# 13 Auditory Sequence Complexity and Hemispheric Asymmetry of Function in Rats

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Language in humans is characteristically manifested by the left cerebral *LANG = LEFT* hemisphere. This fact must reflect properties of the left hemisphere that make it a relatively natural site for language behavior. The same fact may be taken as the basis for a stronger claim: Certain properties of the left hemisphere are unique to humans and causally related to the existence and nature of language. There are several ways to gain perspective on such a claim, such as the study of cerebral asymmetries in nonhumans and of nonlinguistic behaviors, particularly those bearing some structural similarity to language. If we find that asymmetries occur for these behaviors, and in nonhumans, we must conclude that functional hemispheric differences as such are not unique to humans, nor are they the sufficient cause of the existence of language.

The comparative study of auditory sequence learning and perception provides one approach to the study of this problem. The study of simple sequential stimuli in nonhuman species may reveal general psychological mechanisms underlying the structure of natural serial systems such as human language, and general features of brain organization, such as asymmetries in function. A preliminary goal for such research is to develop tasks and methods suited for comparative research. Monaural and dichotic presentation of acoustic stimuli have revealed asymmetries in hemispheric function on a variety of tasks in humans, in which both the direction and degree of hemispheric asymmetry
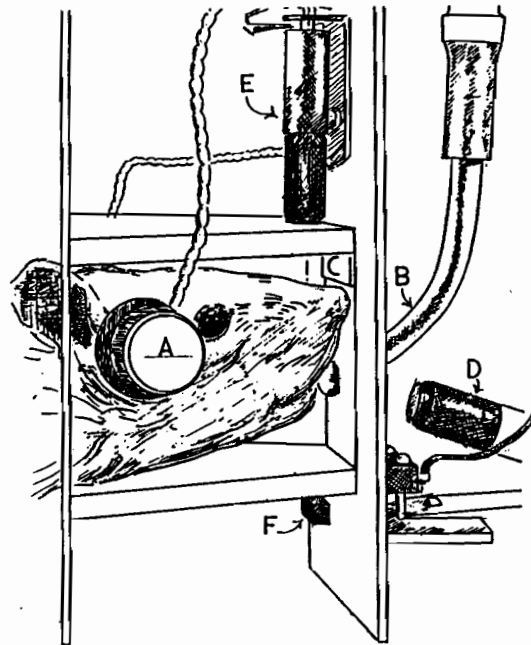
Figure 13.1. The dichotic hood is illustrated: (A) earphone, (B) drinking tube, (C) response key, (D) key lamp, (E) hood lamp, (F) light detector.

are related to the complexity of an acoustic stimulus. Discriminations involving simple, serially presented or temporally varying information, on the other hand, tend to be particularly dramatic in subjects with unilateral brain damage (Chedru, Bastard, & Efron, 1978; Gordon, 1967; Lackner & Teuber, 1973; Van Allen, Benton, & Gordon, 1967), but have also been revealed in studies using intact human subjects and monaural and dichotic techniques (Efron and Yund, 1974; Halperin, Nachson, & Carmon, 1973; Mills & Rollman, 1979a, 1979b; Murphy & Venables, 1970; Sidtis, 1980; Simon, 1967; Vroon, Timmers, & Tempelaars, 1977).

The monaural and dichotic techniques involve presenting different, sometimes conflicting signals simultaneously to both ears through headphones. The term *monaural* generally refers to the presentation of some stimulus of interest to one ear, while a different stimulus (typically white-noise) is simultaneously presented to the other ear. The word *dichotic* refers to a technique in which the two stimuli are similar, such as two different vowels or tones. Because the information originating at the level of the auditory receptors in one ear is projected to both sides of the brain in mammals, though asymmetrically in favor of the contralateral side, these forms of stimulus presentation are believed to interfere or perhaps compete with each other within a hemisphere. Superiority is assigned to the hemisphere contralateral to the ear that "performs better."

The experiments described in this chapter address the problem of auditory sequential complexity and hemispheric asymmetries in intact rats using the monaural presentation technique. As is the case with humans, an ear advantage would imply superior performance by the contralateral side of the brain. If auditory processing in rats parallels that found in humans we would predict an asymmetry to be revealed on the task; further, we would expect the degree and direction of the asymmetry to depend on sequence complexity.

## METHOD

Intact albino rats (*Rattus norvegicus*) were used in these studies. They were trained and tested in an operant chamber modified by the addition of a hood just large enough to accommodate a rat's head (see Figure 13.1). Auditory stimuli were presented to each ear of the rat through subminiature speakers mounted on the hood. The hood underwent modification in design in each of the experiments, in order to improve the control of sound delivery. In the first (3-tone) experiment, the hood consisted of a tapered cubicle with a single light-sensing circuit at the distal end with the speakers mounted on the sides opposite the position of the ears. In Experiment 2 (1-tone) and 3 (2-tone) the hood consisted of a cylinder with two cutouts large enough to accommodate each ear, and each with its own light-sensing circuit. Additionally, in Experiment 3, a rectangular cap with attached speaker was mounted over each cutout, providing an enclosed delivery system for each ear.

