Functional role of the human inferior colliculus in binaural hearing

Ruth Y. Litovsky [a,*], Brian J. Fligor [a], Mark J. Tramo [b]

[a] *Boston University, Hearing Research Center, Boston, MA, USA*
[b] *Massachusetts General Hospital and Harvard Medical School, Boston, MA, USA*

Abstract

Psychophysical experiments were carried out in a rare case involving a 48 year old man (RJC) with a small traumatic hemorrhage of the right dorsal midbrain, including the inferior colliculus (IC). RJC had normal audiograms bilaterally, but there was a marked decrease in wave V amplitude on click-evoked brainstem auditory evoked potentials following left ear stimulation. RJC demonstrated a deficit in sound localization identification when the loudspeakers lay within the auditory hemifield contralateral to his IC lesion. Errors showed a consistent bias towards the hemifield ipsilateral to the lesion. Echo suppression was abnormally weak compared with that seen in control subjects, but only for sources contralateral to the lesion. Finally, speech intelligibility tests showed normal ability to benefit from spatial separation of target and competing speech sources. These results suggest that: (1) localizing sounds within a given hemifield relies on the integrity of the contralateral IC, (2) unilateral IC lesions give the illusion that sound sources in the 'bad' hemifield are displaced towards the 'good' hemifield, (3) the IC mediates aspects of echo suppression, and (4) lesion in the IC does not impede spatial release from masking in speech intelligibility, possibly due to that ability being more heavily mediated by cortical regions. © 2002 Elsevier Science B.V. All rights reserved.

Key words: Binaural; Inferior colliculus; Lesion; Precedence; Localization; Speech

1. Introduction

Humans spend a majority of their time in complex environments, where the auditory system must resolve competition for perception and localization between an important sound source and other sources. These include extraneous noise, both human-made and machine-made, and echoes of the source which result from the presence of hard surfaces in the room. The neural mechanisms involved in these complex perceptual tasks are not well understood, although over the years studies have attempted to draw correlates between physiological mechanisms, anatomical organization and psychophysical phenomena (e.g., Cariani and Delgutte, 1996; Litovsky and Yin, 1998a; Furst et al., 2000). Numerous studies have also used ablation methods to study the effect of removal of specific brain tissue on animal behavior (e.g., Heffner and Masterton, 1975; Jenkins and Masterton, 1982; Whitfield, 1978).

Reports of humans with selective lesions that are not accompanied by other severe dysfunctions are extremely rare, hence little is known about the effect of specific brain lesions in humans on auditory perception. A series of papers on patients with lesions located in the brainstem have shown some correlations between the site of lesion and inability to perform on binaural tasks (Aharonson et al., 1998; Furst et al., 1995, 2000). Specifically, patients with lesions in the inferior colliculus (IC) and/or lateral lemniscus (LL) showed abnormal sound source lateralization, although the results did not emphasize the relation between the side of lesion and performance for sounds in the contralateral hemifield. Similar studies on echo suppression have not been conducted to date.

* Corresponding author. Present address: University of Wisconsin-Madison, Waisman Center Room 567, 1500 Highland Ave., Madison, WI 53706, USA. Tel.: +1 (608) 262-5045; Fax: +1 (608) 263-2918.
E-mail address: litovsky@waisman.wisc.edu (R.Y. Litovsky).

In this paper we present a recent set of experiments conducted on an individual who sustained a traumatic hemorrhage in the right dorsal midbrain, including the IC. This case study presented a rare opportunity to investigate auditory psychophysics in a patient with a focal brain lesion who is relatively highly functional in daily life. This case is especially interesting given that the locus of the lesion is in a nucleus that is known to be crucial for binaural and spatial hearing as well as for echo suppression. The IC contains arrays of neurons tuned to different interaural time differences (ITDs) that provide a coding mechanism for locating sources in space (see reviews by Kuwada et al., 1997; Yin et al., 1997). Lesion studies have shown that the ability of animals to localize sounds in space is impaired after unilateral lesions in the dorsal midbrain, including the IC and dorsal nucleus of the LL (Kelly and Kavanagh, 1994; Kelly et al., 1996; Jenkins and Masterton, 1982). Here we tested the hypothesis that a unilateral lesion in the IC would disrupt sound localization, in particular for sound sources contralateral to the lesion site.

There is growing evidence that the IC mediates the initial stages of the precedence effect (PE) (see Yin, 1994; Fitzpatrick et al., 1995; Litovsky, 1998; Litovsky and Yin, 1998a,b). In psychophysical terms, the PE refers to a group of auditory phenomena that are thought to account for listeners' abilities to function in reverberant spaces. For instance, a source (lead) and a single reflection (lag) are simulated by presenting two sounds with a brief delay in their onsets (1–5 ms for clicks). The lead and lag perceptually fuse into one auditory event whose perceived location is dominated by that of the leading source. In addition, at short delays changes in the location or interaural parameters of the lag are difficult to discriminate compared with changes in characteristics of the lead, presumably due to suppression of the directional information contained in the lag (for review see Litovsky et al., 1999). Physiological studies have shown remarkable correlates of these effects. In virtually all IC neurons responses to the lag are suppressed at short delays, and the spatial receptive field of the neuron is dominated by the position or ITD of the lead (Yin, 1994). We therefore hypothesized that a unilateral lesion in the IC would disrupt the PE, in particular for sound sources contralateral to the lesion site.

Finally, an important aspect of auditory function is the ability to understand speech in noisy environments, also known as the 'cocktail party effect' (Cherry, 1953; Yost, 1997). In psychophysical terms, signal detection and speech perception improve when the target and competing noise are spatially separated. While physiological correlates of this effect have not been extensively studied, recent evidence suggests that IC neurons exhibit a form of masking for a signal in the presence of noise (e.g., Jiang et al., 1997; Palmer et al., 2000). However, it is not clear that IC neurons also demonstrate a correlate of the 'spatial release from masking' phenomenon (Litovsky et al., 2001). In addition, spatial release has both monaural and binaural components, hence a subject with an IC lesion may still be able to perform well on this task. We hypothesized that a lesion of the type seen in our patient may not disrupt speech perception in noise.

The purpose of the present investigation was to determine the functional role of the IC in binaural tasks and to provide a link between psychophysics and physiology related to spatial hearing. Three psychophysical
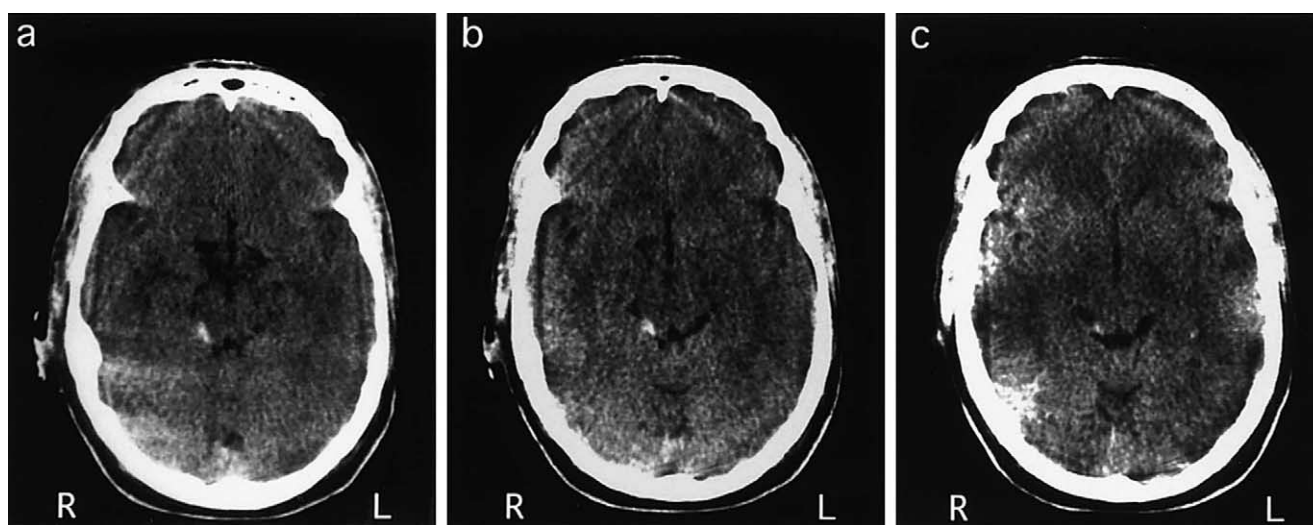

