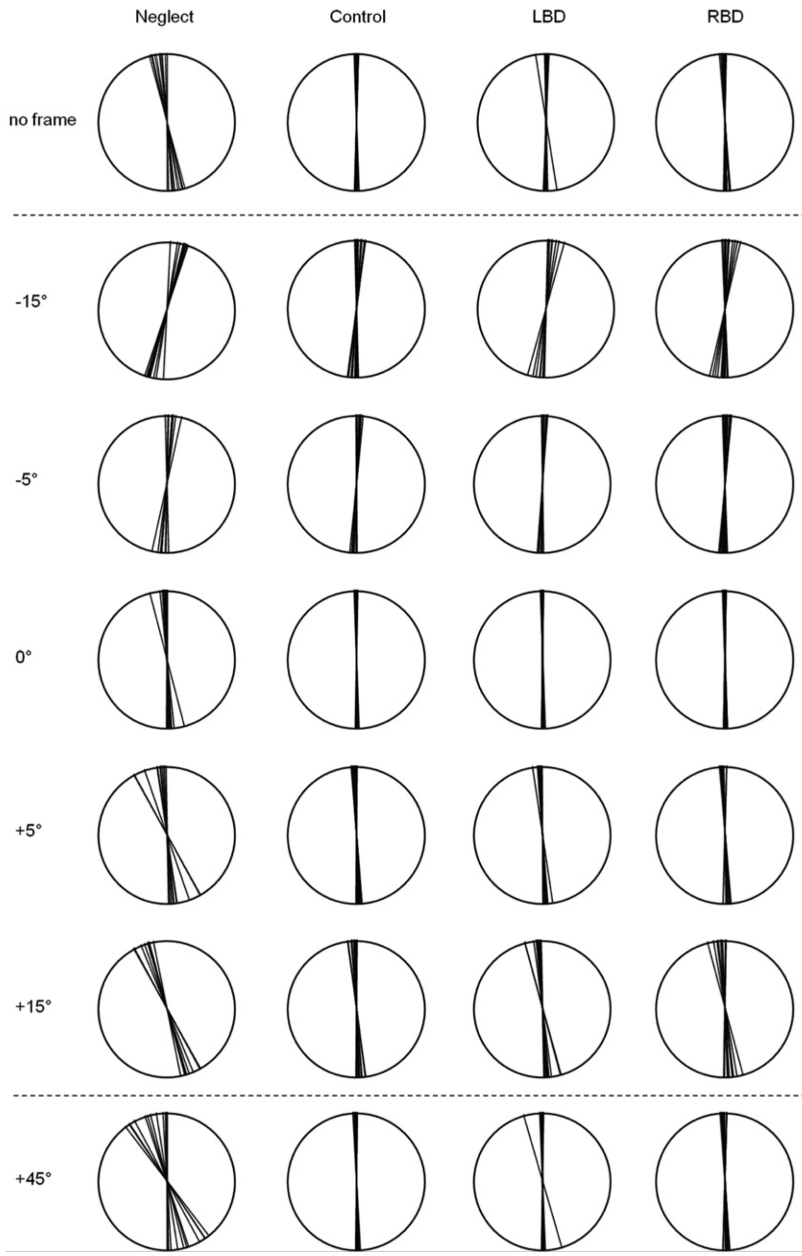

Fig. 2. Performance of neglect patients, LBD and RBD control patients, and healthy controls in the visual-spatial orientation task for the six different frame orientation conditions (−15°, −5°, 0°, +5°, +15° and ±45°); the lines within the circles display the mean SVVs of individual patients and control subjects.

