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Research report

Selective tuning of the left and right auditory cortices during spatially directed attention

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Abstract

Effects of spatially directed auditory attention on human brain activity, as indicated by changes in regional cerebral blood flow (rCBF), were measured with positron emission tomography (PET). Subjects attended to left-ear tones, right-ear tones, or foveal visual stimuli presented at rapid rates in three concurrent stimulus sequences. It was found that attending selectively to the right-ear input activated the auditory cortex predominantly in the left hemisphere and vice versa. This selective tuning of the left and right auditory cortices according to the direction of attention was presumably controlled by executive attention mechanisms of the frontal cortex, where enhanced activation during auditory attention was also observed. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Attention; Auditory cortex; Human; Regional cerebral blood flow (rCBF); Positron emission tomography (PET)

1. Introduction

When the auditory environment contains sounds differing from each other in location or pitch, selective attention can be voluntarily directed to designated sounds [18,19]. For example, one can focus attention on a speaker's voice that differs in location or pitch from voices of other concurrent speakers, and to select only the attended voice for further, semantic processing. In such conditions, stimulus selection presumably occurs in the human auditory cortex as suggested by event-related brain potentials (ERPs) and magnetic fields (ERMFs) [1,6,12,14,17,20,28,33,39] recorded noninvasively with electroencephalographic (EEG) and magnetoencephalographic (MEG) techniques, respectively. In the present study, we sought direct support for these findings by measuring, during different selective-attention tasks, changes in regional cerebral blood flow (rCBF) with positron emission tomography (PET), which has been successfully used in studies locating brain areas involved in auditory processing [8,22,24,44].

Subjects in the present study selectively attended to left-ear tones, right-ear tones, or visual stimuli presented in three concurrent stimulus sequences. Since stimulation was identical in each condition, the effects of the direction of attention on the rCBF could be assessed by determining differences in the brain's activation pattern among the three attention conditions. Moreover, a much faster stimulus rate (on the average 6 Hz in each of the three stimulus sequences) than that used in the previous PET studies of selective auditory attention [30,38] allowed us to study brain activity during strongly focused auditory attention [3,29,40].

2. Materials and methods

2.1. Subjects

A total of 15 healthy subjects (18–45 years; 13 males and 2 females) were studied. All subjects were right-handed and had normal vision and hearing, and at least a secondary school education. Subjects signed an informed consent for their voluntary participation.

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2.2. Stimuli and procedure

The stimulation always consisted of two independent sound sequences delivered dichotically through earphones concurrently with a visual stimulus sequence. For each ear, the sound sequence consisted of 400-Hz standard tones (probability of occurrence 0.85) and 500-Hz deviant tones (probability 0.15), each with a duration of 100 ms and an intensity of about 75 dB SPL. The silent interval between consecutive tones varied randomly between 30–120 ms in each ear. The visual stimuli were produced with a matrix (width: 5 cm, height: 7 cm) of 35 green light emitting diodes (LEDs) placed at a distance of 50 cm from the subject's eyes. The visual stimuli were two letters of the Russian alphabet presented with the same temporal parameters and probabilities as the auditory stimuli, with the letter A being the standard stimulus and the π being the deviant stimulus. There were three different experimental conditions, the subject being instructed to silently count either the number of the deviant tones occurring in the right ear ('Attend Right Ear'), the deviant tones in the left ear ('Attend Left Ear'), or the deviant visual stimuli ('Attend Visual'). In each condition, the subject was instructed to fixate at the LED matrix. In the experimental session, there were six trials, two for each attention condition. Each trial had a duration of about 2 min, and the

