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Brain activity during auditory backward and simultaneous masking tasks¹

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Abstract

Normal-hearing adult subjects performed a simultaneous and a backward auditory masking task, while their brain activity was recorded using functional magnetic resonance imaging. No differences between these tasks were observed in the auditory brain regions on the superior temporal lobes. Brain activity was larger for simultaneous than backward masking in the left inferior parietal lobe, the left inferior frontal cortex, the posterior cingulate cortex, and the cerebellum. In contrast, backward masking gave more activation in the left and right anterior temporal poles, and the anterior cingulate cortex. Apparently, backward and simultaneous masking tasks activate different auditory processing streams and require different cognitive brain resources.

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Key words: Human; Hearing; Backward masking; Simultaneous masking; Brain; Functional magnetic resonance imaging

1. Introduction

The performance of a psycho-acoustic listening task requires the activity of a number of brain areas. A subject has to listen to the auditory stimuli and analyze the acoustical information. Subsequently, the subject will choose, organize and execute his actual response.

Obviously, acoustical perception requires the activity of the auditory nuclei in the brainstem, and of the primary auditory cortex (Brodmann areas, BA 41) (e.g. Gazzaniga et al., 1998). Evidence suggests that acoustical analysis follows a hierarchical processing scheme (Hall et al., 2002; Wessinger et al., 2001), in which ‘pre-processing’ of fundamental sound characteristics takes

place in subcortical areas and in the primary auditory cortex. The subsequent processing of descriptive features of auditory stimuli involves non-primary auditory association areas (BA 42 and 22; Hall et al., 2002) and may activate different processing streams depending on the nature of the stimuli (Rauschecker, 1998; Rauschecker and Tian, 2000).

A subject performing a listening task attends the stimuli and makes a decision based on the information provided by the auditory brain areas. This involves an attentional network, which includes prefrontal and cingulate brain areas (Posner and Dehaene, 1994; Pugh et al., 1996). As a last step in the performance of the listening task, motor areas in the brain will be involved in response organization and execution.

The large number of brain areas involved in the performance of a listening task implies that a deficit in any of the stages described above may result in poor performance of the task. This is particularly relevant in the study of language-impaired children. Auditory studies have shown specific differences between the auditory perception of these children and of controls (Tallal and Piercy, 1973; Wright et al., 1997). Some of these

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Abbreviations: BA, Brodmann area; BOLD, blood oxygen level-dependent contrast; fMRI, functional magnetic resonance imaging

differences are not mediated by conscious perception, and consequently must derive from differences in ‘early’ processing in primary auditory brain regions (Kraus et al., 1996). Nevertheless, language impairment is present in parallel with a range of sensory and motor deficits, which affect the performance of these children (reviewed in Tallal et al., 1998). Thus, for the interpretation of auditory tests it is important to know to what extent non-auditory functions are involved in the test execution.

The current study was designed to gain understanding of brain function during auditory task performance. We did not test language-impaired children, but measured brain activity in a group of adult subjects without language problems. Our subjects performed a backward and a simultaneous masking task, while their brain activity was recorded by functional magnetic resonance imaging (fMRI). The same masking tasks were studied in language-impaired children by Wright et al. (1997). They showed a deficit in auditory backward masking in language-impaired children, while simultaneous masking was not impaired. As discussed above, the difficulty of performing a backward masking task may result from a deficit in any of the brain areas involved in the task performance. Possibly, the backward masking task activates a particular subset of auditory and cognitive brain functions, which happens to be impaired in the language-impaired children. For example, if backward and simultaneous masking require different auditory functions, but cognitive functions are identical, our study would show differences in auditory brain areas, but not in the cognitive (e.g. attention-related) areas in the cingulate and prefrontal cortex. In contrast, if the two tasks require different cognitive functions, we expect differences in the activation of prefrontal and cingulate cortex.

2. Materials and methods

We measured brain activity during auditory masking experiments by fMRI of the blood oxygen level-dependent (BOLD) effect. Our subjects were eight right-handed young adults (ages 22–32, two males, six females) with normal hearing and no history of language problems. For each subject, brain activity was recorded for both a backward and a simultaneous masking task, each in a separate run.