Table 2. Mean constant errors (and standard deviations) for the six different frame orientation conditions (−15°, −5°, 0°, +5°, +15° and ±45°) in healthy, LBD, and RBD control subjects and neglect patients (N+); positive constant errors indicate CCW tilts of the SVV, negative constant errors CW tilts

	Healthy	LBD	RBD	N+
−15°	−2.7° (SD=3.0)	−5.5° (SD=4.2)	−3.5° (SD=4.9)	−13.3° (SD=4.1)
−5°	−1.6 (SD=1.9)	−2.3° (SD=1.6)	−1.7° (SD=2.5)	−4.4° (SD=3.4)
0°	0.2° (SD=0.6)	0.2° (SD=0.8)	0.2° (SD=0.9)	3.0° (SD=4.0)
5°	1.8° (SD=1.5)	2.8° (SD=2.1)	2.4° (SD=1.8)	12.4° (SD=10.9)
15°	2.7° (SD=2.5)	5.5° (SD=4.7)	4.8° (SD=4.4)	18.2° (SD=5.5)
±45°	0.7° (SD=1.0)	1.7° (SD=4.7)	1.3° (SD=1.6)	16.2° (SD=13.9)

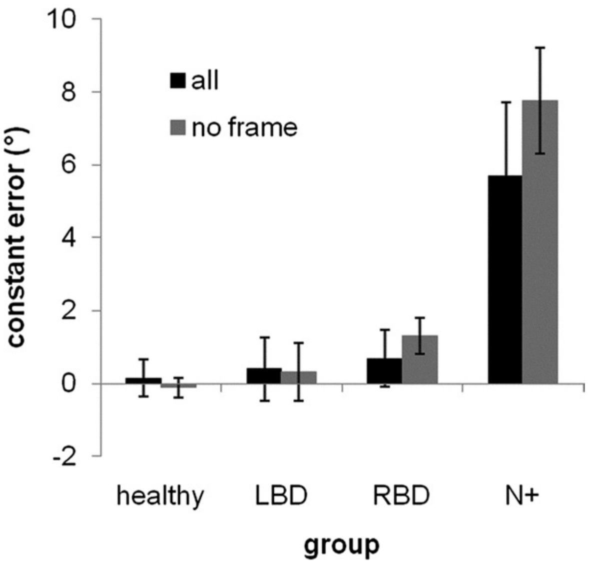

Fig. 3. Constant errors (means and standard errors) in the SVV for the "no frame" condition (grey bars) and across all frame conditions (black bars) in neglect patients (N+), healthy, LBD, and RBD control subjects; positive constant errors indicate CCW tilts of the SVV, negative constant errors CW tilts.

Group differences and general direction of SVV tilt. Fig. 3 displays the average constant errors of the SVV across all frame conditions and separately for the "no frame" condition for each subject group. While the normal subjects and also the RBD and LBD controls show only marginal deviations of their SVV, neglect patients display systematically positive constant errors, indicating a marked CCW tilt of the SVV. A one-way ANOVA with post-hoc Scheffé tests for the between-group comparison of SVV judgments in the "no frame" condition revealed a significant effect of group ($df=3$, $F=17.66$, $P<0.01$). Performance of neglect patients differed significantly from all control groups (all $P<0.01$), while performance of the control groups was highly comparable (all $P>0.70$). Furthermore, to assess the systematic direction of tilt without contextual information, one-sample *t*-tests were calculated for the constant errors of each group in the "no frame" condition. Constant errors of healthy, LBD and RBD controls did not differ significantly from zero (all $P>0.05$). By contrast, those of neglect patients were significantly larger than zero ($t(11)=5.35$; $P<0.01$). Positive constant errors indicating CCW tilts of the SVV were shown by 11 of 12 neglect patients (one did not show any tilt). That is, without additional contextual information, neglect patients displayed reliable, substantial, and systematic CCW tilts of the SVV.

