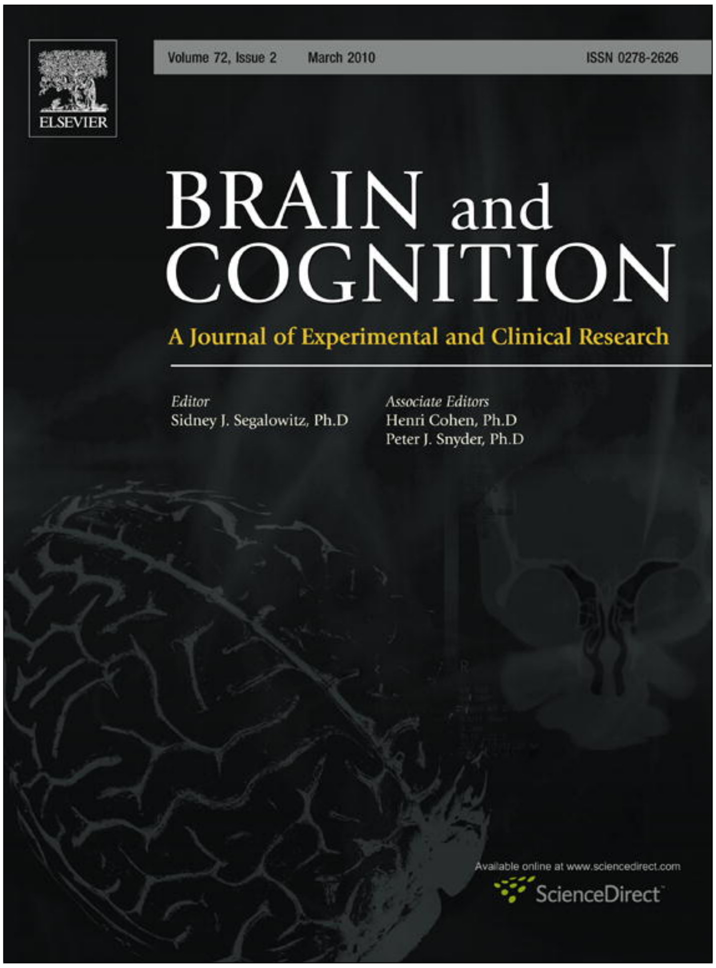
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Brain and Cognition 72 (2010) 210–217

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Auditory space perception in left- and right-handers

Sebastian Ocklenburg [a,*], Marco Hirnstein [b], Markus Hausmann [b], Jörg Lewald [c]

[a] Department of Biopsychology, Faculty of Psychology, Ruhr-University Bochum, D-44780 Bochum, Germany
[b] Department of Psychology, Durham University, South Road, Durham DH1 3LE, United Kingdom
[c] Leibniz Research Centre for Working Environment and Human Factors, Institute for Occupational Physiology at the University of Dortmund, Ardeystr. 67, D-44139 Dortmund, Germany

ARTICLE INFO

Article history:
Accepted 26 August 2009
Available online 27 September 2009

Keywords:
Handedness
Hemispheric asymmetry
Lateralization
Sound localization

ABSTRACT

Several studies have shown that handedness has an impact on visual spatial abilities. Here we investigated the effect of laterality on auditory space perception. Participants (33 right-handers, 20 left-handers) completed two tasks of sound localization. In a dark, anechoic, and sound-proof room, sound stimuli (broadband noise) were presented via 21 loudspeakers mounted horizontally (from 80° on the left to 80° on the right). Participants had to localize the target either by using a swivel hand-pointer or by head-pointing. Individual lateral preferences of eye, ear, hand, and foot were obtained using a questionnaire. With both pointing methods, participants showed a bias in sound localization that was to the side contralateral to the preferred hand, an effect that was unrelated to their overall precision. This partially parallels findings in the visual modality as left-handers typically have a more rightward bias in visual line bisection compared with right-handers. Despite the differences in neural processing of auditory and visual spatial information these findings show similar effects of lateral preference on auditory and visual spatial perception. This suggests that supramodal neural processes are involved in the mechanisms generating laterality in space perception.

© 2009 Elsevier Inc. All rights reserved.

1. Introduction

Handedness is one of the most obvious manifestations of functional cerebral asymmetries in humans and strongly related to other lateralized brain functions such as language and spatial abilities. Typically, the left hemisphere is dominant for language in both right- (RHs) and left-handers (LHs), but an unusual right-hemisphere superiority is more frequently observed in LHs (Corballis, 2003) and its incidence linearly increases with the degree of left-handedness (Isaacs, Barr, Nelson, & Devinsky, 2006; Knecht et al., 2000). Atypical functional cerebral asymmetries in LHs are not restricted to language but can be found in various cognitive functions. For example, a recent meta-analysis of 4278 studies has shown that the right-hemispheric superiority in visuospatial abilities which is typically found for RHs was not present in LHs on a population level (Vogel, Bowers, & Vogel, 2003).

A link between handedness and functional cerebral asymmetries in spatial abilities has also been shown by studies on pseudoneglect, the systematic tendency of neurologically healthy individuals to misbisect a horizontal line leftward of its objective center (Bowers & Heilman, 1980). Jewell and McCourt (2000) conducted a comprehensive meta-analysis of performance factors in visual line-bisection tasks. They reported that both RHs and LHs demonstrate an overall leftward bias. The leftward bias in LHs, however, was slightly shifted to the right relative to that in RHs, a finding that has been replicated by several more recent studies (e.g., Brodie & Dunn, 2005; but see also Hausmann, Waldie, Allison, & Corballis, 2003).

Remarkably, almost all studies dealing with the impact of handedness on spatial abilities have been conducted using visual tasks, whereas the relationship of handedness and spatial processing in the auditory modality has remained largely unclear. In order to reveal potential functional cerebral asymmetries in auditory spatial processing, Burke, Letsos, and Butler (1994) assessed sound localization in free-field space in LHs and RHs, using a task of sound-source identification. Participants verbally reported the horizontal and vertical number of the active sound source within an array of 104 loudspeakers. Sound localization was more accurate in the left than in the right hemispace for all participants, suggesting a right-hemisphere superiority in auditory spatial processing, as the auditory cortex contralateral to the sound source may be preferentially concerned with the processing of its location (Jenkins & Masterton, 1982; Woldorff et al., 1999). However, Burke et al. (1994) did not observe any differences between performances of LHs and RHs.

Evidence for a general right-hemisphere superiority in auditory spatial processing also comes from a study with brain damaged patients (Hausmann, Corballis, Fabri, Paggi, & Lewald, 2005) and

* Corresponding author. Fax: +49 234 32 14377.
E-mail address: sebastian.ocklenburg@rub.de (S. Ocklenburg).