In all these experiments a single-response "go/no-go" procedure was used. On each trial the subject was signaled to insert and correctly orient its head in the listening hood (monitored by the light sensing circuits) for the duration of the stimulus presentation. The discriminative stimulus or sequence

was then presented followed by a 3-s response interval. A response made during this interval was reinforced with water if it followed a stimulus designated as positive and punished with a time-out if it followed a negative stimulus. The tone stimuli consisted of square waves generated by a microcomputer and amplified. Broad-band thermal noise was presented continuously to the contralateral ear receiving tone stimuli. Noise was presented bilaterally during the training sessions in order to train the rat to fixate its head during the stimulus. Movement of the head or responses made during the stimulus resulted in a 5-s time-out before representation of the stimulus.

The subject's task in Experiment 1 ($N$ = 8) was to discriminate a sequence consisting of a specific series of three tones (1.1, 1.5, and 2.33 kHz) in nonmonotonic order, from all other possible combinations (26) of the three elements. The subjects in Experiment 2 (N = 8) were required to discriminate a high pitch (2.33 kHz) from a low pitch (1.1 kHz) tone, one presented on each trial. Six subjects from Experiment 2 were then successfully transferred to a task in which they were required to discriminate a sequence comprising two different tones (1.1 and 2.33 kHz) from the other four combinations of the these elements. The tones in Experiments 1 and 2 were 0.5 s in duration (with 0.5-silent intervals between the elements). To promote transfer in Experiment 3, the tones were briefer, 0.25 s in duration, with an equivalent silent interval between them. In all experiments an equal number of positive and negative trials were randomly presented within each session and ear presentation was counterbalanced in blocks of trials across sessions and subjects. Subjects were tested for 36 sessions in Experiments 1 and 3, and for 30 sessions in Experiment 2.

Correct and incorrect responses, and their latency, were recorded on each trial. It was noted early in Experiment 1 that responses to positive sequences (hits) were, on average, faster than those to negative sequences (false alarms), a common finding supporting the notion that false alarms are executed with less confidence. This prompted us to employ a powerful analysis based on signal detection theory (SDT) which exploits both response accuracy and latency information (Carterette, Friedman, & Cosnides, 1965; Emmerich, Gray, Watson, and Tanis, 1972; Kulics, 1977). The use of latency information as an index of confidence or response criterion may be useful in cases of a difficult discrimination (Green & Swets, 1966), and also addresses the problem of obtaining a sufficient number of probability values for accurate determination of a receiver operating characteristic (ROC).
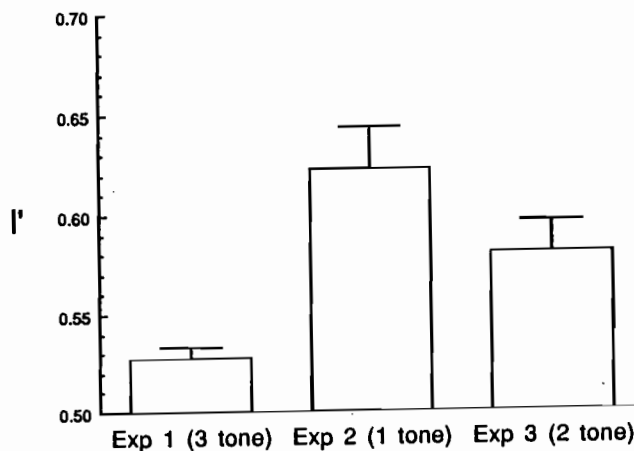
Figure 13.2. Discriminative performance is expressed in mean $l'$ values for each of the experiments. Bars = 1 standard error.

For this analysis, a key press was defined as either a hit or a false alarm depending on whether it followed a positive or negative tone. Hit and false alarm probabilities were calculated for each 300-ms epoch during the 3-s response interval. The corresponding cumulative probability values in each bin were then plotted on unit axes to yield an ROC. These ROCs are linear when plotted on normal deviate (double-probability) scales (O'Connor, 1990), supporting the usual assumption of underlying Gaussian signal and noise functions of SDT. The area falling under the ROC was calculated as a measure of discrimination and will be referred to as $l'$. Random performance is revealed by a characteristic falling on the positive diagonal, bisecting the unit square and yielding an $l'$ value of 0.5, while better than random performance is shown by values between 0.5 and 1 (optimal performance).

## RESULTS

Figure 13.2 illustrates that the rats were able to discriminate a three-tone sequence but their performance was poor relative to the two-tone, and particularly the single-tone task. A right ear (RE) advantage emerged early in training on the three tone task. This result was apparent across both subjects and sessions, and manifested itself during roughly the first half (18) of the total number of training sessions. The mean performance of 14 out of 18 sessions was better for the RE, and these differences were significant Wilcoxon $t(18) = 21.5, p < .05$]. This bias was fairly consistent over subjects—seven out of eight rats exhibited better RE performance for the first 18 sessions (sign test, $p < .05$).