Fig. 1. Case RJC. Serial, 10 mm thick horizontal CT sections extending from the rostral pons to the quadrigeminal plate (a–c). Small hyperdensity in the right dorsolateral pons and midbrain represents a traumatic intraparenchymal hemorrhage involving the IC and rostral LL. Images were obtained hours after RJC's closed head trauma in 1987. R = right, L = left.
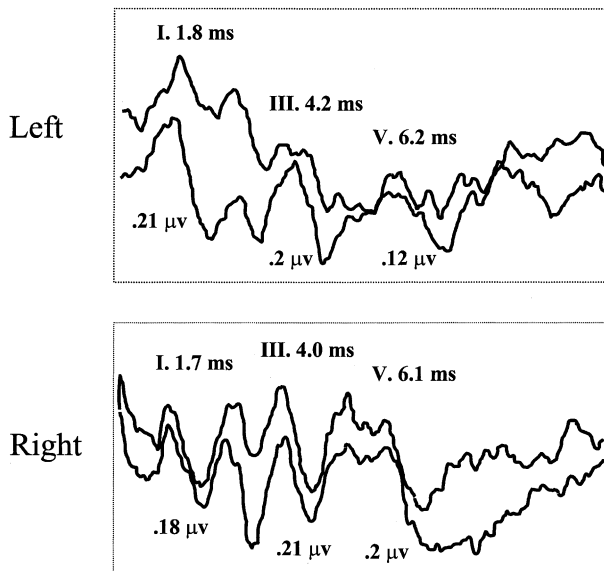
Fig. 2. BAEPs are shown for left (top) and right (bottom) ear stimulation. Examples of two traces are shown in each case. Wave numbers with corresponding average delays are indicated above each peak, and average peak amplitude is indicated below each peak.

phenomena were investigated in an individual with a selective lesion in the right dorsal midbrain. We tested the hypotheses that deficits in sound localization and the PE should occur when the sources are on the side of the head contralateral to the lesion side, i.e., in the left hemifield, but that speech intelligibility in noisy may not be affected by the lesion. Three types of experiments were carried out. First, sound localization accuracy was measured in a sound field lab containing an array of seven loudspeakers. Second, the PE was studied by measuring the strength of echo suppression, as well as the listener's ability to extract information regarding the ITD of the lag in the presence of the lead. Third, speech intelligibility was studied in the presence of competing sounds, and the listener's ability to benefit from spatial separation of the target and competitors was measured.

2. Materials and methods

2.1. Subjects

2.1.1. RJC case report

RJC, a 36 year old right-handed man, suffered a small traumatic hemorrhage of the right brainstem involving the inferior colliculus in 1987 (Fig. 1). RJC complained of difficulty localizing sound and balancing his car stereo while listening to music. He denied difficulty recognizing speech, music, or environmental sounds. Neurological examination was within normal limits except for tenderness and decreased light touch sensation over the supraclavicular region, which was also injured in his motor vehicle accident. Pure tone detection thresholds were within normal limits. Brainstem auditory evoked potentials (BAEPs) showed an abnormally low wave V amplitude following left ear click stimulation at all stimulus intensities (Fig. 2). Wave V to wave I ratio was < 50%, consistent with damage to the right IC and/or rostral LL (Durrant et al., 1994). At the time of the present experiments, RJC was being treated with verapamil and paroxetine.

Pure tone detection thresholds were within the normal limits in both ears at frequencies ranging from 250 to 8000 Hz (Fig. 3). A bilateral notch was observed at 4000 Hz, but is still within the range of normal hearing. Additional audiometric testing showed speech reception thresholds of 0 dB HL bilaterally, and word recognition scores of 100% and 96% in the right and left ears, respectively.

2.1.2. Control subjects

Three subjects with normal pure tone thresholds at frequencies ranging from 250 to 8000 Hz in each ear were tested. These subjects have no known neurological deficits, but brain images were not obtained from these individuals.

For these listeners as well as the lesion patient, testing on the various conditions was interspersed to minimize fatigue or other psychological factors. Hence, testing on most days included conditions from the various experimental conditions, but in some cases certain days were more heavily laden with one condition than another.
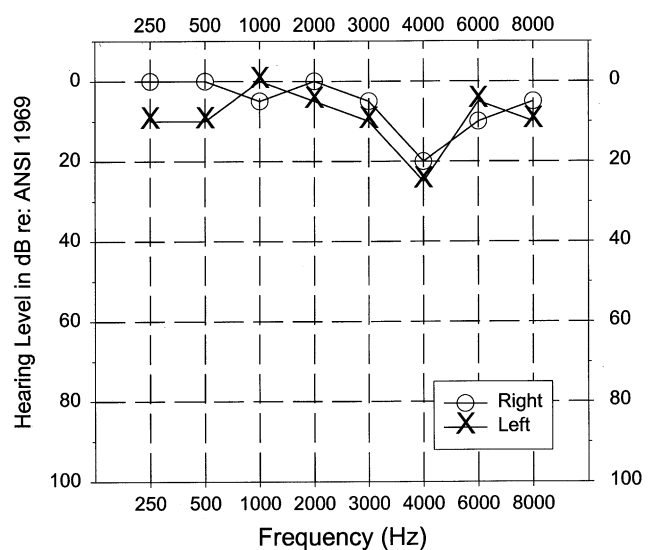

Fig. 3. Subject RJC's pure tone audiogram. Hearing level in dB relative to the standards of ANSI (1969) are shown at each frequency for the right and left ears.

