# Interactions between auditory 'what' and 'where' pathways revealed by enhanced near-threshold discrimination of frequency and position

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## Abstract

Partially segregated neuronal pathways ("what" and "where" pathways, respectively) are thought to mediate sound recognition and localization. Less studied are interactions between these pathways. In two experiments, we investigated whether near-threshold pitch discrimination sensitivity ($d'$) is altered by supra-threshold task-irrelevant position differences and likewise whether near-threshold position discrimination sensitivity is altered by supra-threshold task-irrelevant pitch differences. Each experiment followed a $2 \times 2$ within-subjects design regarding changes/no change in the task-relevant and task-irrelevant stimulus dimensions. In Experiment 1, subjects discriminated between 750 Hz and 752 Hz pure tones, and $d'$ for this near-threshold pitch change significantly increased by a factor of 1.09 when accompanied by a task-irrelevant position change of 65 μs interaural time difference (ITD). No response bias was induced by the task-irrelevant position change. In Experiment 2, subjects discriminated between 385 μs and 431 μs ITDs, and $d'$ for this near-threshold position change significantly increased by a factor of 0.73 when accompanied by task-irrelevant pitch changes (6 Hz). In contrast to Experiment 1, task-irrelevant pitch changes induced a response criterion bias toward responding that the two stimuli differed. The collective results are indicative of facilitative interactions between "what" and "where" pathways. By demonstrating how these pathways may cooperate under impoverished listening conditions, our results bear implications for possible neuro-rehabilitation strategies. We discuss our results in terms of the dual-pathway model of auditory processing.
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## 1. Introduction

Several lines of evidence from human and non-human primate studies support a dual-pathway model of audition, wherein the processing of a sound's identity and location relies on partially segregated cortical networks, commonly referred to as "what" and "where" processing streams (e.g. Adriani, Bellmann, et al., 2003; Adriani, Maeder, et al., 2003; Alain, Arnott, Hevenor, Graham, & Grady, 2001; Altmann, Bledowski, Wibral, & Kaiser, 2007; Barrett & Hall, 2006; Clarke, Adriani, & Tardif, 2005; Clarke & Thiran, 2004; Degerman, Rinne, Salmi, Salonen, & Alho, 2006; Kaas & Hackett, 2000; Rauschecker & Tian, 2000; Anourova et al., 2001). Hemodynamic and electrophysiological studies in humans have shown that these two cortical streams partially overlap, suggesting that some auditory areas are actually involved in the processing of both auditory features (e.g. Arnott, Binns, Grady, & Alain, 2004; Barrett & Hall, 2006; De Santis, Clarke, & Murray, 2007). Single-unit recordings in the parabelt area of the macaque monkey have shown that while some neurons selectively respond to the identity of specific vocalizations (independent of the position) or to specific spatial positions (independent of their identity), others display selectivity for both features (Tian, Reser, Durham, Kustov, & Rauschecker, 2001). These findings raise the question about the nature and extent of interactions between "what" and "where" networks.

Some perceptual phenomena indicate that manipulating basic localization cues such as interaural time differences (ITD) can induce pitch perception from a binaurally presented background noise. In this phenomenon, known as the Huggin's pitch, the same white noise is presented to both ears with the exception of a narrow band of frequencies time-delayed between the two ears, producing the emergence of a faint pitch within the noise background corresponding to the center frequency of the shifted band. This perception may be regarded as an auditory analogue of Julesz's stereograms in the visual modality (Akeroyd, Carlyon, & Deeks, 2005; Cramer & Huggins, 1958; Culling, Summerfield, & Marshall, 1998; Hartmann & Zhang, 2003; Licklider, 1956; see also Kubovy, Cutting, & McGuire, 1974; Kubovy & Howard, 1976 for related auditory phenomena). This demonstrates that binaural cues for sound localization (e.g. the change in interaural correlation induced by interaural time differences; ITD) can impact not only the perceived position of a sound source, but also "what" is actually perceived. As such, perceptual outcomes in audition appear to be multidimensional, combining both spatial and pitch information. A lateralized pure tone can be considered as a multidimensional stimulus, because it creates a sound image representation that has both a particular pitch and position. Dimensions of a stimulus are considered *integral* when subjects are unable to attend selectively to one (task-relevant) dimension while ignoring variations in the other (task-irrelevant) dimension. By contrast, dimensions are considered *separable* when subjects can successfully ignore the task-irrelevant dimension and attend to the relevant one (Garner, 1974, 1976).

Discrepant conclusions have been drawn from psychophysical studies on the extent to which pitch and position are integral or separable auditory dimensions. Reaction times (RTs) were slower on a go/no-go task that required subjects to detect a 1000 Hz tone in the left ear while ignoring concurrent task-irrelevant tones of various frequencies (Näätänen, Porkka, Merisalo, & Ahtola, 1980). This was particularly pronounced when task-irrelevant frequency values approached 1000 Hz (i.e. the target frequency). This effect was only present if the task-relevant and task-irrelevant stimuli were presented to the same ear; dichotic conditions showed no effect of frequency. They concluded that the two dimensions were processed separately because frequency could be ignored when presented at an opposite position than the target. Further studies by Dyson and Quinlan (2002, 2003) using a simple target–nontarget discrimination task also concluded that frequency and position were separable auditory dimensions.

By contrast, Mondor, Zatorre, and Terrio (1998) found that adding random task-irrelevant changes in one dimension impaired performance in judgments on the other dimension and concluded that frequency and location are integral. Further studies showed that judgments of whether two successive tones had the same pitch or position were slowed when task-irrelevant changes were added in the other dimension, again supporting the integrality of the two dimensions (Dyson & Quinlan, 2004). However, these authors also found that RTs were faster for position than frequency judgments when the relevant dimension differed, suggestive of some degree of separation

between frequency and position processing. Dyson and Quinlan concluded that frequency and position processing may entail multiple stages, such that at an early stage the two dimensions are integrally bound together and at a later stage they become separable.

Conjoint with the above discrepancies concerning whether position and frequency are separable or integral auditory dimensions is the fact that prior psychophysical studies used perceptual differences well above threshold and based their interpretations solely on RT changes across conditions. The main drawback of such a design is that (nearly) error-free performance does not provide information regarding subjects' discrimination sensitivity, which is arguably more informative, particularly in clinical populations. The consequence is that studies based solely on RT may be severely limited to situations involving the discrimination of supra-threshold differences. In the present study, we investigated whether auditory frequency and position processing interact during the performance of a discrimination task with near-threshold stimulus differences, which would speak in favor of cross-talk between auditory "what" and "where" pathways. Specifically, we examined (1) whether near-threshold discrimination sensitivity along one auditory dimension would be impaired or enhanced by the inclusion of small, supra-threshold changes in the other, task-irrelevant dimension and (2) whether such changes in discrimination sensitivity were independent of changes in subjects bias in their response criterion, which would in turn indicate if either frequency or position information predominates auditory processing.

