Research Report

HEMISPHERIC DIFFERENCES IN AUDITORY PERCEPTION ARE SIMILAR TO THOSE FOUND IN VISUAL PERCEPTION

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Abstract—*In a pitch discrimination task, subjects were faster and more accurate in judging low-frequency sounds when these stimuli were presented to the left ear, compared with the right ear. In contrast, a right-ear advantage was found with high-frequency sounds. The effect was in terms of relative frequency and not absolute frequency, suggesting that the effect arises from postsensory mechanisms. A similar laterality effect has been reported in visual perception with stimuli varying in spatial frequency. These multimodal laterality effects may reflect a general computational difference between the two cerebral hemispheres, with the left hemisphere biased for processing high-frequency information and the right hemisphere biased for processing low-frequency information.*

Research in visual perception has indicated a computational difference between the left and right cerebral hemispheres in humans. In experiments with both normal (Sergent, 1982) and neurological (Robertson, Lamb, & Knight, 1988) populations, the left hemisphere has been associated with processing local aspects of a visual stimulus and the right hemisphere with processing global information from the same stimulus. Additional support for an asymmetry in visual perception has come from experiments using stimulus sets defined on the basis of component spatial frequencies. Subjects are faster at identifying high-frequency stimuli when these stimuli are presented in the right visual field (left hemisphere) and are faster at identifying low-frequency stimuli when these stimuli are presented in the left visual field (right hemisphere; Kitterle, Christman, & Hellige, 1990; Kitterle & Selig, 1991).

We report here a similar interaction with auditory stimuli. Subjects were asked to judge whether a tone was lower or higher in frequency than other members of a stimulus set. The stimuli were presented monaurally, the primary projection of information assumed to be to the contralateral hemisphere (e.g., Lauter, Hersovitch, Fromby, & Raichle, 1985; Tanguay, Taub, Doubleday, & Clarkson, 1977). For stimuli defined as low in frequency, judgments were more accurate and faster when presented to the left ear/right hemisphere. In contrast, a performance advantage was found for stimuli defined as high in frequency when these tones were presented to the right ear/left hemisphere. Thus, the laterality effect with stimuli varying in sound frequency parallels that reported in visual perception studies using stimuli varying in spatial frequency (Kitterle et al., 1990).

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GENERAL METHODS AND ANALYSIS

Stimuli

The auditory stimuli were modeled on those used in visual experiments in which each stimulus contains both low and high spatial frequency information (Sergent, 1982; Robertson et al., 1988). Each stimulus was composed of two 150-ms sine-wave tones (except in Experiment 4, in which the stimuli were composed of a single pure tone). Across stimuli, the mean frequency of one tone was 200 Hz, and the mean frequency of the other tone was 1,900 Hz. In each experiment, there were two sets of tones, each set composed of several pairs of tones. Within each set, the frequency of the irrelevant tone was always set to one of the mean frequencies and the frequency of the target tone was either slightly lower or slightly higher than the other mean frequency. (See Table 1 for an example of the stimulus sets.)

The stimuli were generated on a 286 personal computer using an 8-bit D-to-A converter. Linear onset and offset ramps of 10-ms duration were included to eliminate transient signals. Loudnesses of the two frequencies were equated based on the judgments of two observers. The duplex waveforms were stored in digital form, and the sounds were produced on-line by the computer during the course of the experiment.

Procedure

Subjects were instructed to respond "low" to the three members of each set in which the target frequency was lower than the mean frequency of targets in that set, and respond "high" to the three members in which the target frequency was higher than the mean frequency of targets in that set. Each trial began with the presentation of a visual alerting stimulus for 500 ms. Then, a duplex stimulus was presented to either the left or the right ear over headphones; no sound was presented to the other ear. Responses were made using the thumb and index finger of the right hand. The response board was oriented orthogonally to the body axis to minimize stimulus–response compatibility effects. In addition, the mapping between digits and response labels was counterbalanced across subjects. Visual feedback was provided after each trial, and the intertrial interval was 1,000 ms.