A **Initial Train**   **"Test Click"**

ISI one
(250 ms)

ISI two
(750 ms)

Time

B **Initial Train**   **"Test Click"**

ISI one
(250 ms)

ISI two
(750 ms)

Delay

Time

C **Reference**   **Comparison**

Lead   Lag

Left ear   Inter-Stimulus Interval (500 ms)   2 ms

Right ear

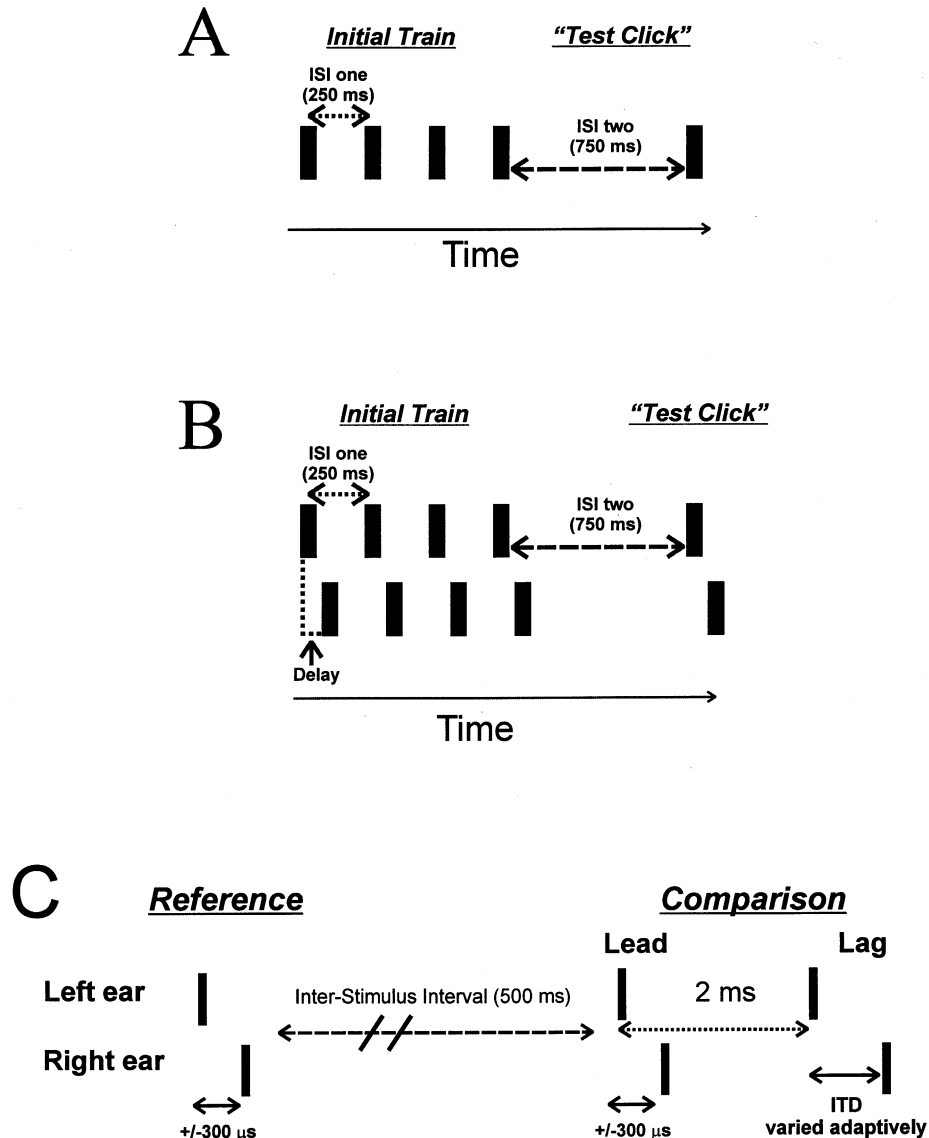+/-300 µs   +/-300 µs   ITD
varied adaptively

Fig. 4. Stimulus configurations used in the localization and precedence experiments. (A) An initial train of clicks occurred with inter-stimulus intervals (ISI) of 250 ms between clicks, followed by a 750 ms ISI and an additional 'test click'. (B) Same as in A, but two identical trains of clicks were presented, with their relative onsets delayed by a variable delay, so that the leading and lagging trains represent the 'lead' and 'lag' stimuli, respectively. (C) In the discrimination suppression task stimuli consisted of two intervals. In the first, a *reference* click pair was presented with a delay of either +300 µs or −300 µs between the two ears (which remained constant within a run). Following the reference, an ISI of 500 ms occurred, followed by the *comparison* stimulus, which consisted of two dichotic click pairs; the first pair had the same ITD as the reference, and the second pair had an ITD that varied adaptively to the right or left of the reference.

2.2. Experiment I: sound localization

Measurements were conducted in a sound field laboratory (12×13 feet and reverberation time of $T_{60} = 250$ ms). The apparatus consisted of seven loudspeakers (Radio Shack Minimum 7), matched for levels with front-end filters at frequencies of 100–10 000 Hz. Loudspeakers were positioned at 30° intervals in the frontal hemifield at ear level and a distance of 5 feet from the center of the listener's head. A Tucker–Davis Technologies (TDT) System-II was used to construct the stimuli. The output was fed through a 16-bit DAC to pro-

grammable filters, amplified (TEAC) and presented to loudspeakers through seven independent channels. Stimuli consisted of 20 µs clicks with peak amplitude of 60 dB SPL. Subjects were seated on a chair with a headrest to constrain head movement during testing. Testing was conducted in the light and listeners were aware of the seven possible locations.

On each trial, a train of five clicks (see Fig. 4A) was presented from one of the seven loudspeakers, with inter-stimulus intervals of 500 ms between the first four clicks, and 750 ms between the fourth and fifth clicks. The subject's task was to identify the perceived position

of the fifth (test) click, by pressing a number (1–7) on a keyboard. No feedback was provided. Testing was conducted under three speaker configurations. In the first, subjects sat facing the seven loudspeakers, which spanned 90° on the right and left. In a second condition the chair was rotated 90° to the right, such that the seven positions spanned from 0° (front) to 180° (behind) in the listener's left hemifield, contralateral to RJC's damaged IC. In a third condition, the chair was rotated 90° to the left, with loudspeakers in the right hemifield, ipsilateral to the damaged IC. Testing was conducted in blocks of 35 trials, containing five repetitions of each location, presented in random order. For each of the three conditions two blocks of trials occurred, with order of the six blocks randomized.

2.3. Experiment II: echo suppression

The apparatus and hardware were identical to those used in experiment I. On each trial a train of five lead–lag click pairs was presented, with inter-stimulus intervals of 500 ms between the first four click pairs, and 750 ms between the fourth and fifth pairs (see Fig. 4). When presented in isolation each click had peak amplitude of 60 dB SPL. The subject's task was to indicate how many sounds were heard (one or two) on the fifth click pair. The delay between the onsets of the lead and lag was varied randomly across trials to include delays ranging from 0 to 20 ms (0, 1, 4, 6, 8, 10, 15, and 20), with 20 repetitions of each delay. The lead and lag sources were presented either from −60° (left) and +60° (right) or vice versa.

2.4. Experiment III: discrimination suppression

Testing was conducted in a double-walled soundproof booth (IAC). The TDT AP2 array processor and PD1 Power DAC were used to generate the stimuli. The sampling rate was 200 kHz, thereby allowing interaural differences as small as 5 μs. Stimuli were amplified by a TDT HB6 headphone amplifier and presented at a level of 60 dB SPL via Sennheiser HD520II headphones.

The task was a two-interval two-alternative forced choice. Each trial consisted of two intervals: interval A, containing the *reference* stimulus, and interval B, containing the *comparison* stimulus, were separated by 500 ms (see Fig. 4C). In the reference stimulus a dichotic click pair occurred with an ITD of either +300 μs or −300 μs. Within each block of trials, this ITD value remained constant. In the comparison stimulus two dichotic click pairs occurred, a lead and a lag, with a delay of 2 ms between their onsets. The lead pair had an ITD identical to that of the reference. The lag pair had an ITD that varied adaptively to the

right or left of the reference, with the end result being an ITD just noticeable difference (JND) threshold. Listeners performed a two-alternative forced-choice task, whereby they reported whether the sound image in the comparison stimulus was perceived to the right or left of the reference stimulus. Feedback was provided on every trial. JND thresholds were estimated using a PEST algorithm (Taylor and Creelman, 1967) with a starting change in ITD difference of 500 μs. In addition to the stimulus configuration shown in Fig. 4C, a single-source condition was run with the lead click pair turned off on the comparison stimulus. For each condition three thresholds were measured with the order of presentation of precedence and single-source conditions randomized.