Auditory stimuli were presented using the piezoelectric element of a tweeter, built into an hearing protection headset (Bilsom Blue). The stimuli were presented to the right ear, in a two-alternative forced-choice paradigm. The two alternatives consisted each of a 300-ms-duration Gaussian noise burst, with spectral components from 1 to 2 kHz, and were separated by a 500-

ms silent gap. In addition, one of the stimuli contained a brief 1500-Hz tone pulse, duration 20 ms, which started either 200 ms after the onset of the noise masker (simultaneous masking) or 20 ms prior to the onset of the noise masker (backward masking). For noises and tones, 10-ms sinusoidal on/off amplitude ramps were used. Noise levels were fixed at 70 dB SPL. For both the backward and the simultaneous masking task, the level of the tone pulse was determined by an adaptive procedure (Green, 1990) aimed at a 94% correct response of the subject. Subjects were instructed to identify which noise contained the tone pulse and respond-

(a) Stimulus timing

(b) Backward masking

(c) Simultaneous masking

Fig. 1. (a) Stimulus timing. MRI scans were conducted using a sparse imaging protocol, in which a scan was performed every 6 s. Each scan lasted 2 s, which leaves a 4-s silent interval to present auditory stimuli. The stimulus presentation started 3 s prior to a subsequent MRI scan. (b) Details of stimulus timing for backward masking. The amplitude envelope of the auditory stimulus is shown. A 20-ms tone was presented prior to one of two 300-ms noise bursts. Here we show the tone prior to the first burst. Subject were asked to identify which of the two noise bursts contained the brief sinusoidal pulse. (c) Details of stimulus timing for simultaneous masking.

ed correspondingly by pushing a button either with their left thumb or with their right thumb. Subjects received no feedback on their performance. Adaptive stimulus control was used both during a practice session 1 week prior to the actual fMRI experiment, and throughout the entire imaging session. At the start of the fMRI session, several responses from the subject were recorded prior to the actual MRI acquisition in order to establish the 94% correct threshold. In this way we could ensure that the MRI scanner recorded brain activity near the target performance level. Each subject practised both tasks in a sound-proof room 1 week prior to the fMRI experiment.

Brain responses were acquired using fMRI at 1.5 T. We used a sparse imaging protocol, in order to minimize the effect of sound produced by the MRI scanner on the auditory performance of our subjects. Full brain T2*-weighted multi-slice echo planar images were acquired every TR = 6 s (see Fig. 1). The parameters were TE 50 ms, 32 contiguous slices, and voxel dimensions $3.5 \times 3.5 \times 3.5$ mm³. Each scan took 2 s. Consequently, a silent period of 4 s was present prior to each scan. Auditory stimuli were triggered by the MRI scanner and started 3 s after the onset of a scan, i.e. 3 s prior to onset of the next scan.

A total of 64 scans was performed. The first four scans were omitted from further analysis, and served

to allow the magnetization to reach a dynamic equilibrium. Following the four initial scans, stimuli were presented in a block design: epochs of five scans taken without prior audio stimulation were followed by five scans with audio stimulation. This sequence was repeated up to the total of 60 scans. For each subject, the 60-scan sequence was used for both the backward and the simultaneous masking task. Four subjects performed the simultaneous masking task first, while the other four started with the backward masking task.

Data were analyzed using statistical parametric mapping (Friston et al., 1995) (SPM99) using a random effects model. First, the data were motion-corrected, spatially normalized to Talairach space, and smoothed (8-mm Gaussian kernel). Talairach coordinates were used to identify brain regions (Talairach and Tournoux, 1988). Subsequently, statistical random-effect group inferences were made on the contrast between the baseline measurement (no stimulus), and the two auditory tasks, respectively. The same analysis was performed for the difference between the auditory tasks, in order to determine in which brain areas simultaneous masking gave more activation than backward masking ($S > B$), and vice versa ($B > S$).