0278-2626/$ - see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandc.2009.08.013

Author's personal copy

neuroimaging studies (Griffiths et al., 1998; Kaiser, Lutzenberger, Preissl, Ackermann, & Birbaumer 2000; Palomäki, Alku, Mäkinen, May, & Tiitinen 2000; Fujiki, Riederer, Jousmäki, Mäkelä, & Hari, 2002). These findings appeared to be related to the general superiority of the right hemisphere in visuospatial tasks (Vogel et al., 2003). The fact that Burke et al. (1994) failed to find differences between LHs and RHs in the auditory modality must not necessarily be in opposition to this view as these authors determined sound-localization performance by the participants' verbal reports on absolute speaker position. This method may be relatively coarse in accordance to the possibly rather subtle differences in functional cerebral asymmetries between handedness groups.

In a more recent study, Dufour, Touzalin, and Candas (2007) found differences between LHs and RHs using an auditory midline task. In this study, sounds were presented simultaneously via two loudspeakers mounted to the left and right of the participants' median plane. Participants were asked to adjust the level difference between the loudspeakers until they perceived the fused sound image located in the median plane. The results revealed that participants perceived sounds centrally when the sound level was higher on the left side, indicating a consistent shift to the right of the veridical center. This bias was found in both groups, but was more pronounced in LHs than RHs, suggesting a relation of handedness and sound localization. However, it should be noted that Dufour et al. (2007) did not investigate the localization of real sound sources in free-field space and, most importantly, did not account for perception of eccentric auditory space. Taken together, there is only sparse and inconsistent empirical data of auditory spatial processing in LHs and RHs.

The primary aim of the present study was to clarify whether LHs and RHs differ in sound localization. For the first time, two tasks (hand-pointing and head-pointing, Lewald, Dörrscheidt, & Ehrenstein, 2000) were used to relate handedness to the variable and constant errors in localization of real sound sources in free-field space covering a range of 160° in azimuth. These two tasks involve different frames of reference for auditory localization. Hand-pointing tasks investigate auditory localization mainly with respect to the trunk and may include effects of hand preferences. One may assume that head-pointing cancels those effects and demonstrates sound localization unbiased by preferential hand use.

Moreover, the present study investigated whether a potential bias in sound lateralization is confounded by lateral preferences other than handedness, such as footedness and ear and eye preferences. Although these latter measures are highly correlated with handedness (McManus, Porac, Bryden, & Boucher, 1999; Reiss, Tymnik, Kögler, Kögler, & Reiss, 1999; Siefer, Ehrenstein, Arnold-Schulz-Gahmen, Sökeland, & Luttmann, 2003), there is some evidence that they are equally or even more reliable predictors of functional cerebral asymmetries than handedness. For example, footedness was assessed because previous research suggests that it may be a more suitable predictor for functional cerebral asymmetries of higher cognitive functions, such as language lateralization (Elias & Bryden, 1998; Searleman, 1980). In addition, ear preference was assessed, as it was found to have the strongest correlation of all lateral preference measures with direction and degree of ear asymmetry in the dichotic listening test (Strauss, 1986). However, it is unknown whether ear preference also affects sound localization. Finally, eye preference was assessed since it has been found to modulate the influence of handedness on lateralization of non-spatial auditory functions (Khalfa, Veuillet, & Collet, 1998).

The aim of the present study was to answer the question whether lateral preferences and the underlying lateralized brain functions do have a similar influence on auditory spatial performance as found in visual tasks. This may allow conclusions about the involvement of supramodal neural processes in lateralization of space perception.

2. Methods

2.1. Participants

Fifty-three volunteers participated in this study. As was evident from the participants' performance in the experiments, all had normal sound-localization abilities. Each participant was assigned to one of two experimental groups, LHs or RHs, according to the result of the hand section of the Laterality Questionnaire (http://www.ergonetz.de/lateralitaet) of Siefer et al. (2003), with individual scores of $\leqslant -3$ for LHs and 3 for RHs. For each lateral preference, a laterality quotient (LQ) was calculated according to the method of Oldfield (1971). The LQ's range was between −100 and +100, with positive values indicating a right-sided preference and negative values a left-sided preference. Two additional participants completed the German version of the Edinburgh Handedness Inventory (Oldfield, 1971) and were assigned to the LHs group based on their negative LQ's. The LH group consisted of 20 participants, 11 females and 9 males, with a mean age of 29.3 years (SD = 8.12, range: 20–46 years) and a mean handedness LQ of −91.62 (SD = 21.23). The RHs group consisted of 33 participants, 18 females and 15 males with a mean age 25.8 years (SD = 6.24, range: 19–48 years) and a mean LQ of 96.21 (SD = 9.10).

All participants were tested on two different tasks in one experimental session: head-pointing to sound sources and hand-pointing to sound sources. Both tasks were conducted in separate blocks, with a short rest between conditions. The order of tasks was balanced across participants.

2.2. Apparatus

In both tasks, the participant sat on a chair in a totally dark, sound-proof and anechoic room ($5.4 \times 4.4 \times 2.1$ m^3). Acoustic stimuli were presented via 21 broad-band loudspeakers (Visaton SC5.9), mounted horizontally along the arc of a circle (radius 1.5 m) with the center near the midpoint of the participant́s interaural distance. One of the loudspeakers was straight ahead of the participant, 10 were on the left, and 10 were on the right with a constant angular separation of 8° (see Fig. 1). The acoustic stimulus was band-pass-filtered frozen noise (lower cut-off frequency 0.8 kHz; upper cut-off frequency 4 kHz; sound pressure level 70 dB re 20 μPa) with a duration of 8 s (rise/fall time 0.1 s). The acoustic stimuli were identical in the head- and the hand-pointing task.

2.2.1. Head-pointing task

The head-pointing task was identical to previous studies (for details, see Lewald, 2002; Lewald et al., 2000). The participant's head was fixed by a swivel-mounted stabilizing rest for the forehead, with an elastic headband attached to the rest and stretched around the occiput, so that the head could rotate freely in the azimuthal plane.

2.2.2. Hand-pointing task

The hand-pointing task was identical to previous studies (for details, see Lewald, 2004; Lewald, Wienemann, & Boroojerdi, 2004; Lewald et al., 2000). A hand-pointer was mounted in front of the participant. This swivel pointer consisted of a metal rod (2×2 cm^2 profile, 50 cm long) that the participant could rotate in both the azimuthal and elevational planes. One end of the rod was linked to the perpendicular axes of two potentiometers that were mounted on the front edge of the participant's chair, with the pivot of the rod located at the level of the abdomen. This apparatus recorded the azimuthal and elevational angles of the pointer. However, in the present study only the pointer azimuth was analyzed as sound elevation was kept constant.