Effects of frame condition on SVV tilt. Fig. 4 presents the average constant errors of the SVV in order to demonstrate the RFEs, separately for each frame condition and for each participant group. As can be seen, all groups showed tilts of the SSV as a function of frame condition: only direct RFEs were obtained, that is, CW frame tilts resulted in a CW tilt of the SVV, while CCW frame tilts resulted in a CCW tilt (relative to the true vertical and relative to the SVV in the "no frame" and in the 0° frame condition). The RFEs increased with increasing frame tilts, that is, small frame tilts led to minor changes in the SVV, whereas large frame tilts led to major changes. Moreover, Fig. 4 shows that neglect patients displayed the most marked SVV modulations as a function of frame condition, that is, their SVV was tilted in the direction of frame tilt to a much larger degree than those of all three control groups.

A mixed-design ANOVA (with the factors subject group and frame condition) revealed significant main effects of group ($df=3$, $F=10.83$, $P<0.01$) and frame condition ($df=5$, $F=71.60$, $P<0.01$), and a significant interaction of group and frame condition ($df=15$, $F=15.54$, $P<0.01$). Neglect patients generally displayed significantly larger constant errors compared to all control groups (all $P<0.01$), whereas the performance of healthy, RBD and LBD controls was highly comparable (all $P>0.95$, n.s.).

One-way ANOVAs revealed that frame tilt significantly affected performance in all subject groups, that is in neglect patients ($df=5$, $F=37.20$, $P<0.01$), RBD ($df=5$, $F=10.92$, $P<0.01$), LBD ($df=5$, $F=16.74$, $P<0.01$), and healthy controls ($df=5$, $F=12.78$, $P<0.01$). In all subjects, a 5° or 15° CW or CCW frame tilt resulted in a significant SVV tilt in the same direction (all $P>0.05$) compared to the 0° frame condition and SVV tilts were generally larger with increasing frame tilt (see Fig. 4). The 45° frame did not cause any SVV tilt in healthy, RBD and LBD controls (all $P>0.05$), but a strong CCW tilt of the SVV in neglect patients ($P<0.01$). Furthermore, the direct RFEs were much larger in the neglect patients compared to all other subject groups. Additional *t*-tests revealed that neglect patients showed a significantly larger CCW tilt of the SVV compared to all control groups in the +5°, +15° and +45° frame conditions (all $P<0.05$) and a significantly larger CW

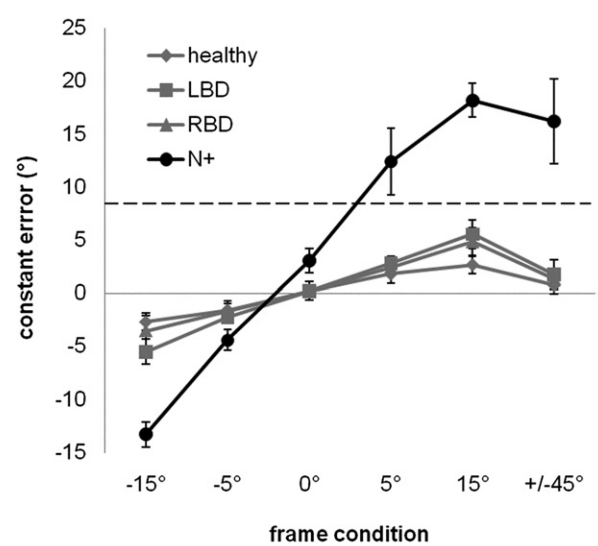

Fig. 4. Constant errors (means and standard errors) in the SVV for the different frame orientation conditions (−15°, −5°, 0°, +5°, +15° and ±45°) in neglect patients (N+), healthy, LBD, and RBD control subjects; positive constant errors indicate CCW tilts of the SVV, negative constant errors indicate CW tilts; the straight line at 0° indicates the true vertical; the dashed line indicates the constant errors of neglect patients in the "no frame" condition.

tilt in the −15° frame condition. Performance in the −5° and the 0° frame condition did not differ significantly between neglect patients and control groups after α-correction (all $P>0.05$). Performance between the three control groups did not differ significantly in any frame condition (all $P>0.05$).