The low and high sets were tested in alternating blocks. Each set was used in one practice block and two test blocks, with the practice block preceding the first test block for that particular stimulus set. The order of stimuli within a set was random. The order of stimulus sets was counterbalanced across subjects in the single-session experiment (Experiment 1) and across subjects and sessions for the multiple-session experiments (Experiments 2–4).

Analysis

This design provided two separate tests of a laterality effect. If a laterality

Table 1. *Stimuli (Hz), response categories, and frequency distinctions for Experiment 1*

Irrelevant tone	Target tone	Correct response	Frequency distinction: Absolute	Frequency distinction: Relative
		Low set		
1,900	192	Low	Low	Low
1,900	195	Low	Low	Low
1,900	198	Low	Low	Low
1,900	202	High	Low	High
1,900	205	High	Low	High
1,900	208	High	Low	High
		High set		
200	1,860	Low	High	Low
200	1,876	Low	High	Low
200	1,892	Low	High	Low
200	1,908	High	High	High
200	1,924	High	High	High
200	1,940	High	High	High

effect exists in terms of absolute frequency, we would expect greater accuracy in judging the stimuli from the low set when these tones were presented to the left ear and greater accuracy in judging the high set of stimuli when they were presented to the right ear. Alternatively, a laterality effect might be observed in terms of relative frequency. Within each set, the target frequency is lower than the mean frequency for half of the stimuli and higher for the other half. A left-ear advantage might be found for the relatively low members of a stimulus set, and a right-ear advantage for the relatively high members of that set. That is, an interaction involving the side of presentation might be expected within each set rather than across sets. Visual studies have shown that the laterality effect is in terms of relative spatial frequency (e.g., Christman, Kitterle, & Hellige, 1991). It should be noted, however, that visual experiments with duplex stimuli have involved an identification task (Robertson et al., 1988; Sergent, 1982), while subjects treat the current task as one of discrimination.

EXPERIMENT 1

Twenty right-handed subjects were recruited in exchange for course credit. Each subject completed a 1-hr session composed of two practice blocks and four test blocks using the stimuli listed in Table 1. For the low set, six stimuli were created by combining an irrelevant tone of 1,900 Hz with target tones of 192, 195, 198, 202, 205, and 208 Hz. For the high set, an irrelevant tone of 200 Hz was paired with frequencies of 1,860, 1,876, 1,892, 1,908, 1,924, and 1,940 Hz. Because each duplex sound was presented to both the left and the right ears, there were 12 stimuli in each stimulus set. Each practice block consisted of four presentations to each ear of the six sounds from a given set, for a total of 48 trials. Each test block consisted of 144 trials, 12 presentations of each stimulus. Subjects were instructed that the dependent variable was accuracy and that they should respond when they had determined whether the stimulus was a low or high member of the set.

A laterality effect in terms of relative frequency was obtained. Subjects made more errors in judging the higher members of each set when these stimuli were presented to the left ear. In contrast, more errors were observed with the lower members of each set when these stimuli were presented to the right ear. This effect can be seen in the results for both the low set of tones (Fig. 1a) and the high set of tones (Fig. 1b). The Ear × Relative Frequency interaction was significant, $F(1, 18) = 5.64$, $p < .03$. In terms of absolute frequency, subjects