Author's personal copy

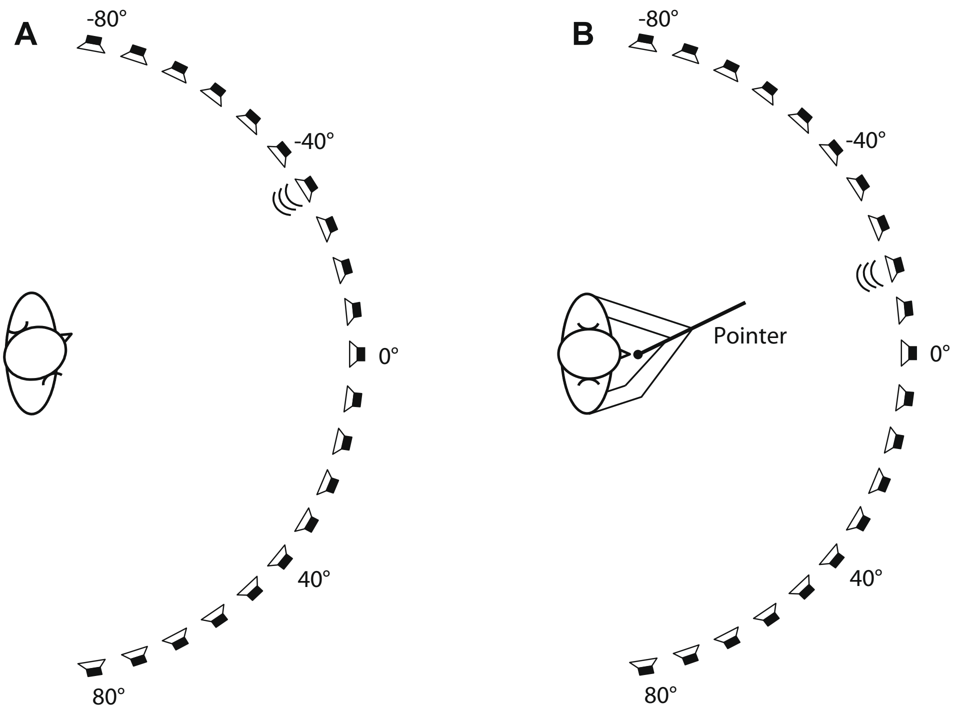


Fig. 1. Experimental set-up for the two tasks. (A) In the head-pointing task, the subject orientated the head such that the subjective median plane of the head was perceived as spatially coinciding with the sound azimuth. (B) In the hand-pointing task, the subject directed a swivel pointer with both hands toward the perceived sound azimuth, with the head fixed in a straight-ahead orientation.

2.3. Procedure

2.3.1. Head-pointing task

Each trial began with the onset of the sound stimulus from one of the 21 loudspeakers. The stimulus position changed in a quasi-random order. The participant was instructed to direct the head toward the perceived stimulus location and "face" it so that an imagined prolongation of the nose pointed as precisely as possible at the stimulus. When this position was reached, the participant pressed a key and the azimuthal head position was measured by a potentiometer linked to the axis of the rotating head restraint.

2.3.2. Hand-pointing task

During the 8 s period of stimulus presentation, participants had to adjust the pointer such that it pointed to the source of the sound as accurately as possible. After completion of the adjustment, a key had to be pressed that was mounted on the upper side of the rod. The position of the pointer at the moment of key-pressing was recorded automatically by the computer program. Two seconds after stimulus offset the next trial began. Participants were explicitly instructed to hold the pointer with both hands and to keep the hand position constant during the test. Compliance with the instruction was monitored on-line by the experimenter via an infrared video camera.

With both tasks, participants were instructed to press the key before the sound stimulus ceased, but were explicitly informed that the accuracy of pointing, not speed, was important for the experiment, and that it was thus not necessary to press the key as fast as possible. If the key was not pressed during the stimulus presentation, the trial was repeated automatically at the end of the session. Two seconds after stimulus offset the next trial began. Participants completed at least 20 practice trials before testing. Each task comprised 210 trials plus repetitions. After completion of 105 trials, the participant was allowed to rest for about 5 min. Thus, the overall duration of an experimental session was about 2 h.

2.4. Data analysis

Data analyses were identical for both tasks. At first, regression lines were fitted to the pointing azimuths for each participant, either across all targets presented, or separately across targets presented in the left (from −80° to −8° azimuth) and right hemispace (from 8° to 80° azimuth). The resulting slope of the regression line (a) was taken as a measure of the mean accuracy of the participant's pointing responses. Deviations of a from the ideal value of one indicate underestimation ($a < 1$) or overestimation ($a > 1$) of sound eccentricity as a function of target azimuth. The coefficient of determination (R^2), indicating the goodness of the fit of the pointing positions to the regression line, was taken as a measure of the participant's precision in pointing. Finally, the y-axis intercept point (y_0) was used as a measure of the mean constant error in pointing to either the left ($y_0 < 0$) or right ($y_0 > 0$).

Furthermore, for each sound-localization task, two different measures of error were calculated from the participant's individual pointing azimuths: (1) the mean of the signed deviations in azimuth from the target (*constant error*) and (2) the standard deviation of the pointing azimuths (*variable error*). Analyses of these measures were conducted for the left (−80° to −8°) and right hemispace (8–80°) separately.

3. Results

3.1. Bilateral asymmetry of sound localization

The mean pointing positions, plotted as a function of sound azimuth, are shown in Fig. 2 for LHs and RHs. In both experiments taken together, linear regression analyses for individual responses over the full range of target positions (from −80° to 80° azimuth) indicated generally high precision in pointing for each participant tested ($R^2 \geqslant 0.954$, $p < 0.0001$).

Author's personal copy

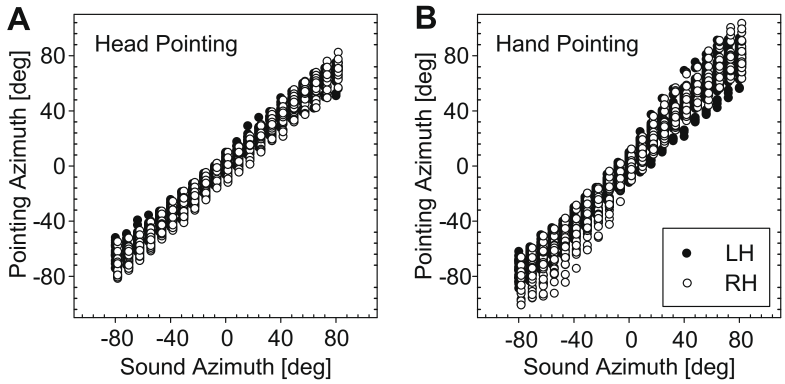


Fig. 2. Mean pointing responses of individual subjects. Final pointing directions in the azimuthal plane obtained with head (A) and hand-pointing (B) in left- (LHs) and right-handers (RHs) are plotted as a function of target azimuth.