## 2. Methods

### 2.1. Experiment 1

#### 2.1.1. Participants

In Experiment 1, the nine participants (three women) were aged 25–36 years (mean ± S.D. 29.9 ± 3.9 years). Two were left-handed, and one was ambidextrous (Edinburgh questionnaire; Oldfield, 1971). None of the subjects had history of neurological or psychiatric illness, and they all reported normal hearing. They all provided written consent to participate in the experiment. All procedures were approved by the Ethics Committee of the Faculty of Biology and Medicine at the University of Lausanne and were conducted in accordance with the Declaration of Helsinki.

#### 2.1.2. Stimuli and paradigm

Stimuli were pure tones of either 750 Hz or 752 Hz (500 ms duration; 10 ms rise/fall envelope to minimize clicks; 44,100 Hz digitization) generated with Adobe Audition 1.0 (http://www.adobe.com) and presented through insert earphones (ER-4P/http://www.etymotic.com). Sound pressure levels in each ear were 88 dB SPL (measured using a CESVA SC-L sound pressure meter; http://www.cesva.com). Sounds were always presented binaurally with an ongoing ITD of either 385 μs or 450 μs, which resulted in perceived positions within the right hemisphere at approximately 40° and 50° from azimuthal midline, respectively (according to Blauert's complex formula, Blauert, 1997). These ITD values were selected based on our previous work, which has shown these values to be supra-threshold but still well below ceiling (Spierer, Tardif, Sperdin, Murray, & Clarke, 2007). On each trial, two tones were presented that were separated by a fixed 280 ms silent inter-stimulus interval (ISI). The first tone was always 750 Hz with an ITD of 385 μs. The features of the second tone varied in their frequency and position according to a 2 × 2 design (see Fig. 1), such that the frequency of the second tone could either be 750 Hz or 752 Hz and the perceived position was induced by either 385 μs or 450 μs ITD. Following the onset of the second stimulus, a response window (maximum 1300 ms) opened. Immediately

## Frequency discrimination
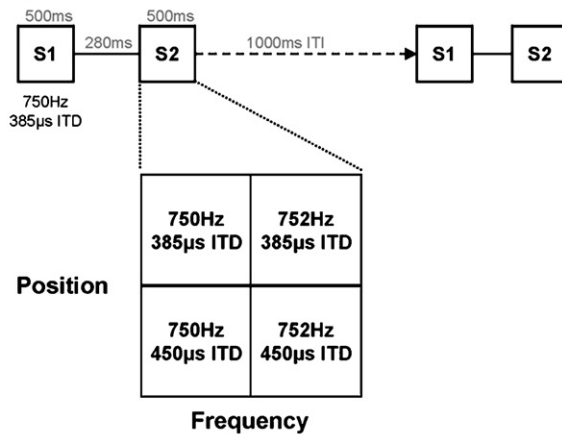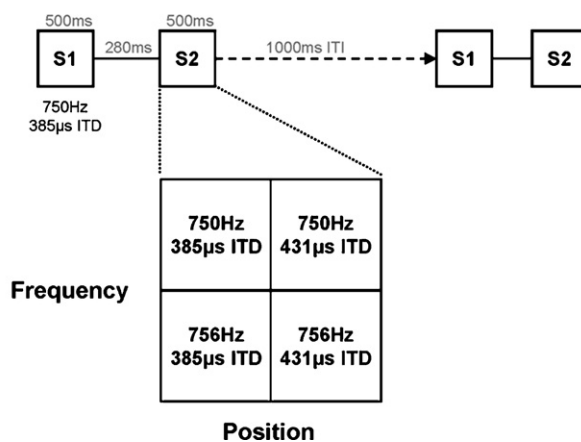


## Position discrimination



Fig. 1. Schematic representation of the experimental paradigms. Sounds were presented in pairs, and the first stimulus (S1) was always a 750 Hz tone with 385 μs ITD. The second stimulus (S2) followed 280 ms later and its properties followed a 2 × 2 design. In Experiment 1 (top panel), S2 had either the same or different frequency (i.e. 750 Hz or 752 Hz) and had either the same or different position (385 μs ITD or 450 μs ITD). Subjects were asked whether the pitch was same or different while ignoring potential changes in position. In Experiment 2 (bottom panel), S2 had either the same or different frequency (i.e. 750 Hz or 756 Hz) and had either the same or different position (385 μs ITD or 431 μs ITD). Subjects were asked whether the position was same or different while ignoring potential changes in pitch. The inter-trial interval was 1000 ms after the subject's response.

after the subject's response, an inter-trial interval of 1000 ms was introduced. In Experiment 1, frequency was the relevant dimension and participants were instructed to indicate as quickly and as accurately as possible whether the second tone had the same or different pitch as the first. That is, participants were instructed to detect a 0.27% change in frequency, which roughly corresponds to the average discrimination threshold in healthy subjects (Delhommeau, Micheyl, & Jouvent, 2005). Each participant completed five blocks of 100 trials. Within a block of trials, each of the four possible types of second tone was equally probable, for a total of 125 trials per condition.

Experiment 1 was conducted in an acoustically attenuated booth (http://www.eckel.ca). Participants sat in a comfortable chair and centrally fixated a cross appearing at the center of a computer monitor. After each trial, visual feedback was given to indicate whether responses were correct, incorrect, or too slow (indicated by 'O', 'X', and '–', respectively). Stimulus delivery, response recording, and accuracy feedback were controlled by E-Prime (Psychology Software Tools, http://www.pstnet.com/eprime).

### 2.2. Experiment 2

#### 2.2.1. Participants

In Experiment 2, the nine participants (four women) were aged 26–36 years (mean ± S.D. 30.2 ± 3.9 years). Three were left-handed, and one was ambidextrous (Edinburgh questionnaire; Oldfield, 1971). None of the subjects had history of neurological or psychiatric illness, and they all reported normal hearing. They all provided written consent to participate in the experiment. All procedures were approved by the Ethics Committee of the Faculty of Biology and Medicine at the University of Lausanne and were conducted in accordance with the Declaration of Helsinki. Five individuals participated in both experiments (always in Experiment 1 first), and for these individuals there was an average of 286 days between their participation in each experiment (range 282–292 days).

#### 2.2.2. Stimuli and paradigm

Experiment 2 was paradigmatically highly similar to Experiment 1 (see Fig. 1). In Experiment 2, the frequency of the second tone could either be 750 Hz or 756 Hz, and the perceived position was induced by either 385 μs or 431 μs ITD. For this, experiment position was the relevant dimension and participants were instructed to respond whether the position of the second tone was the same or different as the first. They had to detect an ITD disparity of 46 μs, which our previous research and pilot data indicated corresponds roughly to the threshold values when the initial position of a stimulus pair is 385 μs (Spierer et al., 2007). All other aspects (i.e. stimulus delivery and number of trials) were identical to those of Experiment 1.