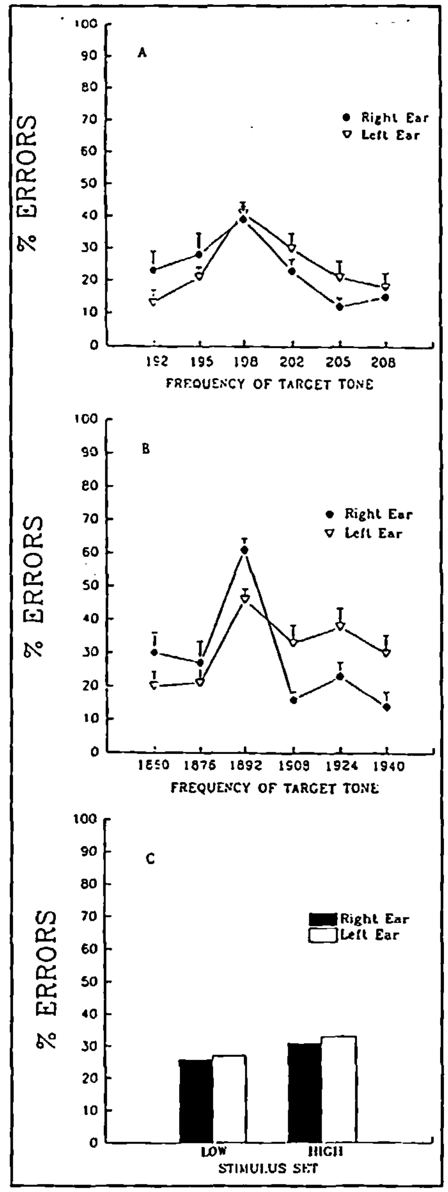

Fig. 1. Percentage of errors in the frequency judgment task of Experiment 1. (a) and (b) Results graphed to highlight the relative laterality effect for the low and high stimulus sets, respectively. (c) Data combined by stimulus set to demonstrate that there was no laterality effect in terms of absolute frequency.

made more errors in judgments involving the high set of stimuli, $F(1, 18) = 8.87$, $p < .01$ (Fig. 1c). The advantage for the low set reflects our failure to select equivalent step sizes for the two stimulus sets. Most important, however, there is no indication of an Ear × Absolute Frequency interaction.

EXPERIMENT 2

Five subjects were each tested in four separate sessions. None of the subjects was familiar with the hypotheses under consideration. Each session consisted of two practice and four test blocks as in Experiment 1. Data from the first session were not included in the final analysis. Given that the subjects were well practiced at this task, the range of test frequencies was reduced. For the low set, the range of the target frequencies was from 197 Hz to 203 Hz in steps of 1 Hz. For the high set, the target component ranged from 1,888 Hz to 1,912 Hz in steps of 4 Hz. The frequencies of the irrelevant tones were as in Experiment 1.

The auditory laterality effect was replicated with these well-practiced subjects. The data are combined across the two stimulus sets in Figure 2a. The Ear × Relative Frequency interaction was significant, $F(1, 4) = 15.79, p < .02$. No laterality effect was found for absolute frequency, although, as before, subjects tended to be more accurate in judging the low set of sounds than the high set (error rates: low set, right ear = 14%; low set, left ear = 11%; high set, right ear = 30%; high set, left ear = 28%).

EXPERIMENT 3

Four subjects, all of whom had been in Experiment 2, completed four additional sessions. The dependent variable was response latency. Subjects were instructed to respond as quickly as possible while keeping errors to a minimum. The number of stimuli in each set was reduced by using only four target frequencies per set, two that were lower than the mean value and two that were higher than the mean value. For the low set, the target frequencies were 192, 196, 204, and 208 Hz. For the high set, the target frequencies were 1,870, 1,885, 1,915, and 1,930 Hz. Since each stimulus was presented monaurally to either the left or the right ear, there were eight stimuli per set. Each stimulus was presented 20 times to each ear per test block. Six presentations of each stimulus were included in the practice block. There were two practice blocks and four test blocks per session. The data from the last three sessions were retained for the analysis.