Participants were more precise with head-pointing (mean $R^2 = 0.988$, SEM = 0.001) than with hand-pointing (mean $R^2 = 0.979$, SEM = 0.001; $t_{(52)} = 8.92$, $p < 0.0001$; paired *t*-test). The mean slope of the regression line differed substantially between pointing conditions ($t_{(52)} = 11.07$, $p < 0.0001$; paired *t*-test). With head-pointing the slope was below the ideal value of one ($a = 0.890$, SEM = 0.010), indicating systematic underestimation of sound eccentricity. This effect is well-known from previous studies (e.g., Lewald, 2002; Lewald & Ehrenstein, 1998a; Lewald, Karnath, & Ehrenstein, 1999; Perrott, Ambarsoom, & Tucker, 1987; Pierce, 1901) and has been related to the illusion of a generally biased space perception with head positions to the side (Aubert, 1888; Delage, 1886; Fischer, 1915; Fookson et al., 1994; Müller, 1923; Reinhold, 1914; for detailed discussion, see Lewald et al., 2000). With hand-pointing the slope was above one ($a = 1.092$, SEM = 0.017) indicating overestimation of eccentricity. This effect has also long been known (e.g., Matsumoto, 1897; Oldfield & Parker, 1984; Pierce, 1901; Preibisch-Effenberger, 1966; Wightman & Kistler, 1989) and has been related to physical factors such as directional properties of the external ears and interaural transfer functions (for detailed discussion, see Lewald & Ehrenstein, 1998b and Lewald et al., 2000). No differences between LHs and RHs were found with respect to R^2 and slope ($t_{(51)} \leqslant 1.44$, $p \geqslant 0.16$ in each case; unpaired *t*-test), thus indicating generally similar accuracy and precision. However, the linear regression analyses revealed different mean constant errors (y_0) for LHs and RHs, with biases opposite to the side of the dominant hand in the hand-pointing task (LH: $y_0 = 4.40°$, SEM = 0.70; RH: $y_0 = -1.98°$, SEM = 0.66; $t_{(51)} = 6.30$, $p < 0.0001$) as well as in the head-pointing task (LH: $y_0 = 1.86°$, SEM = 0.86; RH: $y_0 = -0.82°$, SEM = 0.77; $t_{(51)} = 2.25$, $p = 0.025$; unpaired *t*-test).

3.1.1. Constant error

The mean constant errors of LHs and RHs for all 21 target positions are shown in Fig. 3A and B. RHs perceived the location of the central sound to the left (hand: mean −1.44°, SEM = 0.92; head: mean −0.72°, SEM = 0.93), whereas LHs perceived it to the right (hand: mean 4.61°, SEM = 0.99; head: mean 2.75°, SEM = 1.10). This was confirmed by a 2 × 2 repeated-measures ANOVA for the central position with Handedness (LH, RH) as between-participants factor and Task (hand, head) as within-participants factor that revealed a significant main effect of handedness ($F_{(1,51)} = 15.62$; $p < 0.01$). No other main effects nor interactions were obtained (all $F_{(1,51)} < 2.65$, $p > 0.11$).

A 2 × 2 × 2 × 10 repeated-measures ANOVA with Handedness (LH, RH) as between-participants factor and Hemispace (left, right), Task (hand, head) and Eccentricity (from 8° to 80° to either side, central position analysed separately, see above) as within-participants factors was calculated. Overall, no significant difference between hand- and head-pointing was observed ($F_{(1,51)} = 0.86$; $p = 0.36$). As already evidenced by the linear regression analysis (see above), constant errors of RHs were, on average, to the left of those of LHs ($F_{(1,51)} = 25.76$; $p < 0.001$) with both head-pointing (Fig. 3A) and hand-pointing (Fig. 3B).

To investigate whether participants deviated significantly from veridical pointing, Bonferroni-corrected one-sample *t*-tests against a test score of zero were calculated for both RHs and LHs in both conditions. RHs showed a significant overall bias to the left of the actual sound locations in the hand-pointing condition (mean deviation −2.01°, SEM = 0.62; $t_{(32)} = -3.04$; $p < 0.01$), but not with head-pointing (mean deviation −0.82°, SEM = 0.74; $t_{(32)} = -1.08$; $p = 0.29$). LHs deviated to the right of the target positions in both hand-pointing (mean deviation 4.45°, SEM = 0.8; $t_{(19)} = 6.26$; $p < 0.001$) and head-pointing (mean deviation 2.13°, SEM = 0.95; $t_{(19)} = 2.39$; $p < 0.05$).

The deviation to the right in LHs compared to RHs was larger in the hand-pointing condition than in the head-pointing condition (cf. Fig. 3A and B) as indicated by the interaction Task × Handedness ($F_{(1,51)} = 8.21$; $p < 0.01$). Apart from the differences between handedness groups, the ANOVA revealed that the difference between constant errors in both tasks varied as a function of eccentricity as indicated by the interaction Task × Eccentricity ($F_{(9,459)} = 3.02$; $p < 0.05$). Specifically, participants deviated further rightwards in the hand-pointing task than in the head-pointing task. Eccentricity was underestimated in the head-pointing task and was overestimated in the hand-pointing task, that is, with head-pointing participants deviated to the right in left hemispace and to the left in right hemispace, whereas the opposite pattern was observed in hand-pointing in accordance with an interaction Task × Hemispace ($F_{(1,51)} = 131.02$; $p < 0.001$) and Task × Hemispace × Eccentricity ($F_{(9,459)} = 56.66$; $p < 0.001$). The difference between LHs and RHs decreased with increasing eccentricity as shown by an interaction Eccentricity × Handedness ($F_{(9,459)} = 2.86$; $p < 0.05$). The increasing deviation to the left in the right hemispace and the increasing deviation to the right in left hemispace (across both tasks) was reflected by an interaction Hemispace × Eccentricity ($F_{(9,459)} = 84.85$; $p < 0.001$). This effect was more pronounced in LHs than in RHs as revealed by the three-way interaction Hemispace × Eccentricity × Handedness ($F_{(9,459)} = 4.37$; $p < 0.01$). Although the difference between LHs and RHs was more numerically more pronounced in the left hemispace, the corresponding Hemispace × Handedness interaction only approached significance ($F_{(1,51)} = 2.93$; $p = 0.09$). No further main effects or interactions were obtained (all $F_{(1,51)} < 1.82$, $p > 0.14$).