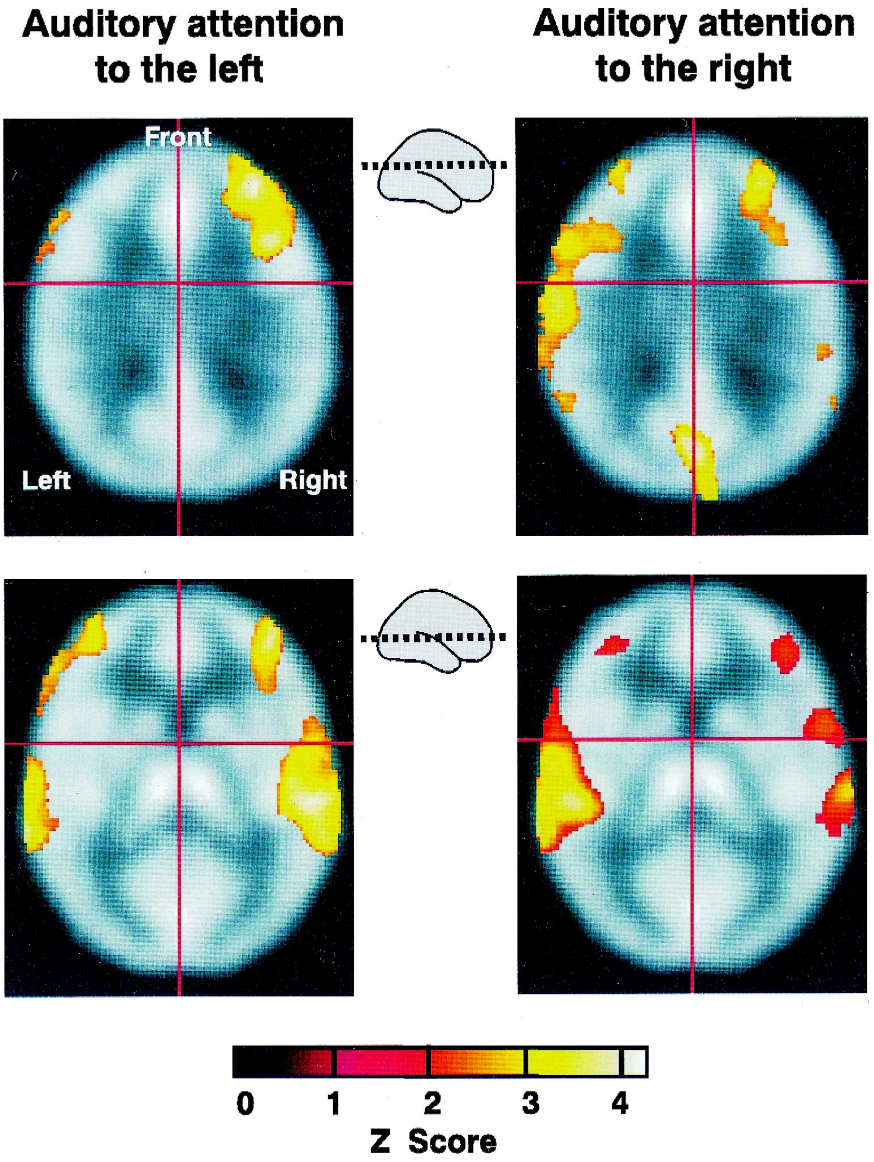

Fig. 1. *Z*-score maps showing brain areas in the temporal and frontal cortices (and in the parieto-occipital cortex for the 'Attend Right Ear' condition) with higher activity in images obtained in the 'Attend Left Ear' condition (left column) and in the 'Attend Right Ear' condition (right column) contrasted with the 'Attend Visual' condition. For each comparison, maps are shown for two horizontal brain slices. The higher one (top row) crosses (from front to back) the frontal and parietal cortices ($z = 28$ mm according to the coordinate system of Talairach and Tournoux [36]) and the lower slice includes (bottom row; $z = 12$ mm) the frontal, superior temporal (auditory), parietal, and occipital cortices. The horizontal and vertical lines indicate the x and y axes, respectively, of the coordinate system of Talairach and Tournoux.

trials occurred at intervals of about 15 min. The order of the attention conditions was counterbalanced among the subjects.

2.3. Pet scanning

The PET camera PC2048b (Scanditronix, Sweden) applied is located in the Institute of the Human Brain, St. Petersburg, Russia. This camera produces 15 slices of 6.5 mm thickness and covers 9.75 cm in the z axis perpendicular to the slices, the spatial resolution being 5.5 mm × 5.5 mm × 6.5 mm.