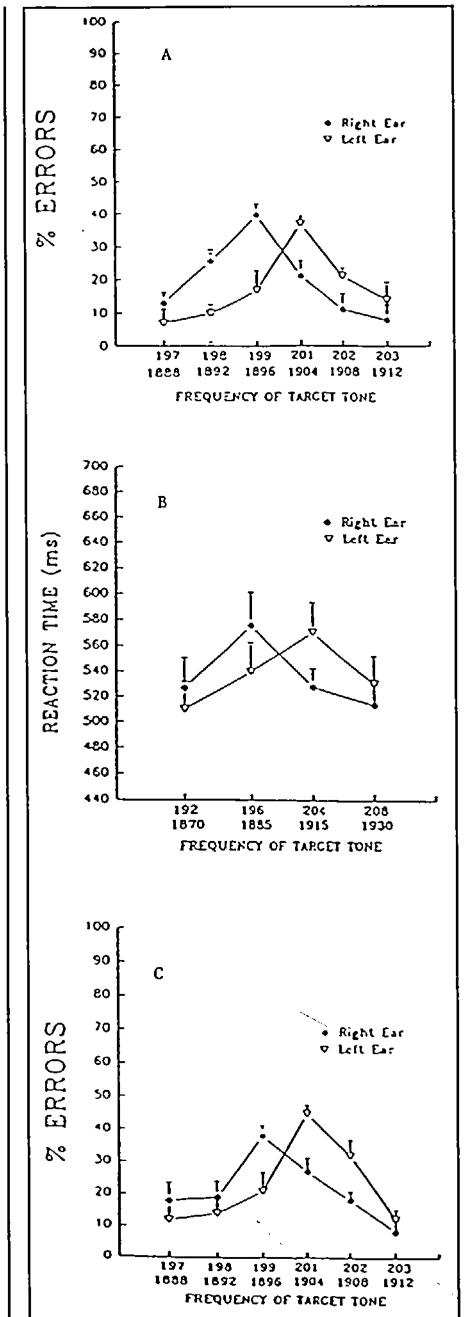

Fig. 2. Results showing laterality interaction in terms of relative frequency. (a) Error data for Experiment 2. (b) Reaction time data for Experiment 3. (c) Error data for Experiment 4.

Only correct responses were included in the analyses. The results with reaction time as the dependent variable essentially mirror the results obtained with an accuracy measure in the first two experiments (Fig. 2b). Subjects were faster when responding to the relatively low members of each set when these sounds were presented to the left ear. When responding to the relatively high members of each set, the subjects were faster following presentations in the right ear. The Ear × Relative Frequency interaction was significant, $F(1, 3) = 11.15, p < .05$. As in the preceding two experiments, judgments of the low set of stimuli were generally easier than judgments of the high set, the difference being marginally significant, $F(1, 3) = 5.79, p < .10$. Nonetheless, there was no laterality effect as a function of absolute frequency.

Given the large steps between stimuli as well as the fact that the subjects had extensive practice, error rates were relatively low. Moreover, there was no evidence of a speed–accuracy trade-off. Low error rates were associated with conditions producing fast responses, and higher error rates were found for conditions producing slower responses.

EXPERIMENT 4

In the final experiment, each stimulus was composed of a single sine-wave tone: The irrelevant tone was eliminated. The target frequencies were the same as in Experiment 2, and the dependent variable was accuracy. Four subjects completed four sessions each. One of these subjects had participated in Experiments 2 and 3. The procedure was the same as in Experiment 2.

The results are presented in Figure 2c. The Ear × Relative Frequency interaction was again significant, $F(1, 3) = 21.15, p < .02$, and the interaction was as in the preceding experiments. Thus, the laterality effect does not depend on the presence of a distractor tone.[1]

1. The finding that the relative laterality effect does not require the presence of an irrelevant tone may need to be qualified. We have conducted experiments using widely spaced frequencies. For the low set, subjects had to discriminate between a 200-Hz and a 700-Hz tone; for the high set, the discrimination was between a 700-Hz and a 1,900-Hz tone. We failed to obtain a relative laterality effect in two versions of this experiment—one in which the target tone was presented alone and one in which the target tone was embedded in white noise. These null results are at odds with data from visual perception experiments in which a relative laterality effect has been obtained with sine-wave gratings in

There were two surprising findings in this experiment. First, removing the irrelevant tone eliminated the difference in difficulty between the two stimulus sets (error rates: low set = 25%, high set = 22%). Second, the error rates were as high in Experiment 4 as they were in Experiment 2, in which the same step sizes had been used with duplex stimuli. However, no statistical comparisons were made between the experiments given the partial overlap in subjects as well as the fact that Experiment 2 was completed prior to Experiment 4.