3.1.2. Variable error

The mean variable errors of LHs and RHs are shown in Fig. 3C and D. As for the constant error, a 2 × 2 × 2 × 10 repeated-mea-

Author's personal copy

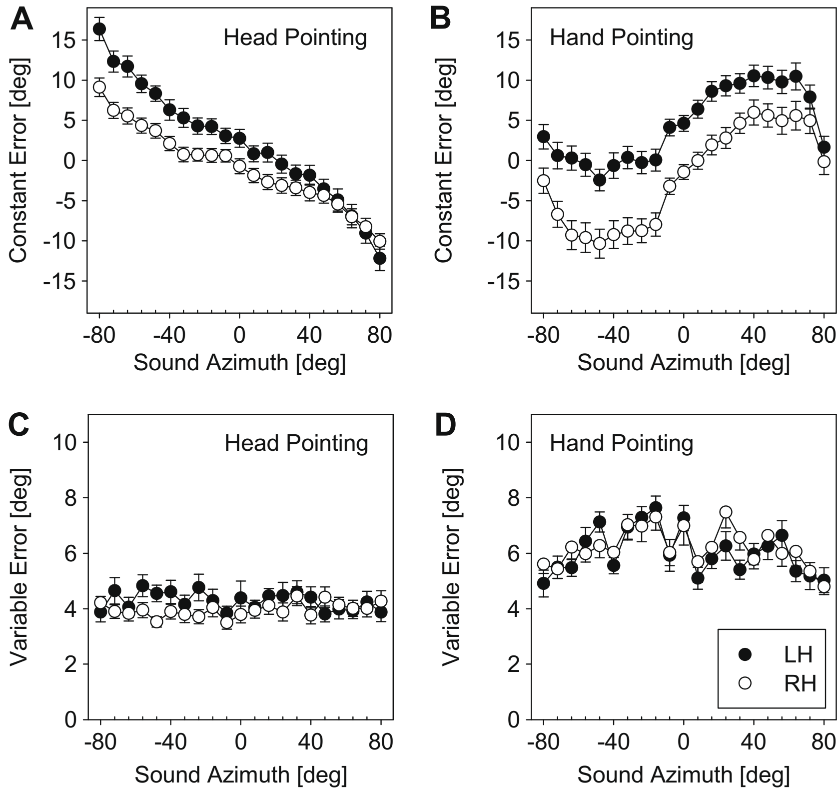


Fig. 3. Mean constant errors (A and B) and variable errors (C and D) derived from head (A and C) and hand-pointing responses (B and D) of left- (LHs) and right-handers (RHs).

sures ANOVA with the between-participants factor Handedness (LHs, RHs) and the within-participants factors Hemispace (left, right), Task (hand, head) and Eccentricity (from 8° to 80° to either side) was calculated for the variable error (Fig. 3C and D). RHs and LHs were equally precise ($F_{(1,51)} = 0.03$; $p = 0.86$), indicating, that the handedness effect observed for the constant error is not due to differences in precision between the two groups. Overall, participants were more precise in the head-pointing condition (mean variable error 4.12°, SEM = 0.18) than in the hand-pointing condition (mean variable error 6.08°, SEM = 0.20; $F_{(1,51)} = 131.98$; $p < 0.001$). This difference was more pronounced in the left (head-pointing: 4.10°, SEM = 0.17; hand-pointing: 6.28°, SEM = 0.22) than in the right hemispace (head-pointing: 4.14°, SEM = 0.20; hand-pointing: 5.88°, SEM = 0.21) as indicated by an interaction Task × Hemispace ($F_{(1,51)} = 6.10$; $p < 0.05$). Furthermore, precision was influenced by target eccentricity ($F_{(9,459)} = 8.44$; $p < 0.001$). Specifically, the variable error was lower at higher eccentricities. This difference was much more pronounced in the hand-pointing task than in the head-pointing task as revealed by an interaction Task × Eccentricity ($F_{(9,459)} = 6.45$; $p < 0.001$). This pronunciation in the hand-pointing task was stronger in right than left hemispace as indicated by a three-way interaction Task × Hemispace × Eccentricity ($F_{(9,459)} = 2.75$; $p < 0.05$). No further main effects or interactions were obtained (all $F_{(1,51)} < 2.63$, $p > 0.11$).

3.2. Relationship between lateral preference and sound lateralization

For each individual, lateral preference for hand, foot, eye, and ear were obtained from the questionnaire (see Section 2) and a laterality quotient (LQ) was calculated according to the method described by Oldfield (1971). The LQ's range was between −100 and 100, with positive values indicating a right-sided preference and negative values a left-sided preference. See Table 1 for mean handedness, footedness, eye and ear preference LQs for RHs and LHs. For the analyses described below LHs and RHs were pooled.

Table 1
Mean handedness, footedness, eye and ear preference LQs for RHs and LHs. Standard errors are given in parentheses.

	Handedness	Footedness	Eye preference	Ear preference
RH	96.21 (1.58)	72.88 (6.10)	53.79 (11.82)	34.19 (11.61)
LH	−91.62 (4.74)	−33.77 (11.16)	−46.67 (13.70)	−40.00 (12.88)

To determine the relation of lateral preferences and the direction of the deviation from the target, multiple linear regressions were carried out for the head- and hand-pointing condition with the constant error in the left and right hemispace acting as dependent variable and the four different LQs acting as predictors. The results of the multiple regressions are summarized in Table 2.

For hand-pointing, multiple regression revealed a significant model for the left hemispace ($F_{(4,48)} = 5.73$; $p < 0.001$) accounting for 32% of the variance. Footedness contributed significantly to the regressions equation ($\beta = -0.45$; $p < 0.05$). For the right hemispace, the regression model was not significant ($F_{(4,48)} = 2.37$; $p = 0.07$). In line with the hand-pointing condition, regression revealed a significant model for the left hemispace in the head-pointing condition, accounting for 27% of the variance ($F_{(4,48)} = 4.42$; $p < 0.01$). However, none of the preference measures approached significance (all $p > 0.08$). Again, no significant model emerged for the right hemispace ($F_{(4,48)} = 0.71$; $p = 0.59$).

The results of the multiple regressions for the variable error are summarized in Table 3. The regression revealed that lateral preferences did not predict the variable error in sound localization. No regression model for both left and right hemispaces approached significance (all $F_{(4,48)} < 1.70$, $p > 0.16$).

Author's personal copy

Table 2
Multiple linear regressions (standardized β coefficients) for hand-, foot-, eye- and ear-LQ as predictors of the constant error. Determination coefficients (R^2) and significances (p) indicate the goodness-of-fit for the regression model.