About 20 s after the beginning of each trial, a bolus injection (0.86 mCi/kg in 1–1.5 ml) of $H_2{}^{15}O$ (half-life: 123 s) was given to the right antecubital vein. PET scanning started automatically at the moment when a sufficient quantity of the tracer had entered the brain, i.e., at about 15–20 s after the injection. Scanning ended about 20–25 s before the end of each trial. In estimating the relative changes in rCBF, the distribution of the ^{15}O tracer was analyzed without arterial blood sampling [9,23]. The position of subject's head was fixed throughout the experimental session with a plastic mask produced individually for each subject and the head position inside the PET camera was determined in the beginning of the session by means of a transmission scan.

The experiments were carried out in accordance with the technical and ethical regulations of the Russian Ministry of Health and the Institute of the Human Brain.

2.4. Data analysis

The emission data were reconstructed with a 7-mm Hanning filter. The axial spatial resolution (FWHM, full width at half maximum) of the resulting images was 6.5 mm × 6.5 mm in the center of the field of view. Further analysis was performed by using Statistical Parametric Mapping [10] software (version SPM96b; Wellcome Department of Cognitive Neurology, London, UK) in a Sun Ultra Model140 computer (Sub Computers Europe, UK) with Matlab version 4.2c software (The Mathworks, USA). The images were reformatted into 43 planes of 128 × 128 voxel matrices (each voxel: 2 mm × 2 mm × 2 mm) with trilinear interpolation. The planes were transformed using linear scaling and rotation into the standard anatomical space of Talairach and Tournoux [36]. Images were smoothed with an isotropic Gaussian filter 16 mm × 16 mm × 16 mm wide. Statistically significant differences in rCBF between the different conditions were assessed by computing the appropriate contrasts with the t-statistic [10].

3. Results

Comparison of PET images during the 'Attend Left Ear' condition with the 'Attend Visual' condition revealed bilaterally enhanced activity in the temporal and frontal cortices during left auditory attention (Fig. 1, left column). In the right hemisphere contralateral to the attended direction, the SPM analysis showed a large activation cluster, which extended from the superior temporal cortex to the frontal cortex, while the ipsilateral left hemisphere showed a smaller cluster also extending from the superior temporal cortex to the frontal cortex (Table 1a; Fig. 1, left column).

In the same way, comparison of the 'Attend Right Ear' condition with the 'Attend Visual' condition showed that auditory attention to the right caused bilaterally enhanced activity in the temporal and frontal cortices (Fig. 1, right column). In the left hemisphere contralateral to the attended direction, a large activation cluster was observed including areas in the superior and medial temporal cortices (Table 1b; Fig. 1, right column). A small cluster was observed in the left frontal cortex, but it did not reach

Table 1
Activation clusters with significant size (in voxels), as indicated by the cluster-level analysis of SPM in the temporal and frontal cortex showing higher activity (a) in the 'Attend Left Ear' condition and (b) in the 'Attend Right Ear' condition than in the 'Attend Visual' condition

Cluster size	x	y	z	Z-score	Brain area
a. Attend Left Ear vs. Attend Visual					
11039, $p < 0.001$	56	22	4	5.42, $p < 0.001$	Right superior temporal gyrus
	26	34	38	4.54, $p < 0.04$	Right medial frontal gyrus
3243, $p < 0.005$	−66	−14	4	4.50, $p < 0.04$	Left superior temporal gyrus
	−38	58	18	3.87, $p < 0.32$	Left medial frontal gyrus
b. Attend Right Ear vs. Attend Visual					
7928, $p < 0.001$	−62	−14	4	6.30, $p < 0.001$	Left superior temporal gyrus
	68	−42	12	4.81, $p < 0.01$	Left medial temporal gyrus
3465, $p < 0.004$	70	−18	6	4.16, $p < 0.13$	Right superior temporal gyrus
	60	8	16	4.10, $p < 0.50$	Right inferior frontal gyrus
1614, $p < 0.04$	32	46	26	3.79, $p < 0.39$	Right superior frontal gyrus

The x, y, and z coordinates according to Talairach and Tournoux [36] and significance level corrected for the cluster size by the SPM are given for Z-score maxima within the cluster.

statistical significance with its size (569 voxels, $p < 0.43$ for the cluster size as indicated by the SPM) or with its highest Z-score ($Z = 3.74$, $p < 0.45$; the significance level corrected for the cluster size by the SPM; Talairach coordinates [36]: $x = -36$, $y = 46$, $z = 20$). In the right hemisphere ipsilateral to the attended direction, there was a smaller cluster than in the left hemisphere, which extended from the superior temporal cortex to the inferior frontal cortex and another small cluster in the right superior and medial frontal cortex (Table 1b; Fig. 1, right column).