DISCUSSION

The rationale of the present study was to investigate the modulation of spatial orientation judgments by visual contextual cues in neglect. Visual-spatial axis orientation performance in a classic rod-and-frame task was analyzed in patients with right hemispheric lesions and left spatial neglect, LBD and RBD control patients without neglect, and healthy control subjects. Our hypotheses were that neglect patients would display a systematic CCW bias in the SSV and that, furthermore, axis orientation judgments would be modulated by frame orientation to a markedly larger degree in neglect patients compared to control groups.

As expected, neglect patients generally showed a systematic and significant CCW tilt in their SVV in the classical, reference condition without frame. Although the oval mask could serve as visual context information also in the condition "no frame," it provides, if any, only vague cues about the cardinal axes indicating the horizontal and vertical orientation. Therefore, the CCW tilt in neglect patients in the present study unlikely represents a bias that is associated with this visual reference. The results in the "no frame" condition replicate findings of previous studies in the field: they show the typical pattern of bias which has already been demonstrated in several studies in the visual domain with (Kerkhoff and Zoelch, 1998; Kerkhoff, 1999) and without an oval shaped mask (Saj et al., 2005b; Yelnik et al., 2002) as well as in the tactile domain (i.e., also without a mask; Kerkhoff, 1999). Interestingly, a vertically aligned frame (0° frame) reduced this bias significantly compared to the "no frame" condition, presumably because it provided a strong orthogonal, external reference for the setting of the vertical.

In all four subject groups, axis orientation performance was significantly and systematically modulated by frame tilt. The RFEs were generally direct, that is, the SVV was biased *in direction of frame tilt*. In line with previous research (e.g., Beh et al., 1971), the control groups showed only slight, but consistent direct effects in case of small, 5° or 15°, CW or CCW frame tilts and no SVV tilt in case of a 45° frame tilt. In neglect patients, the effect of frame orientation was dramatically increased, that is, the magnitude of the direct RFE was approximately three times as large in these patients as in the controls. Since the SVV of neglect patients was already tilted CCW in the "no frame" and also in the 0° frame condition, a CCW tilt of the frame led to a further increase of the subjective bias. By contrast, a CW tilt of the frame led not simply to a reduction, but rather to a reversal of the bias, that is: a CW tilt of the SSV.

An exceptional case was the 45° frame condition: a 45° frame did not bias performance in the healthy, LBD, and RBD control groups, presumably because it can be used efficiently as a helpful reference cue (as the edges of a 45° frame point to the top and the bottom and the frame actually represents a symmetrical diamond; Beh et al., 1971). In neglect patients, by contrast, a 45° frame caused a marked bias, that is, it increased the CCW bias by an amount comparable to the 15° frame. This pattern indicates that neglect patients are not only unable to use the symmetrical contextual information provided by the diamond efficiently; rather, they seem to interpret this frame as a square tilted CCW, leading to a large direct RFE, that is, a large CCW tilt of the SVV. Thus, the 45°-diamond-shaped frame deteriorated the already impaired task performance *selectively* in the neglect group, while it permitted almost normal performance in all other groups (Fig. 4).