3. Results

The subject task performance is expressed in a signal-to-noise ratio, which represents the tone level required for tone detection in the presence of the masking noise. Signal-to-noise ratios reported here correspond to a 94% correct subject button-press response during the two-alternative forced-choice procedure. For simultaneous masking the average difference between performance in the sound-proof room and performance in the MRI scanner was 0.2 dB (± 3.1 dB; S.D. across subjects; see Fig. 2). For backward masking this number was -10.6 dB (± 8.3 dB), which indicates that most subjects performed somewhat better in the scanner.

The analysis of MRI images showed brain activation in several brain regions (see Table 1). For both tasks activation was present in primary auditory regions: the inferior colliculus in the brainstem, and the left primary auditory cortex in the superior temporal gyrus. In addition, several areas outside the primary auditory regions were activated: the inferior frontal gyri, including Broca's area on the left side of the brain, the anterior temporal gyri, and both the left and the right inferior parietal lobes, all of which are presumably involved in language processing (see Section 4). Finally, several brain areas outside the auditory and language centers are involved in both the backward and the simultaneous task: specifically, the cingulate cortex, the right middle frontal gyrus, and the putamen.

Fig. 2. Task performance in a sound-proof room versus in the MRI scanner. Task performance is expressed in dB as the peak level of the tone pulse relative to the rms level (70 dB SPL) of the masking noise necessary for 94% correct detection of the tone. Each symbol represents a task result for one subject. For simultaneous masking (open circles), the task performance in the MRI scanner was similar to that in a sound-proof room. For backward masking (solid circles), most subjects performed better in the MRI scanner.

Table 1
Brain areas activated during auditory masking tasks

Brain region	BA	Side	Simultaneous	Backward	S > B	B > S
Inferior colliculus		M	(−10, −30, 6) 4.2			
Posterior superior Temporal gyrus	22/41/42	L	(−56, −22, 10) 4.4	(−42, −26, 8) 4.4		
Anterior Temporal Gyrus (temporal pole)	21/38	L	(−54, 6, −4) 3.6	(−50, 4, −10) 4.2		(−50, 4, −22) 3.7
		R		(34, 14, −20) 4.1		(34, 16, −3) 3.9
Inferior parietal Lobule	40	L	(−32, −60, 50) 4.5		(−54, −46, 28) 4.7	
		R	(50, −50, 44) 3.6	(58, −44, 46) 4.5		
Inferior frontal cortex	44/45	L	(−48, 12, 38) 4.1	(−54, 6, 36) 5.1	(−34, 22, 8) 4.2	
		R	(38, 20, 6) 4.0	(54, 16, 18) 3.9		
Middle frontal cortex	9/10	R	(26, 52, 8) 4.2	(54, 32, 24) 4.4		
Posterior cingulate cortex	23	M	(8, −42, 26) 4.2		(−12, −52, 18) 4.6	
Anterior cingulate cortex	32	M	(−8, 34, 26) 3.9	(−6, 36, 30) 4.6		(2, 54, 28) 4.0
Cerebellum		L	(−50, −54, −36) 3.9		(−22, −52, −28) 4.5	
		R	(16, −70, −42) 3.9		(28, −40, −34) 3.7	
Putamen		R	(30, 2, 0) 4.3	(28, 6, −6) 4.5		

Only brain areas for which $P < 0.001$ at peak activation are indicated. The activation pattern of each brain region is summarized in the format '(x, y, z) **Z**', which refers to Talairach coordinates [(x, y, z) in mm] of the peak activation, and the **Z** score of the peak activation. Positive x refers to the right hemisphere; positive y is frontal; positive z is superior. The lateralization of activated brain areas is additionally indicated in column 2: L = left for $x < -20$ mm; M = medial for $-20 < x < 20$ mm; R = right for $x > 20$ mm. Column 3: simultaneous masking. Column 4: backward masking. Columns 5 and 6: brain areas where simultaneous masking gave larger and smaller activity, respectively, than backward masking.

The activation patterns discussed so far reflect differences between images obtained during task performance and those obtained during silence. In addition, we analyzed the differences between both tasks. All significant differences between simultaneous and backward masking were observed outside the primary auditory areas (see Fig. 3). Brain activity was larger for simultaneous masking than backward masking in the left inferior frontal cortex (Broca's area), the left inferior parietal lobules, and the posterior cingulate cortex. Simultaneous masking also activated the cerebellum, in contrast to backward masking. Backward masking evoked larger activity bilaterally in the anterior temporal gyrus (temporal poles), and in the anterior cingulate cortex.