As seen in Fig. 1, unlike auditory attention directed to the left, auditory attention to the right caused activation in

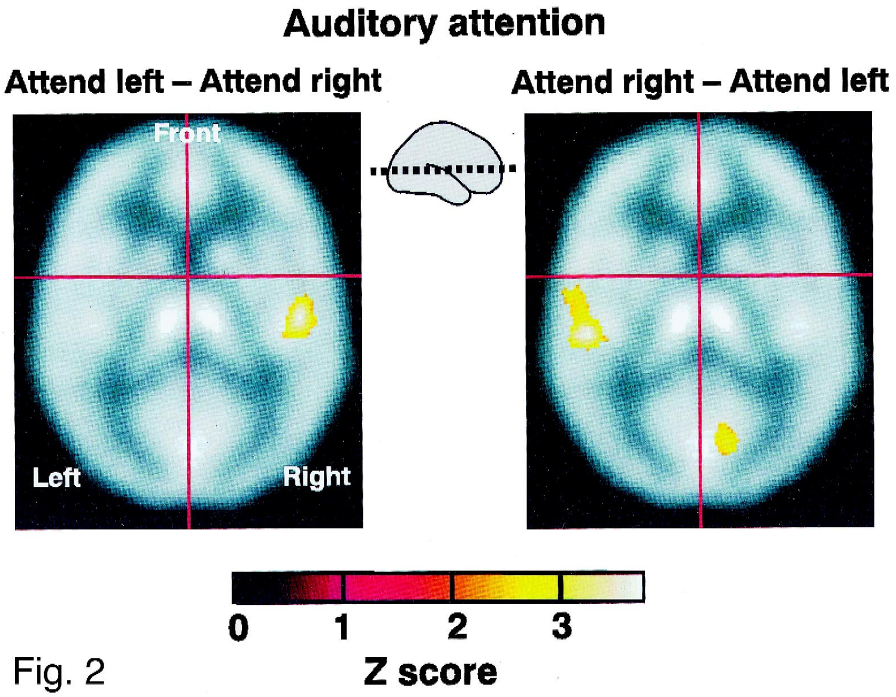

Fig. 2

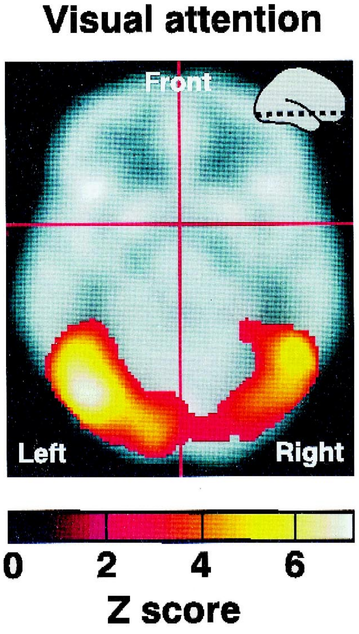

Fig. 3

Fig. 2. Z-score maps ($z = 12$ mm) showing higher activity in the right auditory cortex in the 'Attend Left Ear' condition than in the 'Attend Right Ear' condition and in the left auditory cortex in the 'Attend Right Ear' condition than in the 'Attend Left Ear' condition. In addition, there was an area in the right parietal cortex showing higher activation during attention to the right than during attention to the left. For other details, see Fig. 1.

Fig. 3. A Z-score map including the frontal, temporal, and occipital cortices ($z = -4$ mm) indicating higher activation of the occipital visual areas during visual attention than during auditory attention. The map was obtained by comparing activation during the 'Attend Visual Condition' with the activation averaged across the 'Attend Left Ear' and 'Attend Right Ear' conditions. For other details, see Fig. 1.

the right parieto-occipital cortex close to the midline, this activation cluster, however, not quite reaching statistical significance with its size (1103 voxels, $p < 0.11$) or highest Z-score ($Z = 4.07$, corrected $p < 0.18$, $x = 0$, $y = -72$, $z = 39$).