2.5. Experiment IV: speech intelligibility and spatial release from masking

Speech intelligibility is hampered by the presence of competing sounds such as noise and speech. A well-known phenomenon is the benefit that listeners experience when the target and competing speech are spatially separated, known as the 'spatial release from masking'. The purpose of this experiment was to determine the extent to which a lesion in the IC might affect the subject's ability to experience spatial release from masking.

The methods used here are similar to those in previous studies (e.g., Hawley, 2000; Hawley et al., 2000; Culling et al., 1999). The subject was seated in the same
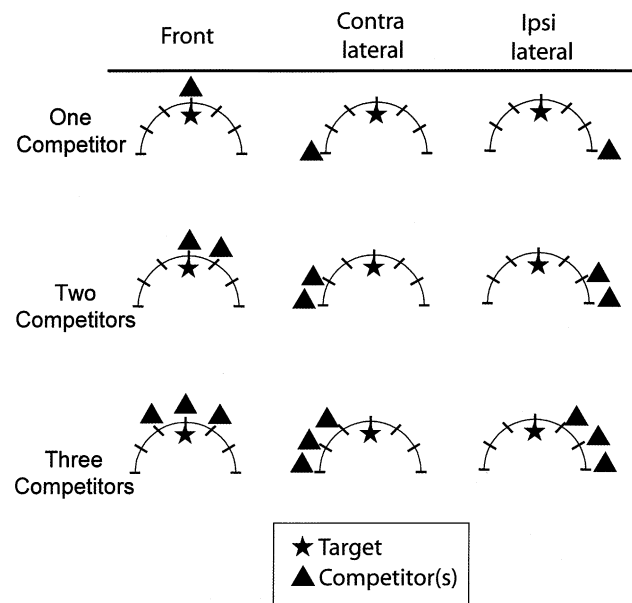

Fig. 5. Stimulus configurations for the speech intelligibility testing. The target location was always in front at 0° (★) and competitor locations varied (▲). Each competitor configuration used is shown, with a different number of competitors in each row, and a different configuration in each column.
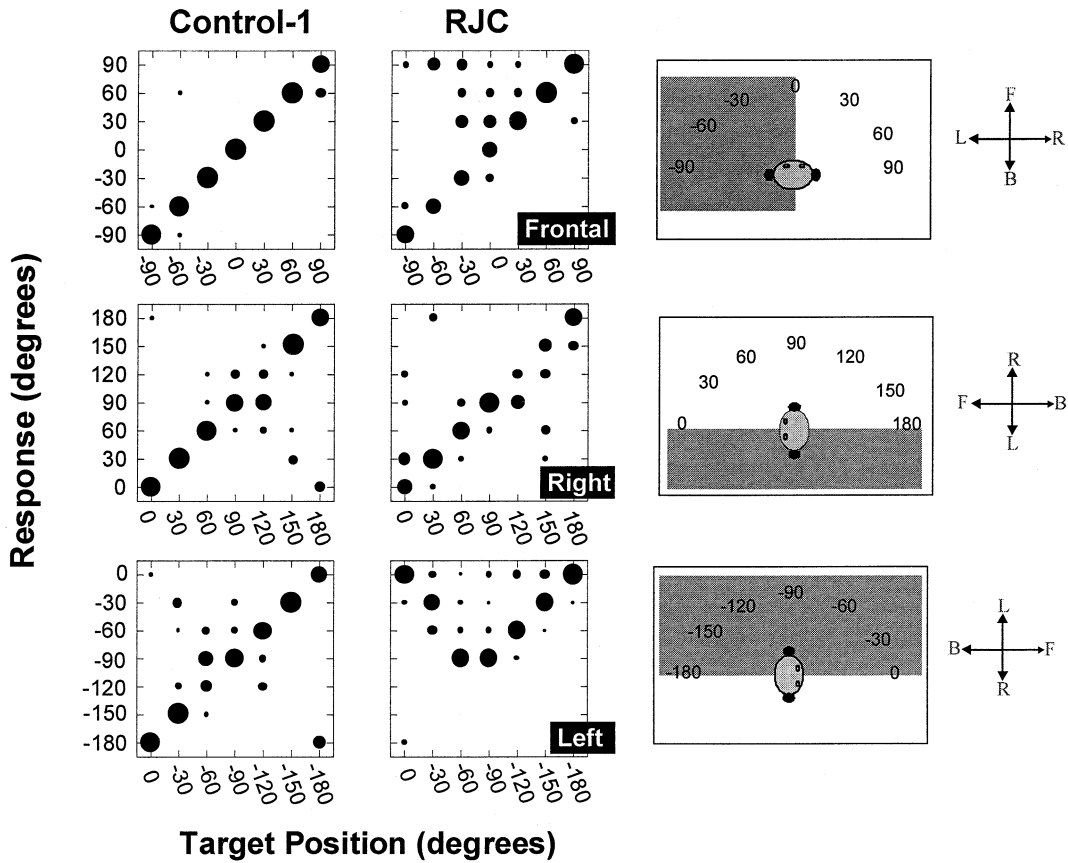
Fig. 6. Single-source localization results. Data for one normal control subject and for RJC are shown in the left and middle columns, respectively, for three stimulus configurations depicted in the right column. From top to bottom, these are the frontal, right and left conditions. The numbers in each configuration represent the angles of the speakers in the room relative to the center of the subject's head. Gray areas denote the hemifield contralateral to the lesion site. Each plot shows the proportion of trials on which responses occurred at each position, as a function of the true (target) source positions, demarcated by dot size.

room as the one used in experiments I and II, with loudspeakers positioned at 30° intervals. Two stimulus types were employed. The 'target' stimuli consisted of sentences from the HINT corpus (Nilsson et al., 1994) spoken by a male voice and were always presented from 0° in front of the listener. The 'competitor' stimuli consisted of sentences from the Harvard IEEE corpus (IEEE, 1969), spoken by a different male voice, and presented in nine spatial configurations (see Fig. 5). The number of competitors was one, two or three, and when more than one competitor was present they consisted of different sentences. For each number there were three spatial configurations, including conditions in which the competitors were near the target in the right hemifield (ipsilateral to the lesion), or in the left hemifield (contralateral to the lesion).

For each condition a speech reception threshold (SRT) was measured by varying the target level adaptively while holding constant the level of the competitor(s). To determine the appropriate competitor levels for each subject, 'quiet' thresholds were measured first, in the absence of a competitor. The competitor level(s)

were then set to 30 dB above the quiet threshold. For most subjects, quiet thresholds were 25–30 dB SPL, hence competitor levels ranged from 55 to 60 dB SPL (exact levels are included in results figure). The nine conditions were each repeated three times in random order. During each threshold measurement the same competitor sentence was repeated on every trial, and new competitors were chosen on each run. During testing the text of each competitor sentence was visually presented on a computer terminal, and the subject was instructed to ignore the competitor(s) and to repeat out loud the content of the sentence that was not displayed. The experimenter (sitting in an adjacent room and listening through an intercom) recorded whether the entire sentence was correctly repeated or not, and the level for the next trial was computed. Feedback was not provided.

