Vestibular Influence on Human Auditory Space Perception

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Lewald, Jörg and Hans-Otto Karnath. Vestibular influence on human auditory space perception. J Neurophysiol 84: 1107–1111, 2000. We investigated the effect of vestibular stimulation on the lateralization of dichotic sound by cold-water irrigation of the external auditory canal in human subjects. Subjects adjusted the interaural level difference (ILD) by varying the ILD by adjusting a potentiometer. The results indicate the involvement of vestibular afferent information on the perception of sound location during movements of the head and/or the whole body. We thus hypothesize that vestibular information is used by central-nervous mechanisms generating a world-centered representation of auditory space.

INTRODUCTION

Auditory localization is based mainly on the evaluation of interaural differences in sound level and time of arrival. Although these directional cues change with all movements of the head, the relative to the source of the sound, the auditory environment is generally perceived as remaining stable, even if additional visual information is not available (Lewald et al. 2000). This phenomenon of perceptual stability implies the neural integration of the spatial information provided to the auditory periphery and of information about the position of the head. One source of such head-position information is proprioception by the muscle spindles of the neck (Lewald et al. 1999), which is, however, restricted to head orientation with respect to the trunk. To take account of movements of the whole body, it must be complemented by information on head position in space, which can be derived from vestibular inputs and may be used for the neural generation of a world-centered coding of auditory space as has been hypothesized for auditory neurons of the hippocampus (Tamura et al. 1990) and multimodal neurons of the posterior parietal cortex (for review, see Andersen et al. 1993).

The preceding neurophysiological findings suggest an influence of vestibular afferent information on the perception of sound location, an issue addressed by few psychophysical studies so far. By using whole-body rotation of subjects as the vestibular stimulus, Münsterberg and Pierce (1894) and Clark and Graybiel (1949), found systematic shifts in free-field sound localization (with closed eyes) that were opposite to the direction of rotation during rotatory movement or in the direction of the former rotation immediately after terminating the movement. However, as noted by the authors, those results may reflect merely kinesthetic illusions of body rotation that usually accompany vestibular stimulation (Clark and Graybiel 1949; Münsterberg and Pierce 1894; for review, see Lackner 1978). Thus no conclusions can be drawn from those findings on any direct vestibular influences on sound localization.

The present study aims to tackle this problem by employing methods that were specifically designed to investigate such vestibular-auditory interactions in isolation from other phenomena. We used cold-water irrigation of the external auditory canal (Bárány 1906), which provides a strong and long-lasting stimulus to vestibular afferents and avoids side effects due to rotatory movements of the subjects. Further, auditory stimuli were presented via headphones to exclude effects of involuntary head movements on sound localization. Finally, a task of visual fixation was applied which is known to suppress both the kinesthetic illusion of body rotation (Münsterberg and Pierce 1894) and the nystagmus evoked by vestibular stimulation (cf. Thurlow and Kerr 1970). The audio-vestibular illusion, demonstrated here for the first time by using these methods, may reflect the operation of neural mechanisms that use the vestibular afferent input to enable a stable perception of auditory space during motion.

METHODS

Main experiment

Thirteen volunteers (7 female, 6 male; mean age 28 yr, range 18–49) participated in the main experiment. None had any known hearing deficiencies, and all were naive with respect to the purpose of the experiments. In a dark and sound-attenuated room, subjects sat on a chair with the head fixed by a chin and forehead rest. The visual fixation target was a dim light-emitting diode, which remained on always, mounted straight ahead of the subject at eye level. The acoustic stimulus consisted of continuous dichotic band-pass-filtered noise (1.5–4 kHz; 70 dB re 20 μPa), presented to the subject via headphones (Sennheiser HD250) and was perceived as an intracranial sound image between the two ears (Blauert 1997). The subject could vary the interaural level difference (ILD) by adjusting a potentiometer.

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ter, thus shifting the sound image toward the left or right (for further details, see Lewald and Ehrenstein 1996).

The psychophysical task was the same in all test conditions employed. The acoustic stimulus was presented for 12 s. Within this period, the subject adjusted the potentiometer such that the sound image was perceived in the median plane of the head, and then pressed a key. The ILD at the moment of key pressing was recorded automatically. Two seconds after sound offset, the next trial began. Each test condition comprised 20 trials (280 s). Initial ILDs were randomly varied between trials.