Thus, auditory attention enhanced the activity in the auditory areas of the superior temporal cortex predominantly in the hemisphere contralateral to the attended direction. This lateralization of attention-related activity was studied further by comparing the 'Attend Left Ear' condition with the 'Attend Right Ear' condition and vice versa (Fig. 2). These comparisons showed higher activity during attention to the left than during attention to the right in the right superior and medial temporal gyri, although the size of this cluster (711 voxels, $p < 0.13$) was not quite statistically significant and the maximal Z-value in this cluster did not quite reach the statistical significance level corrected for the cluster size ($Z = 4.33$, corrected $p < 0.07$). However, in such a focused comparison it is appropriate to rely on uncorrected significance values (see p. 105 in Ref. [10]), which indicated significantly enhanced activity in the 'Attend Left Ear', in relation to the 'Attend Right Ear' condition, for the Z-score maximum located at the right primary auditory cortex ($Z = 4.33$, $p < 0.001$, $x = 52$, $y = -22$, $z = 6$), contralateral to the attended direction. The respective comparison of the 'Attend Right Ear' condition with the 'Attend Left Ear' condition showed a similar pattern of results. Attention to the right caused higher activity in the left superior temporal cortex than attention to the left. The size of this cluster was statistically significant (2120 voxels, $p < 0.018$), but the highest Z-score in this cluster did not quite reach the significance level corrected for the cluster size ($Z = 3.65$, corrected $p < 0.54$). The uncorrected statistics, however, suggested significantly enhanced activity in the 'Attend Right Ear' condition, in relation to the 'Attend Left Ear' condition, for the highest Z-score, which was located in the left primary auditory cortex ($Z = 3.65$, $p < 0.001$, $x = 50$, $y = -24$, $z = 10$), contralateral to the attended direction.

Comparison of the 'Attend Right Ear' condition with the 'Attend Left Ear' also indicated higher activity during attention to the right in the right parietal cortex (Fig. 2), although neither the size of this cluster (691 voxels, $p < 0.31$) nor its Z-score maximum ($Z = 3.47$, corrected $p < 0.74$, $x = 5$, $y = 4$, $z = 38$) reached statistical significance.

Comparison of the PET images in the 'Attend Visual Condition' with the images averaged across the 'Attend Left Ear' and 'Attend Right Ear' conditions (Fig. 3) indicated higher activity during visual than auditory attention only in the occipital and parietal cortices where a large bilateral activation cluster (23,575 voxels, $p < 0.001$) was observed. For each hemisphere, the highest Z-score was located in the Brodmann area 19 (left hemisphere: $Z = 7.17$, corrected $p < 0.001$, $x = -42$, $y = -74$, $z = -4$; right hemisphere: $Z = 6.46$, corrected $p < 0.001$, $x = 52$, $y = -64$, $z = -14$), i.e., outside the primary visual cortex, as was also observed in previous PET and functional magnetic resonance imaging (fMRI) studies [7,16,31,41].

4. Discussion

The present PET results yield direct evidence for the proposal, based on ERP and ERMF recordings [1,6,12,14,20,28,33,39], that auditory selective attention selectively enhances activity in the modality-specific areas of the temporal cortex. Moreover, the present data are in line with other recent PET studies [30,38] showing that the degree of hemispheric lateralization of this attention-related activity depends on the direction of attention. According to the present results obtained with high stimulation rates (on the average 6 Hz for each ear) this lateralization effect is centered at the primary auditory cortex. Previous PET studies on dichotic selective attention used much lower stimulation rates (about 1 Hz for each ear) and found such lateralization of the attention effect in a larger area of the superior temporal gyrus, this area either including [30] or excluding [38] the primary auditory cortex. Thus, partly different auditory-cortex mechanisms might be involved in strongly focused selective attention facilitated by a high stimulation rate than in a less focused attention to sounds occurring at lower rates, as has been suggested also on the basis of ERP data [2].