Each threshold was measured adaptively according to a 1-down-1-up rule, targeting 50% keywords correct with 15 trials per list. Initially, the first sentence in the list was presented at the level of the quiet threshold, and the level was increased in 4 dB steps until the entire

sentence was correctly reported. Subsequently, a 2 dB step size was employed; the level was reduced following correct sentence identification and increased if any of the words in a sentence were not correctly identified. SRT was computed as the average of all but the first sentence.

Experimentation on human subjects was approved by Boston University's Internal Review Board and was carried out in accordance with the Declaration of Helsinki.

3. Results

3.1. Sound localization

The ability to localize a brief click train is shown separately for the three testing configurations. Recall that in the *frontal* condition subjects sat facing the loudspeakers with sources spanning ±90° right to left. In the *right* condition subjects faced the left-most speaker such that the sources spanned front to back in the right hemifield (ipsilateral to the lesion). In the *left* condition subjects faced the right-most speaker such that the sources spanned front to back in the left hemifield (contralateral to the lesion). Data for RJC and for one control subject are shown in Fig. 6. The right-most panels in the figure show a schematic diagram of the speaker configurations relative to listener's head. The gray areas demarcate the hemifield opposite to RJC's damaged IC, denoting the spatial region for which one might expect to find deficit in performance.

Results in the frontal condition suggest that RJC localized sources in the right hemifield quite well, but sources in the left hemifield were somewhat displaced towards the right. This is in contrast to the normal control subject whose performance was nearly perfect with no evidence of bias towards either side. This finding suggests that the hemifield mediated by the healthy IC dominates localization compared with the damaged IC. In the right condition localization performance is fairly accurate, similar to that of the control subject. However, for sounds on the left RJC shows a remarkable inability to perceive sounds coming from behind, and all sources are displaced towards the front. The normal control subject showed no such effect. Two other control subjects were tested and showed extremely accurate performance on all conditions, hence the data are not plotted.

3.2. Echo suppression

The strength of echo suppression was measured by plotting the percent of trials on which a listener reported two sounds as a function of delay. Fig. 7 com-
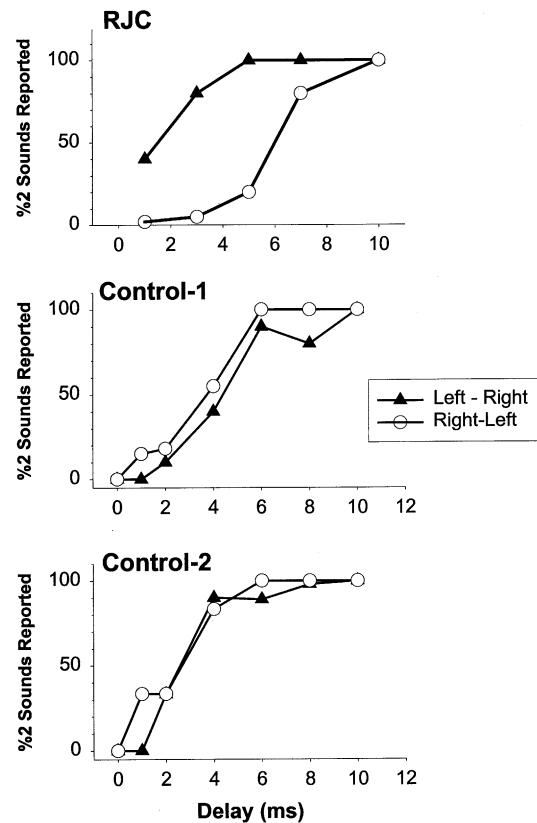

Fig. 7. Echo suppression data from RJC (top) and two normal control subjects (middle and bottom) are shown. Each panel compares conditions in which the lead was on left and lag on right (▲) or the reverse (○). Percent of trials on which listeners reported hearing two sounds is plotted as a function of lead–lag delay.

pares conditions in which the leading source was on the left and lag on the right (▲) or the reverse (○). For RJC (top) there is a clear effect of side, whereby two sounds are reported at much shorter delays when the lead is on the left, contralateral to the lesion, than when the lead is on the right, ipsilateral to the lesion. This finding suggests that the mechanism for suppressing the lag (echo) is much weaker when the leading sound is on the left, i.e., in the right side of the brain. Normal control data for two subjects (center and bottom panels) do not appear to have the same asymmetry; rather, the left–right and right–left curves are quite comparable, suggesting that in a patient with no known brainstem lesion suppression is similar regardless of which side contained the leading source.

3.3. Discrimination suppression

Fig. 8 shows mean and standard deviations for discrimination thresholds in RJC and two normal control subjects (C1 and C2). The top and bottom panels show results for testing in the right hemifield (+300 μs), ipsilateral to the lesion, and the left hemifield (−300 μs),
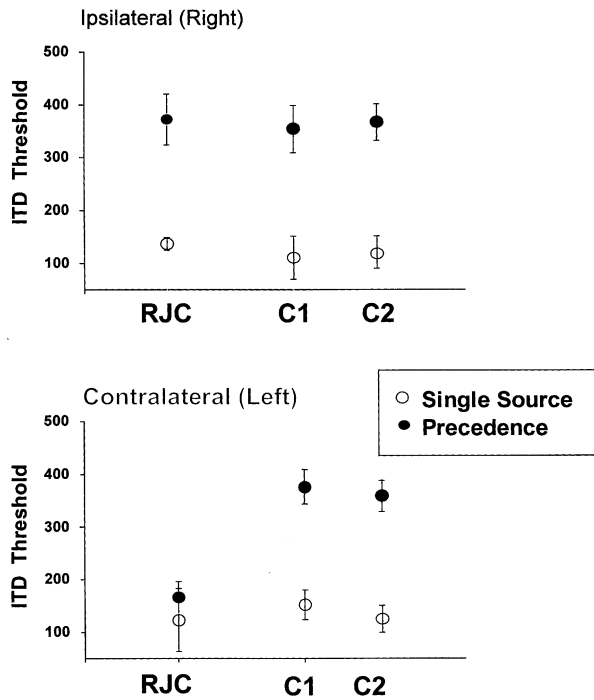
Fig. 8. Discrimination suppression data from RJC and two normal control subjects are compared in each panel. Conditions in which a single source sound was discriminated are plotted in open circles (○), and precedence conditions in which changes in the ITD of the lag were discriminated are shown in filled circles (●). For each condition and subject, the ITD JND thresholds are plotted, marking the change in ITD that listeners could reliably discriminate on 70.9% of trials.

contralateral to the lesion. Performance was expected to be substantially worse on the precedence condition (●) than on the single source condition (○), regardless of which side the stimuli were on (see Litovsky et al., 1999). Note that when the stimuli were on the right side (ipsilateral) the expected result is observed in all subjects: thresholds were on the order of 100–130 μs on single source and 350–375 μs on precedence conditions. In contrast, when stimuli were on the left (contralateral) side only the normal control subjects continued to show elevated precedence thresholds. RJC did not, and was therefore better than the normal controls at extracting binaural information from the simulated echo in the presence of a leading sound. This finding suggests that a patient who has sustained a unilateral brainstem lesion is unable to suppress directional information contained in delayed signals, when the sources are contralateral to the lesion. In fact, such a patient has an abnormally good ability to perform on the precedence task, which in the absence of a lesion is substantially more difficult. This finding is consistent with the echo suppression results, which showed that suppression of echoes is achieved more readily for signals ipsilateral to the lesion, and is weaker for contralateral signals.