Differential effects of contextual modulations on the SVV

Previous research has shown that different reference frames can be selected to define a visual orientation in space (for reviews, see, e.g., Howard, 1982; Rock, 1990; Wade, 1992). Among the egocentric and allocentric reference frames in which spatial orientations can be mapped, most important for the judgment of the subjective visual vertical are probably the gravitational as well as the visual reference frame. Visual, gravitational, and also other (e.g., somatosensory) information is integrated in the intraparietal cortex to generate a subjective percept of space (e.g., Bremmer et al., 2002; Duhamel et al., 1998). If information from different sources is congruent, that is, if the different frames of reference are aligned, the subjective perception of an orientation corresponds to the "veridical" orientation. However, even in participants without disturbed spatial information perception, the information delivered from different sources can be incongruent in certain conditions, as it is the case, for example, in the classic rod-and-frame task. Here, in addition to gravity, the tilted frame serves as a frame of reference for the perception of the upright, that is, it acts as a world surrogate that determines the apparent visual axes of space (e.g., Rock, 1990). The orientation of the rod is consequently perceived with reference to frame orientation and to gravity, so that the resulting rod setting usually is a compromise between the two references. This is exactly the behavior found in healthy, LBD, and RBD controls in the present study. They showed systematic, but only moderate deviations of the SVV (<3° for the ±5° frame condition and <6° for the ±15° frame condition) in the direction of the frame. This pattern of results indicates that frame orientation serves as a frame of reference to a certain extent and therefore biases the rod settings in the control subjects. However, visual information about the orientation of the frame is integrated with intact gravitational information, which is used as a reference for the perception of the upright, too, and thus reduces the effect of frame orientation on the SVV.

By contrast, in neglect patients, the processing of gravitational input is impaired (i.e., asymmetric) and gravitational information cannot be used as an "intrinsic" reference for the perception of the upright to the same extent as in healthy subjects. This is most probably the reason why neglect patients showed such a strong impact of visual contextual information on the SVV. In these patients, the SVV deviations were as large or even larger than the angles of frame orientation tilt (−13.3° and −4.4° deviation in the −15° and −5° frame conditions and 12.4° and 18.2° deviation in the 5° and 15° frame conditions). Larger CCW deviations in comparison to CW deviations can be explained by a general CCW tilt of the SVV of neglect patients. The increased impact of visual contextual information on the SVV in neglect patients is in line with previous findings of enhanced effects of modulations of internal mediators of verticality perception, such as head orientation (Funk et al., 2010b). However, a new and particularly interesting finding of the present study is the reversed bias of the SVV in neglect patients in case of CW frame tilt. In general, the "default mode" of neglect patients is a systematic and substantial CCW bias of the SVV. Previous research (e.g., Funk et al., 2010b; Saj et al., 2006) has demonstrated that this CCW bias can be increased or decreased by modulators of verticality perception. However, to our knowledge, a strong reversal of the spatial bias in neglect patients by visual contextual information as it is revealed here has not been shown thus far. It appears that the spatial performance of neglect patients is not only instable with regard to the magnitude of the pathological bias, but also with respect to its polarity, which is in line with the view that neglect patients are characterized by a loss of spatial orientation constancy. That is, neglect patients display both a consistent CCW tilt of the SVV and a loss of its constancy, which leads to systematic deviations of subjective space as well as an increased reliance on internal and external cues mediating the perception of verticality. The systematic deviations of subjective space are observable under specific (postural) circumstances—in an upright posture with a vertical head position. With lateral head inclination (Funk et al., 2010b), in supine body position (Saj et al., 2005b) or with certain types of visual context (the present paper), the tilt might change, that is be reduced or even reversed.

We suggest that the strong modulations of space/verticality perception in neglect patients might depend upon a central mechanism related to multisensory integration and space representation in intraparietal cortical areas. This idea has for example already been put forward by Rossetti et al. (1998), who reported a larger prism adaptation aftereffect in neglect patients compared to controls. Generally, it appears that the performance of neglect patients in various spatial tests, including the SVV, is influenced more than the one of other brain-damaged patients or healthy controls by many internal (e.g., prism adaptation, neck muscle vibration, vestibular stimulation) and external (e.g., visual or auditory cues) cues mediating space representation. This abnormal weighting of cues mediating space/verticality perception might be the consequence of an impaired integration of multimodal information in the parietal cortex due to a pathological processing of graviceptive information.