4. Discussion

In auditory fMRI experiments, the acoustic pulses produced by the MRI scanner will themselves produce auditory brain responses and may make the performance of subjects worse. In order to minimize these unwanted effects, we applied a sparse imaging protocol, in which scans are taken with 6-s intervals, and stimuli are presented during the silent period in between. In 6 s,

the BOLD response to the scanner sound will be reduced to 40–50% of its peak amplitude (Belin et al., 1999; Backes and Van Dijk, 2002). For a block-design study as described here, this is sufficient to build up a response signal and to allow for adequate registration of the responses to the task stimuli.

The acoustic pulses from the scanner did not degrade subject performance (Fig. 2). The result obtained both during scanner sessions and in a sound-proof room are in agreement with other auditory masking studies (Elliot, 1962; Fastl, 1976; Buss et al., 1999). In fact, for backward masking subjects performed better in the MRI scanner than during a practice session. This may be a learning effect, which specifically occurs for backward masking (Wright et al., 1996). However, the two test sessions were separated by about 1 week without training in the interval. Consequently, the learning effect may not be expected to be significant (Roth et al., 2001).

An alternative explanation for the improved performance relates to the presence of the scanner acoustic pulses. For backward masking, a three-interval two-alternative forced-choice procedure is easier than the two-interval procedure used in our study (Bishop et al., 1999). In the three-interval backward masking para-

Fig. 3. Activity patterns; differences between simultaneous and backward masking. For each panel, an y or z distance (in mm) indicates the Talairach coordinate of the cross-sectional plane. Simultaneous masking gave more response than backward masking in the left inferior frontal gyrus (panel a, arrow 1), the posterior cingulate gyrus (arrow 2), the left inferior parietal lobe (arrow 3), and the left and right cerebellum (panel b, arrow 1 and 2). The small arrows in panel b point to the posterior cingulate gyrus and the left inferior parietal lobe, which are also illustrated in panel a. Backward masking resulted in more response in the anterior cingulate gyrus (panel c, arrow), and in the left and right anterior temporal gyrus (panel d, arrows).

digm, three noise bursts are presented to the subject, and the target tone is hidden in either the second or the third noise burst. Presumably, the first noise burst helps the subject since he knows when to expect the target tone. The control group of Bishop et al. were children aged 7–13 years, and improved on average by 5.2 dB when the additional noise was presented. It is conceivable that during MRI acquisition the acoustic scanner pulse, which precedes each stimulus presentation, plays a similar role: when the subject hears the MRI scanner, he knows when to expect the stimulus. Thus, rather than worsening subject performance the scanner pulse somewhat helps the subject in the backward masking task.

As is to be expected, both the backward and the simultaneous masking task gave activation in several auditory areas; a significant response in the inferior colliculi, with peak activation on the left side. For backward masking, the activation in the colliculus did not reach statistical significance (Z -score 2.8), and also the differences between backward and simultaneous mask-

ing were not significant. Responses in the superior temporal gyrus (BA 41, 42, 22) were also only significant in the left hemisphere, that is contralateral to the side of stimulation.

The activation of the left and right inferior parietal lobules (BA 40), the anterior temporal gyrus (BA 21/38), and the inferior frontal gyrus (BA 44/45) presumably reflects further analysis of the acoustical stimuli, and is consistent with a hierarchical processing model (see below). The involvement of middle frontal (BA 9/10) and cingulate (BA 23 and 32) areas reflects the activation of an attentional network necessary to execute the task (Posner and Dehaene, 1994; Pugh et al., 1996).

After listening to the auditory stimuli, subjects responded by pressing a button. The activation of the cerebellum and the putamen is consistent with a role of these areas in motor control, particularly in movement planning and initiation (e.g. Gazzaniga et al., 1998). No response was observed in the primary motor cortex, presumably since subjects pressed the response

button approximately during the scan following each stimulus presentation. Thus, the motor cortex hemodynamic response was maximal after the image acquisition, and consequently was not recorded.