3.4. Speech intelligibility and spatial release from masking

The purpose of this experiment was to determine the extent to which a lesion in the IC might affect the subject's ability to experience spatial release from masking. For the nine conditions diagrammed in Fig. 5, Fig. 9 shows data from RJC (top) and two normal control listeners. Data consist of average and standard deviations for SRTs relative to the competitor level (demar-
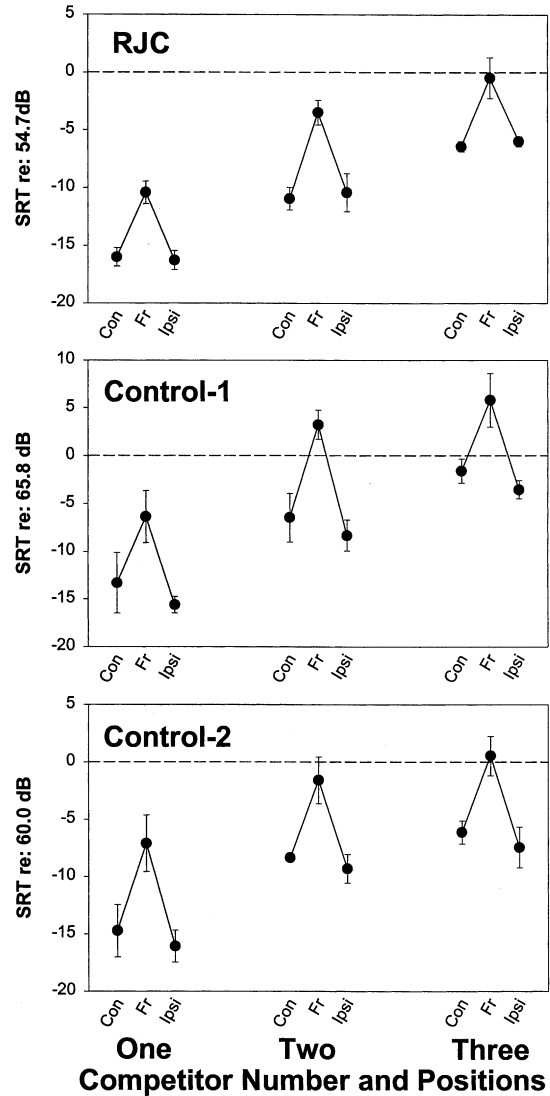

Fig. 9. Speech intelligibility data are shown for RJC (top) and two normal control subjects (middle and bottom). Viewing each plot from left to right, data are grouped according to the number of competitors, which increased from one to three. In all cases, the target was positioned at 0° in front of the listener. For each number, three configurations are compared in which the competitor(s) were contralateral to RJC's lesion (left), in front, or ipsilateral to RJC's lesion (right). For each condition, the listener's SRT relative to the level of each competitor is plotted. The horizontal dashed line in each plot denotes the level at which each competitor was played.

cated by the horizontal dashed line at 0 dB in each plot). Recall that each subject was tested with competitor levels set to 30 dB above their quiet thresholds. RJC's competitor level was set to lower levels than the control subjects, suggesting that his hearing in quiet is better. In addition, data from subject control-1 ascend above the horizontal line, suggesting that her SRTs were worse than RJC's.

Note that for all subjects SRTs increase as the number of competitors increases, consistent with the idea that added competition introduces more energy in the maskers as well as additional linguistic interference, which leads to intelligibility being more difficult. Within each number of competitors, thresholds were highest for the frontal conditions in which the competitor(s) and targets are physically near each other. Thresholds decrease when the competitor(s) were on either side of the target. Interestingly, the decrease is symmetrically distributed about the front, with benefit in speech intelligibility apparent regardless of whether the competitors are displaced towards the ipsilateral or contralateral sides. While this finding is expected in normal listeners, it differs from the other results obtained in RJC that showed a marked asymmetry for all measures.

4. Discussion

Two of the most important functions served by the auditory system are the localization of sound sources in space and the ability to separate sounds that compete for perception in order that the one of interest may be perceived. The binaural system has been identified as a likely candidate for the initial mediation of the processes involved in these abilities (Durlach and Colburn, 1978; Blauert, 1997; Bronkhorst, 2000). In this study we attempted to determine the functional role of the IC in binaural abilities and speech perception in noise, by investigating the effect of a unilateral brainstem lesion on sound localization, the PE and spatial release from masking in speech.

Several main results are worth noting. First, a subject with a unilateral brainstem lesion showed abnormal sound localization for a single-source click train. Sources presented in the front were localized with a bias towards the hemifield ipsilateral to the lesion. In addition, front/back discrimination was abnormal in the hemifield contralateral to the lesion, with a bias towards hearing sounds in the front rather than behind. Second, the PE in RJC was abnormally weak for sources contralateral to the lesion compared with sources ipsilateral to the lesion, which fell within a normal range of both echo suppression and discrimination suppression. Third, a brainstem lesion does not seem to interfere with the benefit that listeners experience in

speech intelligibility when the target and competing sounds are spatially separated. Regardless of the side towards which the competitor(s) were displaced, RJC showed a robust benefit. In the paragraphs that follow we attempt to relate our findings to what is known about auditory mechanisms and to link psychophysics and physiology related to binaural and spatial hearing.

4.1. Sound localization

The abnormal localization abilities observed in RJC are consistent with the subject's own report of having trouble balancing the stereo system in his automobile and localizing sound sources in the environment. Although it is not possible to determine the exact structures that were damaged in subject RJC, the radiology report suggests that they most likely include the IC and/ or its inputs from the LL. The latter include contralateral inputs from the ventral nucleus, and bilateral inputs through the dorsal nucleus (DNLL), both of which are most likely inhibitory, and involved in shaping the directional properties of IC neurons (Shneiderman et al., 1988; Shneiderman and Oliver, 1989; Glendenning et al., 1981). As one might expect, damage to those regions would most likely impair directional selectivity of neurons that mediate sound localization. In the frontal and left hemifield cases, neurons in the right IC (mediating the left hemifield) were worse at providing an accurate representation of space, hence the errors and bias towards the right and front. In contrast, in the right hemifield case performance was comparable to that of normal control subjects, suggesting that the intact IC was perfectly capable of providing accurate directional cues. These findings are consistent with animal lesion work which suggests that the ability of animals to localize sounds in contralateral space is impaired after unilateral lesions in the dorsal midbrain, including the IC and DNLL (e.g., Kelly and Kavanagh, 1994; Kelly et al., 1996; Jenkins and Masterton, 1982). Finally, the fact that the lesion seemed to have no effect on localization in the ipsilateral hemifield is interesting, given the fact that the LL sends major inhibitory projections to the IC. Since a more refined image of the lesioned area was not available, it is impossible to rule out an incomplete destruction of projections to and from the IC. The ones mediating ipsilateral responses may have incurred greater damage than contralateral ones, which would be consistent with findings presented here.

4.2. Echo suppression and discrimination suppression

One of the most compelling auditory illusions is related to the suppression of echoes and the prominence of the source in perception and localization. Although

we are aware of the presence of echoes in rooms, we are unable to identify their location. More compelling is the PE paradigm, where the 'echoes' are presented at the same intensity as the 'source'; nonetheless listeners subjectively report that only one auditory event has occurred (Freyman et al., 1991; Litovsky et al., 1999; Litovsky and Shinn-Cunningham, 2001). Neurophysiological studies on this topic have shown that the IC is a likely site for mediating initial stages of precedence. Neurons in the IC show suppression of responses to the lagging sound, which extends to delays much beyond simple adaptation or refractoriness (see Litovsky et al., 1999 for review). Yin (1994) suggested that for very short delays, where both lead and lag contribute to the perceived location of the fused auditory event, the discharge rates of IC neurons are related to the location at which the animal would perceive the sound. In addition, the extent of suppression mimics psychophysical findings related to stimulus parameters such as the relative and absolute levels, duration, frequency content and locations of the lead and lag (Litovsky and Yin, 1998a,b). It is therefore not surprising that RJC had substantially weaker echo suppression when the leading source was contralateral to the lesion.