Experiment 2 was conducted in an acoustically attenuated booth (http://www.eckel.ca). Participants sat in a comfortable chair and centrally fixated a cross appearing at the center of a computer monitor. After each trial, visual feedback was given to indicate whether responses were correct, incorrect, or too slow (indicated by 'O', 'X', and '–', respectively). Stimulus delivery, response recording, and accuracy feedback were controlled by E-Prime (Psychology Software Tools, http://www.pstnet.com/eprime).

### 2.3. Data analyses for both experiments

Accuracy rates and RTs were analyzed from each experiment separately with a 2 × 2 repeated measures analysis of variance (ANOVA) using frequency and position as within-subject factors. In the case of significant interactions between these factors, follow-up contrasts were conducted using the Wilcoxon signed ranks test, which is a non-parametric equivalent of a paired t-test.

The main analyses in this study were based on signal detection theory (Green & Sweets, 1966; Macmillan & Creelman, 2005; Wickens, 2002). In particular, we compared sensitivity $(d')$[1] to the task-relevant dimension in the absence of contemporaneous task-irrelevant changes, with sensitivity to changes in the relevant dimension in the presence of contemporaneous changes in the task-irrelevant dimension. Sensitivity was calculated as the difference between the z-score transformation of the hit and false alarm rates [i.e. $d' = z(H) - z(FA)$]. A correct answer to a trial in which the second stimulus of a pair differed with regard to the task-relevant dimension (i.e. answering "different") was considered as a hit. A false alarm was computed when a subject responded "different" in trials where no difference between the two stimuli was present with regard to the task-relevant dimension. As illustrated in Fig. 1, the first stimulus of a pair was always the same and the second one had four possibilities: (1) with neither task-relevant nor task-irrelevant differences (i.e. the two stimuli of the pair were identical and the correct response was "same"); (2) with only a task-relevant difference (correct response = "different"); (3) with only a task-irrelevant difference (correct answer = "same") and (4) with both task-relevant and task-irrelevant differences (correct answer = "different"). Hits in trials (2) and false alarms in trials (1) were used to calculate $d'$ without task-irrelevant change; hits in trials (4) and false alarms in trials (3) were used to calculate $d'$ including task-irrelevant change. Values of $d'$ with and without task-irrelevant change were compared using the

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[1] Macmillan and Creelman (2005) describe on p. 460 the following two definitions of sensitivity: (1) "the ability to discriminate, that is, to capture the experimenter-defined correspondence by appropriate responding" and (2) "A measure of discriminability that is not affected by response bias".

Wilcoxon signed ranks test. We also evaluated participants' bias in response criterion ($c$), which is calculated as $-0.5[z(H) + z(FA)]$ (Macmillan & Creelman, 2005). Response criterion was calculated in order to determine if participants were more prone to respond "same" or "different" in the presence or absence of a contemporaneous change in the task-irrelevant dimension. A criterion score of 0 would indicate that participants made an equivalent proportion of "misses" (i.e. responding "same" when an actual change in the relevant dimension was present) and false alarms. A positive criterion score would indicate a bias to respond "same", whereas a negative criterion score would indicate a bias to respond "different". Criterion scores obtained with and without task-irrelevant change were compared using the Wilcoxon signed ranks test as above, and deviation of these values from 0 was likewise evaluated using the Wilcoxon signed ranks test.

## 3. Results

### 3.1. Experiment 1: effect of position changes on near-threshold frequency discrimination

The mean accuracy rates and mean RTs are shown in Table 1. In terms of response accuracy, trials including only a frequency change showed the lowest performance (near chance levels), confirming that the discrimination task was near-threshold. A main effect of position change was observed ($F_{(1,8)} = 15.54$; $p = 0.004$) as well as an interaction between frequency and position changes ($F_{(1,8)} = 13.20$; $p = 0.007$). Follow-up contrasts showed that while the addition of a task-irrelevant position change did not significantly affect "same" responses, it did significantly increase accuracy rates for "different" responses ($p = 0.008$). As will be shown in the analysis based on signal detection theory below, this interaction followed from the fact that participants predominantly responded and were in fact biased to respond that the sounds were the same frequency when no ITD difference was introduced. By contrast, when an ITD difference was introduced participants more accurately responded that the sounds were different frequencies but showed no bias in doing so. In terms of the analysis of mean RTs, the main effect of (relevant) frequency change did not meet the 0.05 significance criterion ($F_{(1,8)} = 2.94$; $p > 0.10$). There was a significant main effect of (task-irrelevant) position change ($F_{(1,8)} = 6.56$; $p = 0.034$), with RTs being generally faster when the position changed between the first and second sounds of each trial. The interaction between factors of position and frequency was marginally significant ($F_{(1,8)} = 5.21$; $p = 0.052$). Follow-up contrasts showed that while the addition of a task-irrelevant position change did not significantly affect RTs for responding "same", it did significantly facilitate RTs for responding "different" ($p = 0.038$). This pattern of results is consistent with a redundant signals effect (e.g. Miller, 1982; Raab, 1962). Furthermore, these RT data indicate that performance

improvements did not follow from a simple speed-accuracy trade-off.

Following a signal detection theory approach, sensitivity ($d'$) and bias in response criterion ($c$) to frequency changes with and without contemporaneous position changes were also analyzed (Fig. 2; see Methods). On average, sensitivity to frequency changes increased by a factor of 1.09 when the position of the sound also changed. Mean $d'$ values ($\pm$S.E.M.) were $0.68 \pm 0.29$ when no position change was present and $1.43 \pm 0.35$ when position changes were present. A non-parametric contrast (Wilcoxon signed ranks test) confirmed that sensitivity was significantly greater with contemporaneous position changes induced by ITD (Fig. 2a; $p = 0.004$). In addition, analyses of response criterion ($c$) revealed that the mean values of ($c$) with and without task-irrelevant position change were significantly different from each other (Fig. 2b; $p = 0.020$). In addition, the mean value of $c$ when no position change was present was significantly greater than zero ($c = 0.25 \pm 0.08$; $p = 0.020$), indicating that subjects were biased to respond that the frequency of the second sound did not change. In other words, when no task-irrelevant position change was present, subjects had more misses (i.e. responding "same" when an actual frequency difference was present) than false alarms, reflecting the fact that the 2 Hz difference was not discriminated in a high number of trials. By contrast, subjects showed no response bias in terms of frequency discrimination when the position of the second sound changed ($p = 0.203$), indicating that subjects made equal numbers of misses and false alarms. To illustrate this point, Fig. 2c shows $z$-score transformations of hit and false alarm rates for both the conditions without a task-irrelevant position change and with a task-irrelevant position change. While the hit rate increased across conditions, the false alarm rate was unchanged. The improvement in hit rate is therefore the basis for the significant sensitivity enhancement following the introduction of task-irrelevant position changes.