Of particular interest are the differences between simultaneous masking and backward masking. Two types of differences may occur. Firstly, a brain region could be activated for one condition, while no significant response is present for the other condition. Such brain regions are easily identified by comparison of each condition to silence (Table 1, columns labeled ‘simultaneous’ and ‘backward’). Secondly, if a brain region is active for both the backward and the simultaneous condition, differences could still be present in strength or spatial extent of the activation. Contrasting backward and simultaneous masking identifies both types of differences (see Table 1, columns ‘S > B’ and ‘B > S’).

Note that the differences we identified occurred only because of a subtle temporal difference between the simultaneous and backward masking stimuli. Apart from this minor difference, all other conditions were kept identical. Specifically, both tasks were performed (1) at the same masker noise levels, (2) at a 94% correct performance level, and (3) requiring the same motor action from the subjects (button pressing). Thus, the observed differences must result from the temporal differences between the stimulus characteristics alone.

The differences between backward and simultaneous masking were only observed outside the primary auditory cortex (BA 41) and its nearby association areas (BA 42, 22). While simultaneous masking gave more response in posterior areas, backward masking activated anterior areas. These results may be compared to the concept of separate ‘what’ and ‘where’ processing streams via an anterior and a posterior pathway, respectively (reviewed by Rauschecker and Tian, 2000). The anterior pathway, which processes language-related information, includes the anterior temporal poles (BA 21 and 38). This pathway was more activated for backward masking than simultaneous masking. In contrast, the posterior pathway, which includes the inferior parietal lobules (BA 40), is more activated for simultaneous masking. Our results indicate that backward masking relied on the ‘what’ pathway, while simultaneous masking gave more response in the ‘where’ pathway.

For some areas, the activation differences are not at the peak location of either simultaneous masking or backward masking. For example, simultaneous and backward masking peaked in the left anterior temporal lobe at $z = -4$ cm and $z = -10$ cm, respectively. However, the difference between backward and simultaneous masking reached a maximum more than 1 cm inferior to these locations, at $z = -22$ cm. This is a consequence of the activation pattern subtraction. Apparently, while the anterior superior temporal gyrus (BA 38, $z = -4$,

-10 cm) is active for both tasks, the middle temporal gyrus (BA 21, $z = -22$ cm) is most active for backward masking. The middle temporal gyrus plays a role in word recognition tasks (Maeder et al., 2001). Consequently, our result suggest that backward masking involves the same neural circuitry used for word recognition.

Our study was originally motivated by the observation that language-impaired children exhibit a deficit in backward masking (Wright et al., 1997). Since we did not study language-impaired children, a discussion on the implications of our results for language impairment must remain speculative. Nevertheless, we point out the relation between our results and those of Wright et al. They showed that when language is impaired, backward masking may be impaired too. This is consistent with our observation that backward masking specifically activates the language-related ‘what’ pathway. However, while the activation of the ‘what’ pathway by backward masking correlates with the finding of Wright et al., at present it remains unclear why simultaneous masking activated the ‘where’ pathway.

In addition to differences related to the ‘what’ and ‘where’ processing streams, we observed differences for the cognitive brain areas in the cingulate and the frontal cortex. The anterior cingulate cortex and frontal cortex play a role in ‘executive functions’ and attention (Posner and Dehaene, 1994; Pugh et al., 1996; e.g. Gazzaniga et al., 1998). Memory functions have been attributed to the posterior cingulate cortex (e.g. Duzel et al., 1999). Our results indicate that backward and simultaneous masking require activity of different cognitive brain areas, although their exact role is presently unclear. A consequence of this finding is that a deficit in backward masking performance may be related to an impairment of the cognitive functions specifically used in that task.

5. Conclusion

We measured brain activity during an auditory simultaneous masking task and a backward masking task. The two tasks activated auditory processing streams differently (i.e. ‘where’ and ‘what’ streams; Rauschecker and Tian, 2000). In addition, cognitive brain regions were activated differently by the two tasks. Apparently, backward and simultaneous masking tasks require different cognitive brain resources.

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