Task	Area	Hand	Foot	Eye	Ear	R^2	p
Hand-pointing	Left	−0.30	−0.45*	0.14	0.23	0.32	<0.001
	Right	−0.40	0.24	−0.01	−0.25	0.17	ns
Head-pointing	Left	−0.20	−0.13	0.05	−0.31	0.27	<0.01
	Right	0.00	−0.29	0.09	0.12	0.06	ns

Note: ns (non-significant).
* $p < 0.05$.

Table 3
Multiple linear regressions (standardized β coefficients) for hand-, foot-, eye- and ear-LQ as predictors of the variable error. Determination coefficients (R^2) and significances (p) indicate the goodness-of-fit for the regression model.

Task	Area	Hand	Foot	Eye	Ear	R^2	p
Hand-pointing	Left	−0.14	0.44	−0.30	−0.08	0.12	ns
	Right	−0.12	0.44	−0.02	−0.21	0.10	ns
Head-pointing	Left	−0.26	0.22	−0.27	0.01	0.11	ns
	Right	−0.28	−0.04	0.03	0.12	0.07	ns

Note: ns (non-significant).

4. Discussion

The present study revealed clear differences in sound localization between LHs and RHs. Both groups showed a constant error in sound localization that was to the side contralateral to the preferred hand. As this effect of handedness on constant error occurred in the hand-pointing task and in the head-pointing task it is independent of the frame of reference (head or trunk) used for auditory localization. Moreover, since the effect was observed in the head-pointing task, it can be assumed that it is caused by a central asymmetry that is related to handedness, rather than asymmetries in peripheral processes such as manual skills. Also, since differences in the variable error between LHs und RHs were not found, precision in sound localization may not be a factor in this respect.

Moreover, regression analyses revealed sound localization not only to be related to absolute handedness, but also to the degree of lateral preference in general. Taken together, handedness, footedness, eye preference and ear preference significantly predicted the constant sound localization error in the left hemispace, but not in the right hemispace. This may reflect a right hemisphere dominance for auditory spatial performance, as has been previously reported for RHs in different visuospatial tasks (Vogel et al., 2003). Again, these relations were independent of possible peripheral asymmetries that might be related to preferential hand use since they were found in both pointing conditions. Also, there was no relation to localization precision as lateral preference measures were independent of the variable error.

In hand-pointing, footedness was a more reliable predictor of the direction of the bias in sound localization than was handedness or eye and ear preference. This greater predictive value of footedness is in accordance with findings on other functional domains, such as language lateralization (Elias & Bryden, 1998; Searleman, 1980). With head-pointing, the combination of all four lateral preferences predicted the direction of the bias and R^2 was slightly smaller than in the hand-pointing task. Since the head-neck motor system may not be as lateralized as the hand motor systems, correlations between head-pointing and functional asymmetries might be lower than between hand-pointing and functional asymmetries.

At first glance, the results of the present study might be in opposition to those of Burke et al. (1994) who did not find any differences between LHs and RHs in sound localization. However, methodological issues may account for this inconsistency. As already mentioned above, participants in the study of Burke et al. (1994) verbally reported the absolute position of the speaker to the experimenter. Such a sound-source identification task does not allow assessing more subtle deviations in localization from the actual sound position and the differentiation between constant and variable errors. Recently, Dufour et al. (2007) reported a significant difference between LHs and RHs in an auditory midline task. In contrast to the present results, these authors obtained a general leftward bias of the auditory median plane for interaural level differences that was stronger in LHs than in RHs. This discrepancy to our results could be explained by the fact that the present experiment investigated localization of real sound sources in free-field space and perception of eccentric sound locations and thus on genuine asymmetries in spatial performance.

In the present study, RHs showed a leftward bias in the hand-pointing task, while a bias to the right was found in LHs with both hand- and head-pointing. This partially parallels findings in the visual modality. Although a leftward bias was typically observed in visual line bisection of both RHs and LHs, the deviation of RHs was found to be stronger than that of LHs, that is, bisection marks of LHs were to the right of those in RHs (Jewell & McCourt, 2000).

The leftward bias in visual line bisection has been explained by means of the activation–orientation model of Kinsbourne (1970). According to this model, a right hemisphere dominance for visuospatial tasks biases attention to the left visual hemispace. However, a right-hemispheric dominance for visuospatial tasks was mainly observed in RHs, whereas LHs may show a less clear-cut hemispheric functional cerebral asymmetry (Vogel et al., 2003). On the one hand, the present data suggest that this model could, at least for the RHs, be applicable to the auditory effects found here, by assuming a right-hemisphere superiority for auditory spatial tasks. On the other hand, our finding of a bias to the right in LHs points towards an even inverted functional cerebral asymmetry in this group, that is, a left-hemisphere superiority, rather than a merely reduced right-hemisphere superiority, as was assumed for the visual modality (Brodie & Dunn, 2005; Jewell & McCourt, 2000).

We have no clear-cut explanation for this inversion of functional asymmetry between RHs and LHs. Most previous studies observed weaker asymmetries in LHs, whereas an inversion was rarely found. However, there is at least some evidence for such an inversion in the visual modality. A large-scale meta-analysis (Vogel et al., 2003) revealed a right-hemispheric advantage in visuospatial abilities in RHs and no asymmetry in LHs on population level. However, as Vogel et al. (2003) pointed out, many of the studies included in their analysis evenly distributed LHs and RHs, which does not mimic the true population where only about ten percent are left-handed. When they re-analysed the data taking the true population distribution of LHs and RHs into account, they found a left-hemispheric advantage in LHs, as was obtained in the present study.

We cannot exclude the possibility that factors other than cerebral asymmetry played a role in the emergence of the observed behavioral asymmetry pattern. For example, one might assume that a shift in subjective median plane tied to handedness might have caused the observed effects. RHs might have an enlarged rep-

Author's personal copy

resentation of their right hemispace, such that their subjective median plane is shifted leftwards. In a recent study (Lewald, Peters, Tegenthoff, & Hausmann, 2009), the position of auditory straight ahead, measured in a control group of healthy RHs, was found to deviate only insignificantly from the physical straight-ahead position to the left. Most important is, however, that the assumption of a leftward bias of the subjective median plane would rather predict the opposite of what was found here. A potential leftward bias of the subjective median plane of the head should necessarily result in a constant error to the right when the head median plane is adjusted to the sound source, which is in opposition to the present results for RHs in the head-pointing task. Similarly, if one assumes that the subjective straight ahead of RHs is shifted to the left, one would expect that a sound source located in the physical median plane (i.e., at 0°) is mislocalized to the right rather than to the left, as was measured here.