While a number of possible circuits may account for such a result, it is unlikely that they bypass the IC. Some of the echo suppression may be mediated in monaural circuits such as the cochlear nucleus (e.g., Wickesberg and Oertel, 1990; Parham et al., 1998), although ultimately that suppression must be relayed through the IC, with or without further refinement. Most likely, target neurons in the IC receive excitation from the ipsilateral medial superior olive and inhibition from the contralateral lateral superior olive, which may be mediated by additional inputs from the DNLL and local circuits within the IC itself (Cai et al., 1998). In the present study, a leading source from the hemifield mediated by the damaged IC did not produce inhibition sufficient for suppressing the lagging source, nor did it maintain suppression that may have been produced at lower levels. Subject RJC served as his own control by showing normal echo suppression performance for the reverse condition in which the lead was presented from the right (ipsilateral) hemifield.

The discrimination suppression results provide a strong line of evidence in support of there being substantial integration of inputs at the level of the IC. While the echo suppression findings may be accounted for by largely monaural inputs, the discrimination suppression task is inherently a binaural task requiring the use of directional cues. For sources contralateral to the lesion, RJC's performance was better than that of control subjects; he was able to extract binaural properties of the lagging source, presumably due to absence of binaural suppression necessary for discrimination sup-

pression to occur (Zurek, 1980; Litovsky et al., 1999). Again, RJC served as his own control by showing the proper suppressive effect for sources ipsilateral to the lesion. While it is unusual for lesion subjects to perform 'better' than control subjects, this difference may not provide a benefit, for it implies increased interference from echoes which is likely to impede performance in reverberant environments.

Finally, we must address the finding that RJC's single-source ITD thresholds were within normal range, even though his localization performance showed deficits. These results are consistent with a recent report (Furst et al., 2000) on patients with brainstem lesions due to multiple sclerosis, whose lateralization performance was severely impaired compared with discrimination performance. A relatively simple model in which two stages of binaural processing occur may account for these results. The first level occurs in the superior olivary complex, where interaural differences are first coded and where binaural characteristics of neurons may be sufficient for discriminating between sources carrying different ITD cues. A second stage, at the level of the IC or higher, integrates binaural cues and provides the organism with a spatial map that operates in localization tasks. The extent to which the response properties of IC neurons are inherited from the superior olivary complex and the extent to which they represent newly formed processes is still unknown. While to some extent physiological properties of IC neurons reflect those of its individual inputs, some novel properties are present which support the idea of there being substantial integration at the level of the IC (e.g., Kuwada et al., 1987).

4.3. Speech intelligibility and spatial release from masking

Let us consider whether the IC and binaural mechanisms are indeed necessary for the speech tasks measured here, for, if they are not, it is no surprise that RJC had a substantial, normal and symmetrical SRM. The benefit gained in speech intelligibility by spatially separating the target and competitor(s) has both a monaural and a binaural component (for review, see Bronkhorst, 2000). The monaural component is derived from what is known as the 'head shadow' effect. A competing source on the side is attenuated by the head once it reaches the opposite ear, producing improved signal-to-noise ratio for the target in that ear. Using the opposite 'better ear' alone, listeners are able to perform quite well on speech intelligibility tasks in the presence of interfering sounds. The binaural component is due to ITD differences between the target and competitor(s), which assist in de-correlating the sources and improving perceptual segregation.

While modeling efforts on this topic have successfully accounted for the effects of head shadow and ITD for one-competitor noise conditions (e.g., Zurek, 1993), they have not addressed conditions such as those used in the present study, in which multiple speech signals were employed as competitors. Similar data do exist though, in which the relative contributions of head shadow and ITDs were compared for speech intelligibility in the presence of multiple competing speech signals (Hawley et al., 1999). Considering the total SRM, 79% could be attributed to monaural 'head shadow' effects, and the remaining 21% to binaural interaction effect. As the number of competitors increased, masking levels increased as well. A variety of factors may have contributed to increased difficulty, such as the added energy in the maskers, as well as the increased confusion due to linguistic interference from additional talkers. The relative contribution of these factors is hard to tease apart using the current paradigm.

Although the IC represents a major station for relaying and refining binaural inputs from the lower brainstem to upper levels in the auditory pathway, it is clear that a unilateral IC lesion does not impair SRM on either the ipsilateral or contralateral hemifields. Since not all auditory inputs ascent through the IC, it is certainly possible that monaural afferents which bypass the IC and project directly to the thalamus can sustain the information for mediating SRM. That is not to say that binaural inputs would not assist a listener. While RJC's performance was quite 'normal' under conditions tested here, his subjective report is that of having trouble understanding speech in noisy environments. The possibility remains that under more stringent testing conditions where binaural inputs must be utilized he might have shown a deficit corresponding to his subjective reports. In our free field study, all spatial cues that are normally available in the world were present, which include interaural time and level differences as well as monaural level cues. Further studies might ascertain the relative importance of binaural and monaural cues in SRM. Meanwhile the present findings confirm psychophysical reports that SRM does indeed include a robust monaural component.

Acknowledgements

References

Aharonson, V., Furst, M., Levine, R.A., Chaigrecht, M., Korczyn, A.D., 1998. Lateralization and binaural discrimination of patients with pontine lesions. J. Acoust. Soc. Am. 103, 2624–2633.

Blauert, J., 1997. Spatial Hearing: The Psychophysics of Human Sound Localization, Revised Edition. MIT Press, Cambridge, MA.

Bronkhorst, A.W., 2000. The cocktail party phenomenon: A review of research on speech intelligibility in multiple-talker conditions. Acustica 86, 117–128.

Cai, H., Carney, L.H., Colburn, H.S., 1998. A model for binaural response properties of inferior colliculus neurons: I. A model with ITD-sensitive excitatory and inhibitory inputs. J. Acoust. Soc. Am. 103, 475–493.

Cariani, P., Delgutte, B., 1996. Neural correlates of the pitch of complex tones. II. Pitch shift, pitch ambiguity, phase invariance, pitch circularity, rate pitch, and the dominance region for pitch. J. Neurophysiol. 76, 1717–1734.

Cherry, C., 1953. Some experiments on the recognition of speech with one and with two ears. J. Acoust. Soc. Am. 25, 975–979.

Culling, J.F., Hawley, M.L., Litovsky, R.Y., 1999. Effects of the spatial distribution of competing sounds in speech reception thresholds. J. Acoust. Soc. Am. 105, 1344.

Durlach, N., Colburn, H.S., 1978. Binaural phenomena. In: Carterette, E.C., Friedman, M. (Eds.), Handbook of Perception, Vol. IV. Academic Press, New York, pp. 405–466.

Durrant, J.D., Martin, W.H., Hirsch, B., Schwegler, J., 1994. 3CLT ABR analyses in a human subject with a unilateral extirpation of the inferior colliculus. Hear. Res. 72, 99–107.

Fitzpatrick, D.C., Kuwada, S., Batra, R., Trahiotis, C., 1995. Neural responses to simple, simulated echoes in the auditory brainstem of the unanesthetized rabbit. J. Neurophysiol. 74, 2469–2486.