### 3.2. Experiment 2: effect of frequency changes on near-threshold position discrimination

Mean accuracy rates and RTs are shown in Table 2. There was a main effect of (task-irrelevant) frequency change ($F_{(1,8)} = 16.72$; $p = 0.003$) with trials including a frequency change yielding generally higher accuracy rates. Moreover, there was a significant interaction between frequency and position factors ($F_{(1,8)} = 43.75$; $p < 0.001$), which followed from participants being more accurate to respond "same" in the absence of a task-irrelevant frequency change ($p = 0.008$) and more accurate to respond "different" when a task-irrelevant frequency change was present ($p = 0.008$). As will be shown

Table 1
Mean accuracy rates ($\pm$S.E.M.) and reaction times (RT; in ms $\pm$ S.E.M.) for the frequency discrimination task (Experiment 1)

| | Mean accuracy rates ($\pm$S.E.M.) | | Mean reaction times ($\pm$S.E.M.) | |
|---|---|---|---|---|
| | Same (%) | Different (%) | Same (ms) | Different (ms) |
| Without a task-irrelevant ITD change | 70.0 ± 4.7 | 53.0 ± 5.9 | 745 ± 42 | 744 ± 39 |
| With a task-irrelevant ITD change | 69.9 ± 5.0 | 76.1 ± 6.8 | 744 ± 43 | 710 ± 40 |

See Fig. 2 for additional results.

## Frequency discrimination

### a. Mean sensitivity (d')



### Position discrimination

### d. Mean sensitivity (d')

### b. Mean bias to criterion (c)

### e. Mean bias to criterion (c)

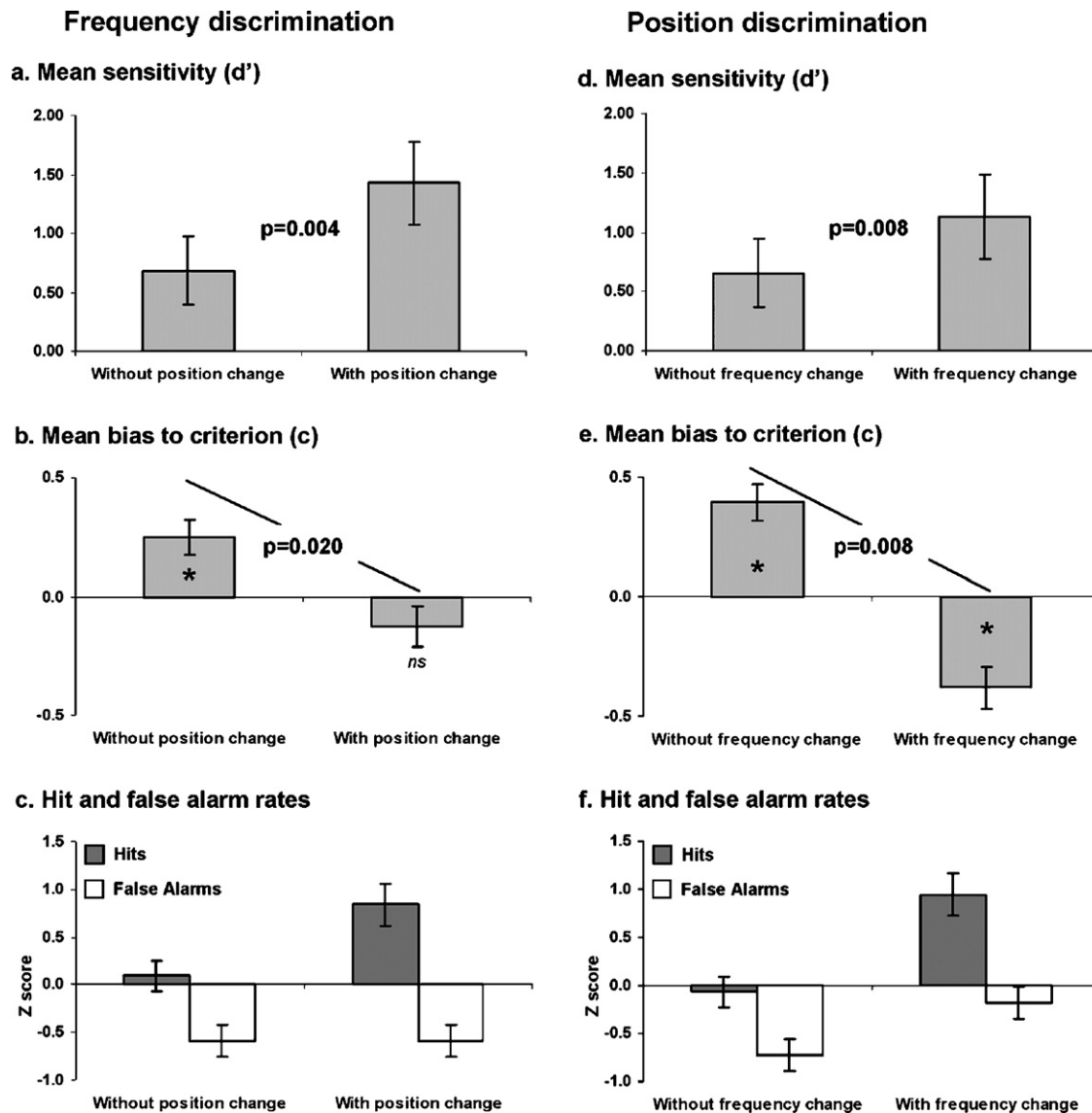### c. Hit and false alarm rates

### f. Hit and false alarm rates

Fig. 2. Group-averaged ($N = 9$) behavioral results on Experiment 1 (a–c; frequency discrimination task) and Experiment 2 (d–f; position discrimination task). (a and d) Mean (±standard error) sensitivity ($d'$). (b and e) Mean (±standard error) bias in response criterion ($c$), with asterisks indicating values significantly different from zero. (c and f) Mean (±standard error) hit and false alarm rates ($z$-score transformation).

below, this pattern was mainly due to the fact that subjects were strongly biased to respond "same". Indeed, when only a task-relevant position change was present, the accuracy rate for responding "different" was at an approximately chance level and lower than all other conditions. Analysis of mean RTs revealed a marginally significant main effect of (relevant) position change ($F_{(1,8)} = 5.02$; $p = 0.055$). There was also a significant interaction between position and frequency changes

($F_{(1,8)} = 15.01$; $p = 0.005$). Follow-up contrasts showed that the introduction of a task-irrelevant frequency change slowed participants when responding that sounds originated from the same location ($p = 0.05$) and speeded them when responding that sounds originated from different locations ($p = 0.008$). As in Experiment 1, this pattern of results would suggest that improved discrimination does not simply follow from a speed-accuracy trade-off.