DISCUSSION

In four experiments, a laterality effect was obtained in an auditory pitch discrimination task. A right-ear/left-hemisphere advantage was found when the target tone was higher in frequency than the average frequency of the stimulus set, and a left-ear/right-hemisphere advantage was found when the target tone was lower in frequency. This interaction was reliable only when the data were analyzed in terms of differences in relative frequency. In all four experiments, no interactions were observed between the side of presentation and differences in absolute frequency.

There is no obvious relationship between spatial frequencies and sound frequencies.[2] Nonetheless, laterality research in visual perception has revealed an asymmetry similar to the one obtained in the current experiments (e.g., Kitterle et al., 1990; see reviews in Robertson & Lamb, 1991; Van Kleeck, 1989). The visual asymmetry has also been found to be a relative effect (Christman et al., 1991). Taken together, the results suggest that in both vision and audition, the right hemisphere is biased for processing low frequencies, and the left hemisphere is biased for processing high frequencies.

This hypothesis is also in accord with a number of other results in the laterality literature. Musical illusions reported by Deutsch (1974, 1985) and Gordon (1980) indicate that people have a preference for localizing low-frequency information to the left ear and high-frequency information to the right ear. Zatorre (1988) has reported that the missing fundamental illusion is more affected in patients with right-hemisphere lesions than in patients with left-hemisphere lesions. In this illusion, the fundamental is perceived even when the stimulus contains power only at harmonic frequencies. The laterality result may reflect the prominent role of the right hemisphere in processing low-frequency information. Similarly, while the left hemisphere is clearly dominant in language tasks (see Geschwind, 1972), damage to the right hemisphere is associated with deficits in the perception of prosody (Blonder, Bowers, & Heilman, 1991; Ross, 1981; Tucker, Watson, & Heilman, 1977). Variation in the fundamental frequency of the speech signal is a primary source of prosodic information (Blumstein & Cooper, 1974). While this selective review is suggestive, experiments are needed to assess directly the generality of the hypothesized difference between how the two hemispheres process frequency information.

Moreover, a computational account of such an asymmetry will be needed. The fact that the effect in both audition and vision is one of relative frequency suggests that the asymmetry arises at a postsensory stage of processing:[3] There may be no difference in the sensory input to the two cerebral hemispheres (Kitterle & Kaye, 1985; Kitterle et al., 1990; but see Previc, 1991). Rather, the laterality effect may reflect the output of an asymmetric filtering operation performed by each hemisphere: Processing in the right hemisphere might include a low-pass filtering operation, whereas processing in the left hemisphere might include a high-pass filtering operation.

Asymmetric mechanisms of this sort would yield a relative laterality effect if the input to the filters were limited to the frequencies that were informative for performing the desired task. For instance, with the low set of stimuli in the experiments described in this report, the filter input would be limited to information near 200 Hz; information from the region of the 1,900-Hz distractor tone would be excluded. In this example, a high-pass filter would emphasize the representation of information just above 200 Hz, while a low-pass filter would emphasize the representation of information just below 200 Hz. When the target is defined by variation in the high-frequency component, the input would be limited to information near 1,900 Hz.

Paradigms have been developed with bilateral stimuli for measuring the bandwidths of visual (Graham, 1989) and auditory (Schlauch & Hafter, 1991) channels. These techniques should prove useful with lateralized stimuli for examining the shape of filtering operations associated with each hemisphere, as well as for evaluating attentional constraints on the input to the filters.

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which the two stimuli were quite distinct (e.g., 1 vs. 9 cycles/deg; Kitterle et al., 1990; Kitterle & Selig, 1991). However, we have recently found a marginally significant laterality effect with sound frequencies using widely spaced frequencies (e.g., 200 vs. 700 Hz) when the target sound is paired with an irrelevant tone (e.g., 1,900 Hz).