Also, when comparing the results from auditory and visual experiments, it has to be taken into account that the auditory and visual systems substantially differ in their bilateral organization. Visual stimuli presented in one hemispace are processed exclusively in the contralateral primary visual cortex. In contrast, contralaterality in the auditory system is less pronounced, with only small differences between activations in unilateral auditory cortex evoked by ipsilaterally and contralaterally presented sounds (Woldorff et al., 1999). Moreover, although sound localization and line bisection are both spatial tasks that require a localization of spatial position, there are critical differences between the tasks, namely in the participants' responses. With line bisection, a subject indicates the midpoint of a line, that is, a location within a given visual frame of reference. With the sound-localization tasks used here, a subject has to indicate a spatial location in the absence of any external reference. Thus, any comparisons between the results of these two approaches must be drawn with caution.

For physical reasons, it seems rather difficult or even impossible to design an auditory experiment that is directly analogous to visual line bisection. In principle, one might conceive a task in which the participant has to point towards the center of two simultaneously active sound sources separated by a variable distance. However, the resulting auditory percepts will not appear as clearly separated as would be adequate to perform such a task (for further details, see Blauert, 1997). In future experiments, it would, therefore, be useful to test the same participants with visual and auditory tasks, in order to support the assumption that supramodal neural processes are involved in lateralization of space perception. This assumption is also supported by the fact that the present results for RHs are in alignment with the observation of a leftward bias in tactile spatial performance (Sampaio & Chokron, 1992). Similar to the visual modality, the tactile bias is also affected by handedness. When blindfolded subjects were asked to estimate the midpoint of a horizontal wooden stick without visual feedback, LHs did not show any hand difference, whereas RHs exhibited a larger leftward deviation from the midpoint with the right hand. Further evidence for a supramodal lateral bias comes from two studies in partial commissurotomy patients with splenial lesions. Pollmann, Maertens, and von Cramon (2004) and Pollmann, Maertens, von Cramon, Lepsien, and Hugdahl (2002) found parallel lateralization effects in the auditory and visual domains in these patients.

Up to now, there are no neuroimaging studies that have compared LHs and RHs using sound-localization tasks and previous neuroimaging studies that aimed to reveal the substrates of spatial hearing did not consider hand preference and other lateral preferences as a relevant factor. However, the majority of imaging studies (in which RHs may have been in vast majority) suggests a general right-hemisphere superiority for the processing of auditory location (Fujiki et al., 2002; Griffiths et al., 1998; Kaiser et al., 2000; Palomäki et al., 2000).

There is also evidence from studies with brain-damaged patients suggesting that severe deficits in auditory spatial abilities are observed more frequently following right-hemispheric lesions, although they also occur in individual patients with left-hemispheric lesions (Bisiach, Cornacchia, Sterzi, & Vallar, 1984; Hausmann et al., 2005; Ruff, Hersh, & Pribram, 1981; Zatorre & Penhune, 2001; Zimmer, Lewald, & Karnath, 2003). Assuming contralaterality of auditory processing, the result may be an imbalance in processing of sound location in favor of the left and right hemispace in RHs and LHs, respectively. This is in accordance with the leftward bias in RHs (rightward bias in LHs) shown in the present study.

In conclusion, the present study is the first that directly demonstrated opposing biases of LHs and RHs in free-field sound localization. Despite differences in neural processing of auditory and visual spatial information, our data argue in favor of similarities, rather than differences, in the effects of lateral preference on auditory and visual spatial perception. This suggests that multimodal or supramodal neural processes are involved in lateralization of space perception.

References

Aubert, H. (1888). *Physiologische Studien über die Orientierung*. Tübingen: Laupp.

Bisiach, E., Cornacchia, L., Sterzi, R., & Vallar, G. (1984). Disorders of perceived auditory lateralization after lesions of the right hemisphere. *Brain, 107*, 37–52.

Blauert, J. (1997). *Spatial hearing: The psychophysics of human sound localization*. Cambridge: MIT Press.

Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: Effects of hemispace on a tactile line bisection task. *Neuropsychologia, 18*, 491–498.

Brodie, E. B., & Dunn, E. M. (2005). Visual line bisection in sinistrals and dextrals as a function of hemispace, hand, and scan direction. *Brain and Cognition, 58*, 149–156.

Burke, K. B., Letsos, A., & Butler, R. A. (1994). Asymmetric performances in binaural localization of sound in space. *Neuropsychologia, 32*, 1409–1417.

Corballis, M. C. (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral Brain Sciences, 26*, 199–208.

Delage, Y. (1886). Études expérimentales sur les illusions statiques et dynamiques de direction pour servir à déterminer les fonctions des canaux demi-circulaires de l'orneille interne. *Archives de Zoologie expérimentale et générale, 2me série, 4*, 535–624.

Dufour, A., Touzalin, P., & Candas, V. (2007). Rightward shift of the auditory subjective straight ahead in right- and left-handed subjects. *Neuropsychologia, 45*, 447–453.

Elias, L., & Bryden, M. P. (1998). Footedness is a better indicator of language lateralisation than handedness. *Laterality, 3*, 41–51.

Fischer, B. (1915). Der Einfluß der Blickrichtung und Änderung der Kopfstellung (Halsreflex) auf den Bárányschen Zeigeversuch. *Jahrbücher für Psychiatrie und Neurologie, 35*, 155–158.

Fookson, O., Smetanin, B., Berkinblit, M., Adamovich, S., Feldman, G., & Poizner, H. (1994). Azimuth errors in pointing to remembered targets under extreme head rotations. *NeuroReport, 5*, 885–888.

Fujiki, N., Riederer, K. A. J., Jousmäki, V., Mäkelä, J. P., & Hari, R. (2002). Human cortical representation of virtual auditory space: Differences between sound azimuth and elevation. *European Journal of Neuroscience, 16*, 2207–2213.

Griffiths, T. D., Rees, G., Rees, A., Green, G. G. R., Witton, C., Rowe, D., et al. (1998). Right parietal cortex is involved in the perception of sound movement in humans. *Nature Neuroscience, 1*, 74–79.

Hausmann, M., Corballis, M. C., Fabri, M., Paggi, A., & Lewald, J. (2005). Sound lateralization in subjects with callosotomy, callosal agenesis, or hemispherectomy. *Cognitive Brain Research, 25*, 537–546.

Hausmann, M., Waldie, K. E., Allison, S. D., & Corballis, M. C. (2003). Line bisection following hemispherectomy. *Neuropsychologia, 41*, 1523–1530.

Isaacs, K. L., Barr, W. B., Nelson, P. K., & Devinsky, O. (2006). Degree of handedness and cerebral dominance. *Neurology, 66*, 1855–1858.