Table 2
Mean accuracy rates (±S.E.M.) and reaction times (RT; in ms ± S.E.M.) for the position discrimination task (Experiment 2)

|  | Mean accuracy rates (±S.E.M.) | | Mean reaction times (±S.E.M.) | |
|---|---|---|---|---|
|  | Same (%) | Different (%) | Same (ms) | Different (ms) |
| Without a task-irrelevant frequency change | 75.8 ± 2.9 | 47.5 ± 3.5 | 704 ± 48 | 707 ± 51 |
| With a task-irrelevant frequency change | 57.2 ± 3.0 | 79.4 ± 4.9 | 733 ± 51 | 667 ± 47 |

See Fig. 2 for additional results.

Signal detection theory applied to the data from Experiment 2 showed that, on average, sensitivity to position changes increased by a factor of 0.73 when the frequency also changed. Mean $d'$ values ($\pm$S.E.M.) were $0.65 \pm 0.16$ when no frequency change was present and $1.13 \pm 0.24$ when frequency changes were present (Fig. 2d). Statistical analysis using the Wilcoxon signed ranks test confirmed that sensitivity to position changes was significantly greater with a contemporaneous task-irrelevant frequency change (Fig. 2d; $p = 0.008$). Analyses of response criterion ($c$) revealed that the mean values of $c$ with and without a task-irrelevant frequency change were significantly different from each other (Fig. 2e; $p = 0.008$). The mean value of $c$ when no frequency change was present was significantly different from zero ($c = 0.39 \pm 0.05$; $p = 0.008$), such that subjects were biased to respond that the position of the second sound did not change. In other words, when no task-irrelevant frequency change was present, subjects produced more misses (i.e. responding "same" when an actual position difference was present) than false alarms, reflecting the fact that the 31 μs ITD difference was not discriminated in a high number of trials. However, when a task-irrelevant frequency change was introduced, subjects were biased to respond that the position of the second sound was different (i.e. more overall "different" responses), as reflected by a mean $c$ value significantly smaller than zero ($c = -0.38 \pm 0.09$; $p = 0.015$). This shows that subjects made more false alarms than misses regarding position changes when a task-irrelevant frequency change was introduced. Nonetheless and importantly for the proposed interpretation of the present results, the positive shift in $z$-scores following the introduction of a task-irrelevant frequency change was larger for hits (gray bars) than for false alarms (white bars; see Fig. 2f), giving rise to the observed significant increase in sensitivity following the introduction of a task-irrelevant frequency change.

## 4. General discussion

The two experiments of this study support the existence of facilitative interactions between auditory "what" and "where" networks. Sensitivity to near-threshold changes in a sound's frequency was enhanced and RTs were facilitated by task-irrelevant, supra-threshold changes in its position (Experiment 1). Likewise, sensitivity to near-threshold changes in sound position was enhanced and RTs were facilitated by task-irrelevant, supra-threshold frequency changes (Experiment 2). These results suggest that in a near-threshold discrimination task, frequency and position dimensions of sounds can interact in a facilitative manner.

The enhanced sensitivity and facilitated RTs measures observed in the present study suggest that adding a task-irrelevant difference between the stimuli of a trial improved sensory processing and/or discrimination capabilities. Previous psychophysical studies also suggest that subjects can benefit from task-irrelevant changes during active discrimination. Mondor and Breau (1999) had their subjects classify the rising time of a target sound (near-threshold task; mean accuracy level of ~65%–70%) and found that task-irrelevant changes between either the frequency or position of the cue and target sounds

facilitated performance measures (RT and accuracy) without introducing a response bias when the stimulus onset asynchrony (SOA) between sounds was 750 ms, which is comparable to the 780 ms SOA in the present study, though these authors also note the crucial importance of SOA on behavioral outcomes (see also Dyson & Quinlan, 2004). These facilitative effects with near-threshold stimuli are in contrast with the interference effects often obtained when extreme supra-threshold have been used (Dyson & Quinlan, 2004; Mondor et al., 1998). An interesting possibility may be that the polarity of interactions (i.e. facilitation vs. interference) may critically depend on whether near-threshold or supra-threshold stimuli are used. Still other data would suggest that the occurrence of interactions may also crucially depend on task demands. Schröger (1995) measured auditory evoked potentials and compared the mismatch negativity (MMN)[2] elicited by deviations in one stimulus dimension (i.e. either frequency or position) with the MMN elicited by simultaneous deviations in both dimensions (i.e. both frequency and position). Under *passive* listening conditions, the MMN elicited by two-dimensional deviants roughly corresponded to the linear summation of the MMNs elicited by one-dimensional deviants. This pattern would suggest that frequency and position are processed independently without apparent interactions. By contrast, under *active* listening conditions sub-additive non-linear effects were evident at relatively late processing stages (i.e. >200 ms post-stimulus onset), indicative of interactions between these stimulus features that are perhaps under the control of top-down modulations from attention- or task-related mechanisms thought to be located within frontal cortices. The dependence on active listening to elicit interactions between frequency and position dimensions is called into question by a recent EEG and fMRI study by Altmann et al. (2007), who identified a region of overlap within the anterior planum temporale and posterior superior temporal gyrus that was activated under passive listening conditions by both position and vocalization changes (see also Barrett & Hall, 2006). While both Schröger (1995) as well as Altmann et al. (2007) used large and supra-threshold feature changes, the results of the present study suggest that similar facilitative interactions may also occur even when subjects perform near-threshold discrimination tasks with much smaller task-irrelevant changes (6 Hz and 65 μs ITD changes here vs. 25 Hz and 600 μs changes in Schröger, 1995). Indeed, near-threshold frequency (Sams, Paavilainen, Alho, & Näätänen, 1985) or ITD-defined spatial (Deouell, Heller, Malach, D'Esposito, & Knight, 2007; Deouell, Parnes, Pickard, & Knight, 2006; Spierer et al., 2007) changes can elicit a MMN. Detailing the neurophysiological mechanisms underlying multidimensional interactions for such small variations (and the processing stage(s) at which they occur) will be the topic of future investigations.

The results we obtained across the two experiments of this study also indicate that in a near-threshold discrimination task,

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[2] The mismatch negativity of MMN is calculated as the potential difference between a frequent (i.e. standard) stimulus and an infrequent (i.e. deviant) stimulus.

task-irrelevant dimensional changes can influence the response pattern in terms of bias. In both experiments, subjects were biased to respond "same" when no task-irrelevant changes were present (as revealed by positive $c$ values). Consequently, subjects had relatively high accuracy rates when the two stimuli of a pair were identical (70% and 75% on average for frequency and position tasks, respectively). However, this high accuracy level is more likely to be explained by the subjects' tendency to respond "same" on all trials without task-irrelevant changes rather than by reliable perceptual discrimination. Indeed, in both experiments, accuracy rates dropped dramatically to chance levels for "different" trials on which only a task-relevant difference was present between the two sounds (53.0% and 49.5% on average for frequency and position tasks, respectively), confirming that the discrimination task was near-threshold.