2. One possible correspondence is that large objects are generally associated with low sounds and small objects with high sounds. Compare the calls of an elephant with those of a bird.

3. In the musical illusion and prosody experiments reviewed above, relative and absolute frequency differences were confounded. For example, in making prosodic judgments of normal speech, the fundamental is the lowest component of the signal in both absolute and relative terms.

REFERENCES

Blonder, L.X., Bowers, D., & Heilman, K.M. (1991). The role of the right hemisphere in emotional communication. *Brain, 114*, 1115–1127.

Blumstein, S., & Cooper, W. (1974). Hemispheric processing of the intonation contours. *Cortex, 10*, 146–152.

Christman, S., Kitterle, F.L., & Hellige, J. (1991). Hemispheric asymmetry in the processing of absolute versus relative spatial frequency. *Brain and Cognition, 16*, 62–73.

Deutsch, D. (1974). An auditory illusion. *Nature, 251*, 307–309.

Deutsch, D. (1985). Dichotic listening to melodic patterns and its relationship to hemispheric specialization of function. *Music Perception, 3*, 127–154.

Geschwind, N. (1972). Language and the brain. *Scientific American, 226*, 76–83.

Gordon, H.W. (1980). Degree of ear asymmetries for perception of dichotic chords and for illusory chord localization in musicians of different levels of competence. *Journal of Experimental Psychology: Human Perception and Performance, 6*, 516–527.

Graham, N. (1989). *Visual pattern analyzers*. New York: Oxford University Press.

Kitterle, F., Christman, S., & Hellige, J. (1990). Hemispheric differences are found in the identification, but not detection of low versus high spatial frequencies. *Perception & Psychophysics, 48*, 297–306.

Kitterle, F., & Kaye, R. (1985). Hemispheric symmetry in contrast and orientation sensitivity. *Perception & Psychophysics, 37*, 391–396.

Kitterle, F.L., & Selig, L.M. (1991). Visual field effects in the discrimination of sine-wave gratings. *Perception & Psychophysics, 50*, 15–18.

Lauter, J.L., Hersovitch, P., Fromby, C., & Raichle, M.E. (1985). Tonotopic organization in the human auditory cortex revealed by positron emission tomography. *Hearing Research, 20*, 199–205.

Previc, F.H. (1991). A general theory concerning the prenatal origins of cerebral lateralization in humans. *Psychological Review, 98*, 299–334.

Robertson, L.C., & Lamb, M.R. (1991). Neuropsychological contributions to theories of part/whole organization. *Cognitive Psychology, 23*, 299–330.

Robertson, L.C., Lamb, M.R., & Knight, R.T. (1988). Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *The Journal of Neuroscience, 8*, 3757–3769.

Ross, E.D. (1981). The aprosodias: Functional-anatomic organization of the affective components of language in the right hemisphere. *Archives of Neurology, 38*, 561–567.

Schlauch, R.S., & Hafter, E.R. (1991). Listening bandwidths and frequency uncertainty in pure-tone signal detection. *Journal of the Acoustical Society of America, 90*, 1332–1339.

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation. *Journal of Experimental Psychology: Human Perception and Performance, 8*, 253–272.

Tanguay, P., Taub, J., Doubleday, C., & Clarkson, D. (1977). An interhemispheric comparison of auditory evoked responses to consonant-vowel stimuli. *Neuropsychologia, 15*, 123–131.

Tucker, D.M., Watson, R.T., & Heilman, K.M. (1977). Discrimination and evocation of affectively intoned speech in patients with right parietal disease. *Neurology, 27*, 947–950.

Van Kleeck, M.H. (1989). Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: New data and a meta-analysis of previous studies. *Neuropsychologia, 27*, 1165–1178.

Zatorre, R.J. (1988). Pitch perception of complex tones and human temporal-lobe function. *Journal of the Acoustical Society of America, 84*, 566–572.

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