Freyman, R.L., Clifton, R.K., Litovsky, R.Y., 1991. Dynamic processes in the precedence effect. J. Acoust. Soc. Am. 90, 874–884.

Furst, M., Levine, R.A., Korczyn, A.D., Fullerton, B.C., Tdmor, R., Algom, D., 1995. Brainstem lesions and click lateralization in patients with multiple scrlerosis. Hear. Res. 82, 109–124.

Furst, M., Aharonson, V., Levine, R.A., Fullerton, B.C., Tadmore, R., Pratt, H., Polyakov, A., Korczyn, A.D., 2000. Sound lateralization and interaural discrimination. Effects of brainstem infarcts and multiple sclerosis lesions. Hear. Res. 143, 29–42.

Glendenning, K.K., Brunso-Bechtold, J.K., Thompson, G.C., Masterton, R.B., 1981. Ascending auditory afferents to the nuclei of the lateral lemniscus. J. Comp. Neurol. 197, 673–703.

Hawley, M.L., 2000. Speech Intelligibility, Localization and Binaural Hearing in Listeners with Normal and Impaired Hearing. Unpublished Doctoral Dissertation.

Hawley, M.L., Litovsky, R.Y., Colburn, H.S., 1999. Speech intelligibility and localization in a multi-source environment. J. Acoust. Soc. Am. 105, 3436–3448.

Hawley, M.L., Litovsky, R.Y., Culling, J.F., 2000. The cocktail party problem with four types of maskers: speech, time-reversed-speech, speech-shaped noise or modulated speech-shaped noise. Assoc. Res. Otolaryngol. Abstr. 105, 1150.

Heffner, H., Masterton, B., 1975. Contribution of auditory cortex to sound localization in the monkey. J. Neurophysiol. 38, 1340–1358.

IEEE, 1969. IEEE Recommended practice for speech quality measurements. IEEE Trans. Audio Electroacoust. 17, 225–246.

Jenkins, W.M., Masterton, R.B., 1982. Sound localization: effects of unilateral lesions in central auditory system. J. Neurophysiol. 47, 987–1016.

Jiang, D., McAlpine, D., Palmer, A.R., 1997. Detectability index measures of inaural masking level difference across populations of inferior colliculus neurons. J. Neurosci. 17, 9331–9339.

Kelly, J.B., Kavanagh, G.L., 1994. Sound localization after unilateral lesions of inferior colliculus in the ferret (*Mustela putorius*). J. Neurophysiol. 71, 1078–1087.

Kelly, J.B., Li, L., van Adel, B., 1996. Sound localization after kainic acid lesions of the dorsal nucleus of the lateral lemniscus in the albino rat. Behav. Neurosci. 110, 1445–1455.

Kuwada, S., Stanford, T.R., Batra, R., 1987. Interaural phase-sensitive units in the inferior colliculus of the unanesthetized rabbit: effects of changing frequency. J. Neurophysiol. 57, 1338–13360.

Kuwada, S., Batra, R., Fitzpatrick, D.C., 1997. Neural processing of binaural temporal cues. In: Gilkey, R., Anderson, T.R. (Eds.), Binaural and Spatial Hearing in Real and Virtual Environments. Lawrence Erlbaum, Hillsdale, NJ, pp. 399–425.

Litovsky, R.Y., 1998. Physiological studies on the precedence effect in the inferior colliculus of the kitten (selected research article). J. Acoust. Soc. Am. 103, 3139–3152.

Litovsky, R.Y., Shinn-Cunningham, B.G., 2001. Investigation of the relationship between three common measures of precedence: fusion, localization dominance and discrimination suppression. J. Acoust. Soc. Am. 109, 346–358.

Litovsky, R.Y., Yin, T.C.T., 1998a. Physiological studies of the precedence effect in the inferior colliculus of the cat: I. Correlates of psychophysics. J. Neurophysiol. 80, 1302–1316.

Litovsky, R.Y., Yin, T.C.T., 1998b. Physiological studies of the precedence effect in the inferior colliculus of the cat: II. Neural mechanisms. J. Neurophysiol. 80, 1302–1316.

Litovsky, R.Y., Colburn, H.S., Yost, W.A., Guzman, S., 1999. The precedence effect. Review and Tutorial paper. J. Acoust. Soc. Am. 106, 1633–1654.

Litovsky, R.Y., Lane, C., Atencio, C., Delgutte, B., 2001. Physiological measures of the precedence effect and spatial release from masking in the cat inferior colliculus. Advances in Hearing Research: 12th International Symposium on Hearing. World Scientific Publishers, Singapore.

Nilsson, M., Soli, S.D., Sullivan, J., 1994. Development of the Hearing in Noise Test for the measurement of speech reception thresholds in quiet and in noise. J. Acoust. Soc. Am. 95, 1085–1099.

Palmer, A.R., Jiang, D., McAlpine, D., 2000. Neural responses in the inferior colliculus to binaural masking level differences created by inverting the noise in one ear. J. Neurophysiol. 84, 844–852.

Parham, K., Zhao, H.B., Ye, Y., Kim, D.O., 1998. Responses of anteroverntral cochlear nucleus neurons of the unanesthetized decerebrate cat to click pairs as simulated echoes. Hear. Res. 125, 131–146.

Shneiderman, A., Oliver, D.L., 1989. EM autoradiographic study of the projections from the dorsal nucleus of the lateral lemniscus: a possible source of inhibitory inputs to the inferior colliculus. J. Comp. Neurol. 286, 28–47.

Shneiderman, A., Oliver, D.L., Henkel, C.K., 1988. Connections of the dorsal nucleus of the lateral lemniscus: an inhibitory parallel pathway in the ascending auditory system? J. Comp. Neurol. 276, 188–208.

Taylor, M.M., Creelman, C.D., 1967. PEST: Efficient estimates on probability functions. J. Acoust. Soc. Am. 41, 782–787.

Whitfield, I.C., 1978. Auditory cortical lesions and the precedence effect in a four-choice situation. J. Neurophysiol. 289, 81P.

Wickesberg, R.E., Oertel, D., 1990. Delayed, frequency-specific inhibition in the cochlear nuclei of mice: A mechanism for monaural echo suppression. J. Neurosci. 10, 1762–1768.

Yin, T.C.T., 1994. Physiological correlates of the precedence effect and summing localization in the inferior colliculus of the cat. J. Neurosci. 14, 5170–5186.

Yin, T.C.T., Joris, P., Smith, P.H., Chan, J.C.K., 1997. Neuronal processing for coding interaural time disparities. In: Gilkey, R., Anderson, T.R. (Eds.), Binaural and Spatial Hearing in Real and Virtual Environments. Lawrence Erlbaum, Hillsdale, NJ, pp. 427–445.

Yost, W.A., 1997. The cocktail party problem: Forty years later. In: Gilkey, R., Anderson, T.R. (Eds.), Binaural and Spatial Hearing in Real and Virtual Environments. Lawrence Erlbaum, Hillsdale, NJ, pp. 329–348.

Zurek, P.M., 1980. The precedence effect and its possible role in the avoidance of interaural ambiguities. J. Acoust. Soc. Am. 67, 952–964.

Zurek, P.M., 1993. Binaural advantages and directional effects in speech intelligibility. In: Studebaker, G.A., Hochberg, I. (Eds.), Acoustical Factors Affecting Hearing Aid Performance. Allyn and Bacon, Boston, MA, pp. 255–276.