The crucial finding of both experiments is that the introduction of task-irrelevant dimensional changes greatly increased the number of hits as well as RTs on these trials. On the frequency discrimination task, subjects showed no response bias when a task-irrelevant position change was introduced; their rates of misses on "different" trials and false alarms on "same" trials were equal and there was no difference between the false alarm rates on trials that included a task-irrelevant change and those that did not. That is, subjects easily ignored the task-irrelevant position change of ~10° on "same" trials, suggesting that the increase in sensitivity was not attributable to the subjects' tendency to respond to the task-irrelevant position change.

In the position discrimination task, subjects had more difficulty ignoring the task-irrelevant frequency change (6 Hz), as revealed by higher false alarm rates for "same" trials that included frequency change and a mean value of $c$ that was below zero. However, the introduction of task-irrelevant frequency changes also increased hit rates on "different" trials to a greater extent than false alarm rates increased in "same" trials (see Fig. 2f). Consequently, mean $d'$ value was nevertheless significantly higher with the presence of task-irrelevant frequency changes. It is also important to note that the higher discrimination sensitivity on trials that included task-irrelevant changes in both experiments cannot be explained in terms of speed-accuracy trade-off.

We interpret the observed sensitivity improvements as a reflection of interactions between brain networks described under the rubric of the dual-pathway model and thought to be involved in auditory recognition and localization functions. For example, despite the accumulating anatomical and functional evidence speaking in favor of specialized pathways, the anatomical infrastructure is also present to support cross-talk between these pathways at both lower and higher cortical levels (c.f. Fig. 1 of Kaas & Hackett, 2000). For example, in addition to the specialized "what" and "where" pathways, a third functional network could be involved in the processing and/or integration of both auditory dimensions. Several cortical regions respond to both frequency and location contexts, albeit perhaps to differing degrees (e.g. Barrett & Hall, 2006; Zatorre, Mondor, & Evans, 1999). Similarly, critics of a strict what/where dual-pathway model have proposed that regions of the caudal superior temporal plane as well as planum temporale, which are often ascribed

to the dorsal 'where' pathway, might not simply be sensitive to spatial information, but also simple changes in frequency (e.g. Binder et al., 2000; Hall et al., 2002), spectral motion[3] (e.g. Belin & Zatorre, 2000; Thivard, Belin, Zilbovicius, Poline, & Samson, 2000), complex spectro-temporal information (e.g. Griffiths & Warren, 2002) and linguistic material (e.g. Hall, 2003; Scott, 2005). One proposition is that these regions act as a "computational hub" for auditory sensory-cognitive functions (Griffiths & Warren, 2002; see also Viceic et al., 2006). Such findings raise the possibility, which will require empirical confirmation that specific neurophysiological pathways may exist that could mediate the enhanced discrimination sensitivity we observed. Another line of evidence, which is not incompatible with the above, demonstrates the preserved use of spatial cues for sound object segregation in a case of spatial deafness (Bellmann Thiran & Clarke, 2003).

One alternative account for our results is that they reflect changes in high-level decision-related processes, rather than facilitative interactions in sensory processing between "what" and "where" systems. One level of argument against this account is that RTs in each experiment were significantly facilitated relative to all other conditions for "different" responses in the presence of a task-irrelevant change. An account based on interactions at a late or decision-level, would not predict such RT facilitation, but rather the fastest RTs when responding "same" (e.g. Dyson & Quinlan, 2002, 2003, 2004). Second, according to a decision-level participants would be using the task-irrelevant information to shift their response criterion such that responding "different" could be reinforced by the presence of a task-irrelevant cue and responding "same" could either be the default mode or could be actively reinforced when stimuli are near-threshold and in the absence of task-irrelevant cues. The use of signal detection theory analyses allowed us to (partially) rule out this alternative, because sensitivity ($d'$) and bias ($c$) are statistically independent measures (i.e. they are separately calculated and are uncorrelated; c.f. Macmillan & Creelman, 2005 for discussion). This was confirmed in both experiments of the present study; there was no evidence of significant correlation between hit and false alarm rates (as assessed by non-parametric Spearman rank correlation tests). Consequently, the improved sensitivity is unlikely to directly follow from a change is subjects' response criterion. Such being said, in each experiment we did observe a significant correlation, using Spearman's rho, between the *change* in $d'$ and the *change* in $c$ with the addition of a task-irrelevant cue (Experiment 1: $p = 0.042$; Experiment 2: $p = 0.010$) such that the more sensitivity increased with a task-irrelevant cue the more response criterion shifted downwards (i.e. *away* from being biased to respond "same"). Disentangling whether (and if so which of) sensitivity or bias is driving the other will require additional experimentation. More importantly, in Experiment 1, we would remind the reader that the downward shift in $c$ was to a value that did not significantly differ from zero (i.e. there was no bias to either respond "same" or

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[3] Spectral motion refers to shifts in the peaks of acoustic energy along the frequency dimension.

"different" following the addition of a task-irrelevant position change), despite sensitivity significantly increasing. This pattern of results in Experiment 1 speaks in favor of facilitative interactions between "what" and "where" networks, rather than late or top-down influences at the decision stage. The pattern observed in Experiment 2 (i.e. a significant increase in sensitivity and a significant bias to respond "different"), by contrast, leaves the possibility that such late/top-down influences may play a role, such that interactions between frequency and position may be asymmetric. In the case of the present study, position would interact in a facilitative manner with frequency discrimination but not forcibly the converse. Lastly, we would add that the currently prevailing anatamo-functional model would suggest that domain specificity between "what" and "where" functions persists in frontal and pre-frontal cortices that have themselves been implicated in memory and decision-making functions (e.g. Goldman-Rakic, 1996; Romanski, 2004), raising the possibility that even if the present effects can be (partially) explained in terms of late or top-down influences they might still reflect interactions between functionally specialized brain networks.

An additional alternative account would be that subjects learned to use the task-irrelevant information during the course of each of the experiments. If such were the case, a prediction would be that any enhancement of sensitivity ($d'$) should increase across blocks of trials. In order to assess this possibility, we submitted $d'$ values from each block of trials to a $2 \times 5$ repeated measures ANOVA, using the absence versus presence of task-irrelevant information and block of trials as within subjects factors. In Experiment 1, there was a main effect of the presence of a task-irrelevant position change ($F_{(1,8)} = 14.386$; $p = 0.005$). Neither the main effect of block nor the interaction reached the 0.05 significance criterion. In Experiment 2, there was a main effect of the presence of a task-irrelevant frequency change ($F_{(1,8)} = 13.038$; $p = 0.007$). Neither the main effect of block nor the interaction reached the 0.05 significance criterion. This pattern of results, observed in both experiments, would argue against the proposition that subjects learned to associate the task-relevant information with the task-irrelevant information.