In ERP and ERMF studies, however, the effects of auditory selective attention have not usually shown higher amplitudes in the hemisphere contralateral to the attended ear than over the ipsilateral hemisphere [1,3,12,29,37,42] and although two studies using very high stimulation rates, like the present study, suggested such lateralization of the attention effect [33,40], three others using similarly high stimulation rates did not [3,29,37]. Therefore it appears that the higher auditory-cortex activity in the hemisphere contralateral to the attended direction than in the ipsilateral hemisphere indicated by the present PET results might be largely invisible in scalp recorded ERPs. It is possible, however, that this lateralization would be associated with attention-related changes in the EEG spectrum [43] or with very slow attention-related brain potentials [13] not usually seen in ERP recordings because of stimulus-locked averaging and high-pass filtering of the data, respectively. Thus, it is not clear whether the present hemispheric lateralization of the attention-related activity was caused by stronger stimulus-induced activity in the auditory cortex contralateral to the attended direction or by preparatory attentional tuning of the left and right auditory cortices preceding the stimulus presentation [27,34], or by both. In any case, this tuning is presumably associated with maintenance of an auditory-cortex representation of the attended stimulus (its location), an 'attentional trace' [28], which selects these stimuli for further processing. However, it should be noted that ERPs elicited in quite similar attention conditions as the present ones indicate that selective attention is also manifested by activity related to rejection of unattended sounds from further processing by the attentional trace mechanism [5]. Therefore some of the present attention-related rCBF might have been caused by active suppression of processing of unattended stimuli rather than by facilitation of processing of attended stimuli.

In this study, no attention-related rCBF changes were observed in the subcortical structures of the afferent auditory pathway, e.g., in the thalamus. This result makes it unlikely that the present effects of selective attention observed in the auditory cortex would have been caused by some precortical mechanism modulating the auditory input from the attended direction to the contralateral auditory cortex [11,28,40].

It might be argued that the present rCBF effects in the primary auditory cortex and in its vicinity were not solely caused by direction of attention, but are partly associated with detection and counting of target tones within the attended input [17,28]. This is unlikely for three reasons, however. First, the target (deviant) stimuli occurred much more infrequently than the non-target (standard) stimuli, the rCBF differences between different conditions being therefore dominated by activity related to attentional selection of the non-target stimuli. Second, any activation caused by target discrimination would have been largely cancelled out by the comparisons between different conditions, because each condition included a discrimination task. Third, ERMF recordings during discrimination of infrequent, higher-pitch target tones [4] do not show any task-related activity elicited by target stimuli in the auditory areas on the superior temporal plane and recent fMRI results [25] derived using similar conditions found activity associated with auditory target discrimination only in the supramarginal gyrus, the anterior cingulate gyrus, and the thalamus, where no significant rCBF effects were seen in the present study.

Prefrontal cortical areas appear to be involved in controlling attention [26,28,32], as indicated by enhanced prefrontal rCBF [35,38] and electrical activity [1,12,28,37,42] during auditory attention and by attenuated attention effects on auditory ERPs in patients with dorsolateral prefrontal lesions [21]. Enhanced prefrontal activity observed in the present auditory attention conditions was presumably associated with the control of attentional tuning of the left and right auditory cortices [28]. Higher frontal activity observed during auditory vs. visual attention might be caused by the higher cognitive effort demanded by the auditory tasks, in which one of the two concurrent sound streams was to be selectively attended, than by the visual task, which required no intramodal selective attention.

There were also signs of increased activity in the right parietal cortex in the 'Attend Right Ear' condition, as compared with the 'Attend Visual' and 'Attend Left Ear' conditions, although these parietal effects did not reach statistical significance. Previous studies have shown that the right parietal cortex has an important role in directing both auditory and visual spatial attention [15,26]. However, it is not clear why the right parietal cortex would be activated more during auditory attention to the right than during auditory attention to the left or during visual attention to the central space. Perhaps higher activity of the right parietal spatial-attention mechanisms is needed during attention to the left than during attention to the right, or to the central space, because the afferent neural activity caused by stimuli occurring in contralateral hemispace or in central space arrives more directly to the right parietal areas than activity caused by stimuli in the ipsilateral hemispace.

In conclusion, selective attention to lateralized sounds delivered at a fast rate enhanced activity of the auditory cortex predominantly in the primary auditory areas in the contralateral hemisphere. Thus, the left and right auditory cortices were selectively tuned according to the direction of attention. This tuning was presumably controlled by prefrontal executive attention mechanisms, as suggested by enhanced prefrontal activity observed during the present auditory attention conditions.

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