Clinical and daily-life consequences of impaired spatial orientation constancy

It is likely that this effect—the loss of spatial orientation constancy and the pathologically increased influence of contextual visual information—has profound consequences in daily life. It can be conjectured that neglect patients have great difficulties in estimating verticality in the presence of additional oblique contours visible in the environment. A typical situation or scene in the daily routine, which contains multiple complex stimuli (and, therefore, also orientations), provides many different sources of context information. It would, thus, to be expected that the perception of such complex visual stimulation will lead to similar biases or even greatly increase the biases observed with the experimentally reduced stimulation in the present study. That is, depending on the predominant contextual information, different orientation biases could result which would in turn continuously change through egomotion or moving scenes/stimuli.

In this context it is worth mentioning that the size of the perceptual tilt of the SSV in the rod-and-frame test was found to predict poor ambulation performance in patients with left hemiplegia (Bruell et al., 1957, 1958; note that, unfortunately, these reports did not mention explicitly whether their patients had left-sided visual neglect). Also, the notable deficits in drawing and copying performance that neglect patients typically display could conceivably stem from (or at least be increased by) given or already drawn orientations that impede the correct drawing of new orientations. The inaccurate and very instable representation of spatial orientations changing rapidly with changes in external visual and internal modulations might therefore profoundly affect performance in clinical tests as well as fundamental competencies indispensable for managing daily life (e.g., ambulation performance).

In the present study, we showed that context information can increase, reduce, or reverse the orientation bias in neglect patients (depending on the frame orientation). Thus, visual contextual information seems to be a good candidate to manipulate this bias and could therefore be possibly used as one component of neglect therapy. Further research is necessary to investigate whether, in therapy, certain types of contextual information (e.g., a visually tilted chamber) might induce positive and desirably also long-lasting effects on orientation performance in neglect patients.

Limitations of the study

The present results, together with findings from other studies in the field, indicate a functional relation between spatial neglect and a CCW bias of the SVV. The neuropsychological methodology used in this study has inherent limitations which concern the conclusion that SVV tilts are a core deficit in spatial neglect rather than a highly correlated epiphenomenon. The high comorbidity along with the correlation between neglect severity and the magnitude of SVV tilt serve as evidence for the former assumption, which is advocated in the present study. However, if neglect is caused by lesions close to structures that are responsible for SVV deviations, we cannot exclude a high comorbidity without a direct functional relationship. In this case, not the presence or absence of spatial neglect, but the exact brain area affected would be crucial for the presence and magnitude of SVV bias. The topographic accuracy of neuropsychological studies based on the individual lesions would be a critical point with regard to this question. Unfortunately, the structural images of the patients' lesions cannot be provided in this paper. Nevertheless, the present study is the first to demonstrate that neglect patients—included on the basis of descriptions of the lesion sites and the presence of the syndrome assessed via behavioral tests—suffer from a spatial deficit which can be significantly modulated by changes in contextual visual information.

CONCLUSION

When combining the present finding of a strong influence of *contextual* visual information on the subjective vertical with previous findings indicating a significant impact of modulations of *internal* mediators of verticality perception (e.g., lateral head orientation: Funk et al., 2010b; and posture: Funk et al., 2010a; Saj et al., 2005b), the emerging picture is one of a loss (or an impairment) of *spatial orientation constancy* in patients with neglect. This impairment of spatial orientation constancy along with a systematic bias of the subjective vertical leads to severe perturbations of subjective space as well as an increased reliance on internal and external cues mediating the perception of verticality in neglect. Put differently: in neglect patients, the (already perturbed) perception of the subjective vertical changes dramatically not only with changes in head- or body-position, but also with modifications of contextual visual information that serve as a reference for the perception of spatial orientation. Modulations of internal and external cues mediating the perception of space do affect orientation performance also in healthy subjects or brain-damaged patients without neglect. However, in neglect patients, this modulation is pathologically exacerbated, since they are not able to use intact gravitational information as a reference for the perception of the upright to accurately integrate and counterbalance other sources of input. The result of this may be an inaccurate and very instable representation of spatial orientations changing rapidly with manipulations of internal and/or external modulators of subjective space perception, which has profound consequences in daily life of neglect patients.

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