The increase in discrimination sensitivity induced by the addition of task-irrelevant dimensional changes could be used as a neuro-rehabilitation strategy. Recently, an increasing number of studies have demonstrated that training can improve both frequency and position discrimination sensitivity (e.g. Ari-Even Roth, Amir, Alaluf, Buchsenspanner, & Kishon-Rabin, 2003; Demany & Semal, 2002; Spierer et al., 2007; Wright & Fitzgerald, 2001). Several studies described patients with cortical lesions who were impaired in frequency (e.g. Johnsrude, Penhune, & Zatorre, 2000; Tramo, Shah, & Braida, 2002) or location discrimination based on interaural cues (e.g. Adriani, Bellmann, et al., 2003; Adriani, Maeder, et al., 2003; Thiran & Clarke, 2003; Yamada, Kaga, Uno, & Shindo, 1996). The present study suggests that using an experimental training design with task-irrelevant dimension changes could be used to enhance performance, particularly given the above evidence that effects are not predicated on learning associations between task-relevant and task-irrelevant information.

## References

Adriani, M., Bellmann, A., Meuli, R., Fornari, E., Frischknecht, R., Bindschaedler, C., et al. (2003). Unilateral hemispheric lesions disrupt parallel processing within the contralateral intact hemisphere: An auditory fMRI study. *Neuroimage*, *20*(Suppl. 1), S66–S74.

Adriani, M., Maeder, P., Meuli, R., Thiran, A. B., Frischknecht, R., Villemure, J. G., et al. (2003). Sound recognition and localization in man: Specialized cortical networks and effects of acute circumscribed lesions. *Experimental Brain Research*, *153*, 591–604.

Ahveninen, J., Jaaskelainen, I. P., Raij, T., Bonmassar, G., Devore, S., Hamalainen, M., et al. (2006). Task-modulated "what" and "where" pathways in human auditory cortex. *Proceedings of the National Academy of Sciences U.S.A.*, *103*, 14608–14613.

Akeroyd, M. A., Carlyon, R. P., & Deeks, J. M. (2005). Can dichotic pitches form two streams? *Journal of the Acoustical Society Of America*, *118*, 977–981.

Alain, C., Arnott, S. R., Hevenor, S., Graham, S., & Grady, C. L. (2001). What" and "where" in the human auditory system. *Proceedings of the National Academy of Sciences U.S.A.*, *98*, 12301–12306.

Altmann, C. F., Bledowski, C., Wibral, M., & Kaiser, J. (2007). Processing of location and pattern changes of natural sounds in the human auditory cortex. *Neuroimage*, *35*, 1192–1200.

Anourova, I., Nikouline, V. V., Ilmoniemi, R. J., Hotta, J., Aronen, H. J., & Carlson, S. (2001). Evidence for dissociation of spatial and nonspatial auditory information processing. *Neuroimage*, *14*, 1268–1277.

Ari-Even Roth, D., Amir, O., Alaluf, L., Buchsenspanner, S., & Kishon-Rabin, L. (2003). The effect of training on frequency discrimination: Generalization to untrained frequencies and to the untrained ear. *Journal of Basic and Clinical Physiology and Pharmacology*, *14*, 137–150.

Arnott, S. R., Binns, M. A., Grady, C. L., & Alain, C. (2004). Assessing the auditory dual-pathway model in humans. *Neuroimage*, *22*, 401–408.

Barrett, D. J., & Hall, D. A. (2006). Response preferences for "what" and "where" in human non-primary auditory cortex. *Neuroimage*, *32*, 968–977.

Belin, P., & Zatorre, R. J. (2000). 'What', 'where' and 'how' in auditory cortex. *Nature Neuroscience*, *3*, 965–966.

Bellmann Thiran, A., & Clarke, S. (2003). Preserved use of spatial cues for sound segregation in a case of spatial deafness. *Neuropsychologia*, *41*, 1254–1261.

Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S., Springer, J. A., Kaufman, J. N., et al. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, *10*, 512–528.

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

Clarke, S., Adriani, M., & Tardif, E. (2005). "What" and "Where" in human audition: Evidence from anatomical, activation and lesion studies. In R. Konig, P. Heil, E. Budinger, & H. Scheich (Eds.), *Auditory cortex—towards a synthesis of human and animal research* (pp. 77–94). Hillsdale, NJ: Lawrence Erlbaum Associates.

Clarke, S., Bellmann Thiran, A., Maeder, P., Adriani, M., Vernet, O., Regli, L., et al. (2002). What and where in human audition: Selective deficits following focal hemispheric lesions. *Experimental Brain Research*, *147*, 8–15.

Clarke, S., & Thiran, A. B. (2004). Auditory neglect: What and where in auditory space. *Cortex*, *40*, 291–300.

Cramer, E. M., & Huggins, W. H. (1958). Creation of Pitch through Binaural Interaction. *Journal of the Acoustical Society of America*, *30*, 412–417.

Culling, J. F., Summerfield, A. Q., & Marshall, D. H. (1998). Dichotic pitches as illusions of binaural unmasking. I. Huggins' pitch and the "binaural edge pitch". *Journal of the Acoustical Society Of America*, *103*, 3509–3526.

De Santis, L., Clarke, S., & Murray, M. M. (2007). Automatic and intrinsic auditory "What" and "Where" processing in humans revealed by electrical neuroimaging. *Cerebral Cortex*, *17*, 9–17.

Degerman, A., Rinne, T., Salmi, J., Salonen, O., & Alho, K. (2006). Selective attention to sound location or pitch studied with fMRI. *Brain Research*, *1077*, 123–134.

Delhommeau, K., Micheyl, C., & Jouvent, R. (2005). Generalization of frequency discrimination learning across frequencies and ears: Implications for underlying neural mechanisms in humans. *Journal of the Association for Research in Otolaryngology*, *6*, 171–179.

Demany, L., & Semal, C. (2002). Learning to perceive pitch differences. *Journal of the Acoustical Society of America*, *111*, 1377–1388.

Deouell, L. Y., Heller, A. S., Malach, R., D'Esposito, M., & Knight, R. T. (2007). Cerebral responses to change in spatial location of unattended sounds. *Neuron*, *55*, 985–996.

Deouell, L. Y., Parnes, A., Pickard, N., & Knight, R. T. (2006). Spatial location is accurately tracked by human auditory sensory memory: Evidence from the mismatch negativity. *European Journal of Neuroscience*, *24*, 1488–1494.

Dyson, B. J., & Quinlan, P. T. (2002). Within- and between-dimensional processing in the auditory modality. *Journal of Experimental Psychology: Human Perception & Performance*, *28*, 1483–1498.