Jenkins, W. M., & Masterton, R. B. (1982). Sound localization: Effects of unilateral lesions in central auditory system. *Journal of Neurophysiology, 47*, 897–1016.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia, 38*, 93–110.

Kaiser, J., Lutzenberger, W., Preissl, H., Ackermann, H., & Birbaumer, N. (2000). Right-hemisphere dominance for the processing of sound-source lateralization. *Journal of Neuroscience, 20*, 6631–6639.

Khalfa, S., Veuillet, E., & Collet, L. (1998). Influence of handedness on peripheral auditory asymmetry. *European Journal of Neuroscience, 10*, 2731–2737.

Kinsbourne, M. (1970). The cerebral basis of lateral asymmetries in attention. *Acta Psychologia, 33*, 193–201.

Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain, 123*, 2512–2518.

Author's personal copy

Lewald, J. (2002). Opposing effects of head position on sound localization in blind and sighted human subjects. *European Journal of Neuroscience, 15*, 1219–1224.
Lewald, J. (2004). Gender-specific hemispheric asymmetry in auditory space perception. *Cognitive Brain Research, 19*, 92–99.
Lewald, J., Dörrscheidt, G. J., & Ehrenstein, W. H. (2000). Sound localization with eccentric head position. *Behavioral Brain Research, 108*, 105–125.
Lewald, J., & Ehrenstein, W. H. (1998a). Influence of head-to-trunk position on sound lateralization. *Experimental Brain Research, 121*, 230–238.
Lewald, J., & Ehrenstein, W. H. (1998b). Auditory-visual spatial integration: A new psychophysical approach using laser pointing to acoustic targets. *Journal of the Acoustical Society of America, 104*, 1586–1597.
Lewald, J., Karnath, H.-. O., & Ehrenstein, W. H. (1999). Neck-proprioceptive influence on auditory lateralization. *Experimental Brain Research, 125*, 389–396.
Lewald, J., Peters, S., Tegenthoff, M., & Hausmann, M. (2009). Dissociation of auditory and visual straight ahead in hemianopia. *Brain Research, 1287*, 111–117.
Lewald, J., Wienemann, M., & Boroojerdi, B. (2004). Shift in sound localization induced by rTMS of the posterior parietal lobe. *Neuropsychologia, 42*, 1598–1607.
Matsumoto, M. (1897). Researches on acoustic space. *Yale Psychology Laboratory Studies, 5*, 1–75.
McManus, I. C., Porac, C., Bryden, M. P., & Boucher, R. (1999). Eye-dominance, writing hand, and throwing hand. *Laterality, 4*, 173–192.
Müller, O. (1923). Über den Einfluß der Kopf- und Augenstellung auf die Lokalisationsbewegung des Armes. *Deutsche Zeitschrift für Nervenheilkunde, 78*, 325–346.
Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia, 9*, 97–113.
Oldfield, S. R., & Parker, S. P. A. (1984). Acuity of sound localisation: A topography of auditory space. I. Normal hearing conditions. *Perception, 13*, 581–600.
Palomäki, K., Alku, P., Mäkinen, V., May, P., & Tiitinen, H. (2000). Sound localization in the human brain: Neuromagnetic observations. *Neuroreport, 11*, 1535–1538.
Perrott, D. R., Ambarsoom, H., & Tucker, J. (1987). Changes in head position as a measure of auditory localization performance: Auditory psychomotor coordination under monaural and binaural listening conditions. *Journal of the Acoustical Society of America, 82*, 1637–1645.
Pierce, A. H. (1901). *Studies in auditory and visual space perception*. New York: Longmans.
Pollmann, S., Maertens, M., & von Cramon, D. Y. (2004). Splenial lesions lead to supramodal target detection deficits. *Neuropsychology, 18*, 710–718.
Pollmann, S., Maertens, M., von Cramon, D. Y., Lepsien, J., & Hugdahl, K. (2002). Dichotic listening in patients with splenial and nonsplenial callosal lesions. *Neuropsychology, 16*, 56–64.
Preibisch-Effenberger, R. (1966). *Die Schallokalisationsfähigkeit des Menschen und ihre audiometrische Verwendbarkeit zur klinischen Diagnostik. Habilitationsschrift*. Dresden: Medizinische Akademie.
Reinhold, J. (1914). Über die Abhängigkeit der Baranyschen Zeigereaktion von der Kopfstellung. *Deutsche Zeitschrift für Nervenheilkunde, 78*, 158.
Reiss, M., Tymnik, G., Kögler, P., Kögler, W., & Reiss, G. (1999). Laterality of hand, foot, eye and ear in twins. *Laterality, 4*, 287–297.
Ruff, R. M., Hersh, N. A., & Pribram, K. H. (1981). Auditory spatial deficits in the personal and extrapersonal frames of reference due to cortical lesions. *Neuropsychologia, 19*, 435–443.
Sampaio, E., & Chokron, S. (1992). Pseudoneglect and reversed pseudoneglect amoung left-handers and right-hander. *Neuropsychologia, 30*, 797–805.
Searleman, A. (1980). Subject variables and cerebral organization for language. *Cortex, 16*, 239–254.
Siefer, A., Ehrenstein, W. H., Arnold-Schulz-Gahmen, B. E., Sökeland, J., & Luttmann, A. (2003). Population statistics and association analysis of sensorimotor lateral preferences and its relevance for various fields of professional activity. *Zentralblatt für Arbeitsmedizin, Arbeitsschutz und Ergonomie, 53*, 346–353.
Strauss, E. (1986). Hand, foot, eye and ear preferences and performance on a dichotic listening test. *Cortex, 22*, 475–482.
Vogel, J. J., Bowers, C. A., & Vogel, D. S. (2003). Cerebral lateralization of spatial abilities: A meta-analysis. *Brain and Cognition, 52*, 197–204.
Wightman, F. L., & Kistler, D. J. (1989). Headphone simulation of free-field listening. II: Psychophysical validation. *Journal of the Acoustical Society of America, 85*, 868–878.
Woldorff, M. G., Tempelmann, C., Fell, J., Tegeler, C., Gaschler-Markefski, B., Hinrichs, H., et al. (1999). Lateralized Auditory Spatial Perception and the contralaterality of cortical processing as studied with functional magnetic resonance imaging and magnetoencephalography. *Human Brain Mapping, 7*, 49–66.
Zatorre, R. J., & Penhune, V. B. (2001). Spatial localization after excision of human auditory cortex. *Journal of Neuroscience, 21*, 6321–6328.
Zimmer, U., Lewald, J., & Karnath, H.-O. (2003). Disturbed sound lateralization in patients with spatial neglect. *Journal of Cognitive Neuroscience, 15*, 694–703.