Prior to data collection, each subject conducted 20 practice trials followed by three experimental test conditions (Fig. 1). First, sound lateralization was tested without additional stimulation. Next, 30 ml of water at body temperature (37°C) was applied to either the subject’s left or right external auditory canal for 1 min. During application, the subject sat upright on the chair with the head tilted 60° backward. Immediately after irrigation, the subject dried the ear canal with cotton swabs and the lateralization test was started. These measurements served as the control condition to cancel any nonspecific effects of water irrigation on hearing. Finally, vestibular stimulation was applied by irrigation of the same external auditory canal in the same manner as in condition 2, but now by using 30 ml of iced water. (Vestibular stimulation with iced water induces a caloric nystagmus with a fast phase to the side opposite of stimulation, a slow phase to the stimulated side, and a sensation of rotation.) Subsequently, eye movements were observed using Frenzel glasses (magnification glasses for observing eye position and suppressing eye fixation), and subjects were asked to report dizziness felt, whether weak, strong, or none at all. This examination allowed us to differentiate between two groups of subjects: those with a brisk nystagmus and subjectively strong dizziness (group 1, n = 8) and those with only weak nystagmus and dizziness (group 2, n = 5).

Control experiment

To exclude the possibility that cold-water irrigation affects not only vestibular but also auditory afferent information, we measured the differences in monaural loudness perception between the two ears in an additional control experiment, conducted with six of the group 1 subjects on a different day. The three experimental conditions were as described in the preceding text. Each trial began with the presentation of the reference stimulus (with a constant sound-pressure level of 70 dB) to the ear opposite to the side of vestibular stimulation (duration, 0.5 s; rise and fall time, 20 ms; all other parameters as in the preceding text). After a 0.5-s period of silence, the test stimulus was presented to the other ear. The test stimulus differed from the reference stimulus only in its level, which was varied between trials, following a quasi-random order over a range from 60 to 80 dB, in 2-dB steps. The subject pressed a “left” or “right” key according to whether the left or the right of the two successive stimuli was perceived to be louder. The next trial began 1.5 s after the sound offset. Each experimental condition was composed of 110 trials (5330 s). The subject’s judgments were determined as a function of the level difference between the two stimuli for each condition, and averages of 22 trials were computed every 66 s. The resulting data were fitted to the sigmoid function: \( F(\Delta L) [\%] = 100(1 + e^{-(\Delta L - \Delta L_{50})/2}) \), where \( F \) is the frequency of the judgement: “test stimulus louder” (given as percentage); \( \Delta L \) is the level difference between the two stimuli (positive

![FIG. 1. Effect of caloric stimulation on adjustments of the interaural level difference (ILD) to the median plane of the head in 3 exemplary subjects of group 1 (A–C). Lateralization was tested over periods of 280 s without additional stimulation (left); after irrigation with water at 37°C (middle left); and after vestibular stimulation with iced water (middle right). “Normalization” was made by calculating the difference between data of the 2 conditions with water application (right). Positive ILD values indicate higher level at the ear with caloric vestibular stimulation; negative values higher level on the nonstimulated side.](http://jn.physiology.org/doi/10.1152/jn.00000.2017)
values indicate a higher level at the side of vestibular stimulation); ∆L50% is that ∆L where F is 50% (i.e., the point of subjective equality); e the base of the natural logarithm. The fit was significant for each individual analysis ($R^2 \geq 0.8, P < 0.0001$). In all subjects tested, ice-water application induced a brisk nystagmus and subjectively strong dizziness as in the main experiment.

**RESULTS**

**Main experiment**

For all group 1 subjects, the comparison of data obtained after irrigation with water at 37°C and with iced water indicated that vestibular stimulation induced a clear tendency of ILD adjustments to be shifted toward the side of stimulation, i.e., to achieve a centered position of the sound image, the sound level was amplified at the cooled ear and was attenuated at the other (Fig. 1). ILD adjustments averaged over the first four trials (=56 s) were, with respect to the control condition (37°C irrigation), significantly shifted toward the side of caloric stimulation (Fisher randomization test for matched pairs, $P = 0.008$), by a mean of 5.7 ± 1.2 (SE) dB (Fig. 2A). This implies that ice-water application induced a shift of the sound image toward the nonirrigated side so that it had to be brought back to the median plane by compensatory ILD adjustments (Fig. 2B). The effect decreased over time, with slopes which differed for each subject (see examples in Fig. 1, A–C). Except for one subject, equivalent shifts in ILD adjustments were also observed in group 2 (1.6 ± 1.1-dB shift averaged over the 1st 4 trials) but with a significantly weaker effect compared with group 1 (Fisher-Pitman randomization test for 2 independent samples, $P = 0.009$; Fig. 2A).

Figure 2C shows the averaged time courses of the effects for both group 1 and group 2 subjects. The latter group exhibits a slight systematic deviation by 1.6 ± 1.6 dB, which remained almost constant over the whole 280-s test period. In contrast, group 1 subjects showed a considerably larger mean shift of 7.3 ± 1.4 dB in the first trial immediately after caloric stimulation, which decreased approximately exponentially to a mean value of 2.5 dB at the end of the lateralization test.