Dyson, B. J., & Quinlan, P. T. (2003). Feature and conjunction processing in the auditory modality. *Perception and Psychophysics*, *65*, 254–272.

Dyson, B. J., & Quinlan, P. T. (2004). Stimulus processing constraints in audition. *Journal of Experimental Psychology: Human Perception & Performance*, *30*, 1117–1131.

Garner, W. R. (1974). *The processing of information and structure*. Maryland: Lawrence Erlbaum Associates.

Garner, W. R. (1976). Integration of stimulus dimensions in concept and choice processes. *Cognitive Psychology*, *8*, 98–123.

Goldman-Rakic, P. S. (1996). Regional and cellular fractionation of working memory. *Proceedings of the National Academy of Sciences U.S.A.*, *93*, 13473–13480.

Green, D. M., & Sweets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Griffiths, T. D., & Warren, J. D. (2002). The planum temporale as a computational hub. *Trends in Neuroscience*, *25*, 348–353.

Hall, D. A. (2003). Auditory pathways: Are 'what' and 'where' appropriate? *Current Biology*, *13*, R406–R408.

Hall, D. A., Johnsrude, I. S., Haggard, M. P., Palmer, A. R., Akeroyd, M. A., & Summerfield, A. Q. (2002). Spectral and temporal processing in human auditory cortex. *Cerebral Cortex*, *12*, 140–149.

Hartmann, W. M., & Zhang, P. X. (2003). Binaural models and the strength of dichotic pitches. *Journal of the Acoustical Society Of America*, *114*, 3317–3326.

Johnsrude, I. S., Penhune, V. B., & Zatorre, R. J. (2000). Functional specificity in the right human auditory cortex for perceiving pitch direction. *Brain*, *123*(Pt 1), 155–163.

Kaas, J. H., & Hackett, T. A. (2000). Subdivisions of auditory cortex and processing streams in primates. *Proceedings of the National Academy of Sciences U.S.A.*, *97*, 11793–11799.

Kubovy, M., Cutting, J. E., & McGuire, R. M. (1974). Hearing with the third ear: Dichotic perception of a melody without monaural familiarity cues. *Science*, *186*, 272–274.

Kubovy, M., & Howard, F. P. (1976). Persistence of a pitch-segregating echoic memory. *Journal of Experimental Psychology: Human Perception & Performance*, *2*, 531–537.

Licklider, J. C. R. (1956). Auditory frequency analysis. In C. Cherry (Ed.), *Proceedings of the Third London Symposium on Information Theory* (pp. 253–268).

Macmillan, N. A., & Creelman, C. D. (2005). *Detection theory: A user's guide* (2nd ed.). Mahwah, NJ: Lawrence Erlbaum Associates.

Maeder, P. P., Meuli, R. A., Adriani, M., Bellmann, A., Fornari, E., Thiran, J. P., et al. (2001). Distinct pathways involved in sound recognition and localization: A human fMRI study. *Neuroimage*, *14*, 802–816.

Miller, J. (1982). Divided attention: Evidence for coactivation with redundant signals. *Cognitive Psychology*, *14*, 247–279.

Mondor, T. A., & Breau, L. M. (1999). Facilitative and inhibitory effects of location and frequency cues: Evidence of a modulation in perceptual sensitivity. *Perception & Psychophysics*, *61*, 438–444.

Mondor, T. A., Zatorre, R. J., & Terrio, N. A. (1998). Constraints on the selection of auditory information. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 66–79.

Näätänen, R., Porkka, R., Merisalo, A., & Ahtola, S. (1980). Location vs. frequency of pure tones as a basis of fast discrimination. *Acta Psychologica (Amsterdam)*, *44*, 31–40.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Raab, D. (1962). Statistical facilitation of simple reaction time. *Transactions of the New York Academy of Sciences*, *43*, 574–590.

Rauschecker, J. P. (1998). Parallel processing in the auditory cortex of primates. *Audiology and Neuro-Otology*, *3*, 86–103.

Rauschecker, J. P., & Tian, B. (2000). Mechanisms and streams for processing of "what" and "where" in auditory cortex. *Proceedings of the National Academy of Sciences U.S.A.*, *97*, 11800–11806.

Romanski, L. M. (2004). Domain specificity in the primate prefrontal cortex. *Cognitive, Affective, & Behavioral Neuroscience*, *4*, 421–429.

Sams, M., Paavilainen, P., Alho, K., & Näätänen, R. (1985). Auditory frequency discrimination and event-related potentials. *Electroencephalography and Clinical Neurophysiology*, *62*, 437–448.

Schröger, E. (1995). Processing of auditory deviants with changes in one versus two stimulus dimensions. *Psychophysiology*, *32*, 55–65.

Scott, S. K. (2005). Auditory processing—speech, space and auditory objects. *Current Opinion in Neurobiology*, *15*, 197–201.

Spierer, L., Tardif, E., Sperdin, H., Murray, M. M., & Clarke, S. (2007). Learning-induced plasticity in auditory spatial representations revealed by electrical neuroimaging. *Journal of Neuroscience*, *27*, 5474–5483.

Thiran, A. B., & Clarke, S. (2003). Preserved use of spatial cues for sound segregation in a case of spatial deafness. *Neuropsychologia*, *41*, 1254–1261.

Thivard, L., Belin, P., Zilbovicius, M., Poline, J. B., & Samson, Y. (2000). A cortical region sensitive to auditory spectral motion. *Neuroreport*, *11*, 2969–2972.

Tian, B., Reser, D., Durham, A., Kustov, A., & Rauschecker, J. P. (2001). Functional specialization in rhesus monkey auditory cortex. *Science*, *292*, 290–293.

Tramo, M. J., Shah, G. D., & Braida, L. D. (2002). Functional role of auditory cortex in frequency processing and pitch perception. *Journal of Neurophysiology*, *87*, 122–139.

Viceic, D., Fornari, E., Thiran, J. P., Maeder, P. P., Meuli, R., Adriani, M., et al. (2006). Human auditory belt areas specialized in sound recognition: A functional magnetic resonance imaging study. *Neuroreport*, *17*, 1659–1662.

Wickens, T. D. (2002). *Elementary signal detection theory*. Oxford: Oxford University Press.

Wright, B. A., & Fitzgerald, M. B. (2001). Different patterns of human discrimination learning for two interaural cues to sound-source location. *Proceedings of the National Academy of Sciences U.S.A.*, *98*, 12307–12312.

Yamada, K., Kaga, K., Uno, A., & Shindo, M. (1996). Sound lateralization in patients with lesions including the auditory cortex: Comparison of interaural time difference (ITD) discrimination and interaural intensity difference (IID) discrimination. *Hearing Research*, *101*, 173–180.

Zatorre, R. J., Mondor, T. A., & Evans, A. C. (1999). Auditory attention to space and frequency activates similar cerebral systems. *Neuroimage*, *10*, 544–554.