**Control experiment**

In group 1 subjects, the mean point of subjective equality (∆L50%) for two monaural sound stimuli, presented successively to the left and right ear, was shifted only slightly (1.2 ± 0.8 dB) toward the side of cooling, within the first 66 s after vestibular stimulation (Fig. 3A) and remained almost constant over the whole 330-s test period (Fig. 3B). This result contrasts significantly with the mean ILD shift of 7.1 ± 0.9 dB found in the main experiment within the first 56 s for the same subjects (Fisher randomization test for matched pairs, $P = 0.03$) but strongly resembles that of group 2 (cf. Fig. 2C).

**DISCUSSION**

It is generally agreed that vestibular stimulation by cooling leads to a gradient of the specific gravity of the endolymph in the horizontal semicircular canal, resulting in a thermal current...
that affects the cupula (Bárány 1906; Bergstedt 1961). The direction of this long-lasting current is equivalent to that which occurs naturally during rapid rotary acceleration of the head opposite to the side of cooling. In the present experiment, cold caloric stimulation e.g., of the right ear (which is equivalent to head rotation to the left), induced a shift in sound lateralization to the left with respect to the median plane of the head (Fig. 2B).

Under natural conditions when the head is rotated to the left, the ILD produced by a stationary free-field sound source in the frontal hemifield shifts to a higher level at the right ear. If we apply the present dichotic results to acoustic free-field situations (Blauert 1997), we could conclude, that with actual head rotation, the resulting vestibular afferent signal may at least partially compensate for the physical shift in interaural difference, in an effort toward maintaining stable perception of sound sources during motion. This interpretation is compatible with the view that vestibular afferent information contributes to the neural generation of body- and world-centered space coding, as has been suggested by neurophysiological studies (Andersen et al. 1993; Tamura et al. 1990) and observations made in patients suffering (predominantly) from parietal lobe lesions (Karnath 1994; Karnath et al. 1996; Rubens 1985; for a recent review, see Vallar et al. 1997).

Several studies have indicated improvements of sound-localization acuity by dynamic (head motion) cues (e.g., Perrett and Noble 1997; Pollack and Rose 1967; Thurlow and Runge 1967). However, the present effect rather suggests systematic errors to result from head movements. A possible solution of this problem may be that vestibular information interacts with proprioceptive information on head-to-trunk position. Static eccentric head position (Lewald and Ehrenstein 1998) as well as transcutaneous neck-muscle vibration (Lewald et al. 1999) have been shown to induce shifts in sound localization. In natural situations, with rotations of the head toward auditory targets, when both head-in-space and head-to-trunk position change in a coordinated manner, such proprioceptive effects may counteract or even totally neutralize the present effect. In any case, our results indicate an integration of vestibular with auditory spatial information, which may represent an essential prerequisite for an efficient use of dynamic cues in sound localization.

To our knowledge, two earlier studies have employed unilaterral caloric stimulation to investigate vestibular influences on free-field-sound localization, but they found either no effect at all (Leisse 1926) or only general deficits in localization accuracy (Rauch 1922). The lack of agreement between these and our data, although unclear, may in all likelihood be due to the different experimental conditions (e.g., the latter studies used no head fixation; presented sound stimuli to the rear of the subject; illuminated the test room). Also in seeming opposition to our results, previous studies using real whole-body rotation of the subjects have reported shifts in free-field sound localization opposite to those expected from the present results (Clark and Graybiel 1949; Frey 1912; Jongkees and Van de Veer 1958; Münsterberg and Pierce 1894). However in those studies, subjects had kept their eyes closed so that a kinesthetic illusion of body rotation must have occurred. The direction of this illusion was opposite to the reported shift in perceived sound location. Consequently one might assume that it was the body position that had apparently shifted with respect to the sound source rather than vice versa. In contrast, the present method suppressed the kinesthetic illusion by providing a visual fixation target. In addition, the centered intracranial...
auditory percep (evoked by the dichotic stimulus), counteracted effects of potential illusory head movements (cf. Lewald et al. 1999) as well as the possibility that an illusory shift of the visual target (induced by vestibular stimulation) influenced the subjects’ perception of the median plane (cf. Graybiel and Hupp 1946; Karnath et al. 1994). We thus interpret our results as reflecting a direct influence of afferent vestibular information on neural substrates of spatial hearing.

This interpretation is justified only if any influence of vestibular stimulation on auditory afferent information can be excluded. Electrophysiological recordings of cochlear potentials have demonstrated both a reduction in amplitude and an increase in latency with decreasing temperature of the cochlea (Brown et al. 1983; Butler et al. 1960; Coats 1965, 1971; Fernández et al. 1958; Inamura et al. 1987; Kahana et al. 1950). As a consequence, the lateralization of dichotic sound should shift in a way similar to that found in the present main experiment. Our control experiment, however, showed only slight effects of cold-water irrigation on monaural intensity coding, and as can be inferred from the above electrophysiological studies, changes in latency are unlikely to occur in isolation from the former effect. Thus since the method of cold caloric stimulation may hardly affect peripheral auditory information, the results of the main experiment obviously demonstrate a primarily vestibular influence on central processes of auditory spatial coding.

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