During the second half of the experiment there was no longer a bias in favor of the RE; in fact, 13 out of these 18 sessions showed better LE performance (Sign test, $p < .05$), though these differences were not significant $(t(18) = 64.5, p > .05)$. The possibility of a reversal in asymmetry is supported by an examination of ear bias over sessions and subject. Over the entire experiment, the number of sessions showing superior RE performance within six session blocks is: 4-4-6-2-0-3 (the value of zero in the fifth block is part of a seven session run of superior LE performance). The number of subjects (out of eight) showing better RE performance within six session blocks is 7-6-5-2-3-4.

Further evidence for an RE, and so, inferred left hemisphere (LH) advantage on the 3-tone task early in training comes from an analysis of discriminative performance for certain negative sequences. Because of the apparent difficulty of discriminating three sequential tones, subjects may have adopted a simpler strategy, such as basing a decision on some subset of the entire sequence (Roitblat, Scopatz, & Bever, 1987). For example (letting the series ABC denote the positive sequence), subjects may have rejected negative sequences on the basis of only a single element (such as those ending in C), or two elements (rejecting all negative sequences ending in elements other than BC, but not those ending in BC). To address this question, discrimination between the positive sequence and various subsets of the entire set of negative sequences was assessed. The entire set of negative sequences was first subdivided on the basis of whether single or double tonal elements matched those of the positive sequence in the same positions. In the case of single elements this produced subsets of negative sequences with element A, B, or C in the first, second or third position respectively, with eight sequences of each type. These sequences may be denoted as Axx, xBx, or xxC, where the letter x stands for any other element, except, of course, those producing the positive sequence. For two element matches, the subsets consisted of sequences ABx,
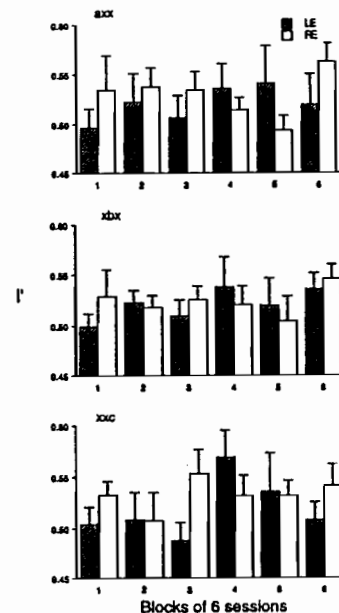
Figure 13.3. $I'$ values calculated over subjects for individual negative sequences containing one matching element are shown.

xBC, and AxC, each subset comprising two sequences. Discrimination was then assessed by determining $I'$ scores between the positive sequence and each subset of the negative sequences.

The results of this analysis are depicted in Figure 13.3 and 13.4 for single- and double-element cases, respectively, in blocks of six sessions across the entire experiment. The analysis indicated that performance was reliably above chance (.5) levels for both single- and double-element subsets, though better in the case of single-element matches, evidence that subjects were not simply basing their decisions on some subset of the entire positive sequence. Inspection of these figures also suggests that this ability was better when stimuli

were presented to the RE during the first half of the experiment. For single-element matches, a comparison of the performance over all negative cases yielded a significant difference between the ears for the first three six-session blocks [$t(9) = 3$, $p < .02$], but not the last three blocks [$t(9) = 16$, $p > .05$]. This difference is greatest during the first six sessions; analysis of performance of subjects within blocks revealed an effect of ear presentation closely approaching significance only in this case [$F(1,7) = 4.94$, $p < .10$].

Ear differences in the case of two element matches also appear more prominent in the first half of the experiment, with the bias again in favor of the RE. A comparison of performance for all negative cases revealed a significant difference between the ears for the first three blocks [$t(9) = 7$, one-tailed $p < .05$], but not the last three [$t(9) = 18.5$, $p > .05$]. This difference is again most apparent during the first six sessions of the experiment, wherein performance is significantly better for RE presentations [$F(1,7) = 7.18$, $p < .05$].

Because the $I'$ measure is based partly on response latency it seems reasonable to ask whether the dichotic difference may have been due to a simple underlying cause such as a latency difference dependent on hemispheric initiation of responses. One reason for rejecting such an explanation is that the $I'$ measure is sensitive to relative response speed, that is, the latency of hits relative to false alarms. A simple response or motoric difference between the hemispheres would cause a shift in both hit and false alarm distributions, so should leave $I'$ unaffected. In any case, an examination of mean overall response latency (the average of hits and false alarms) revealed no consistent difference in mean latency over the course of the experiment.

Analysis of both overall performance and discrimination of negative sequences resembling the positive stimulus in form supports superior discrimination for stimuli presented to the RE early in training, for a 3-tone sequence discrimination. This implies better performance by the LH. The results of this study, therefore, support an LH superiority for learning an abstract sequence discrimination not obviously related-to-natural communicative behavior in the rat. If, as in humans, this advantage is dependent on stimulus complexity, then a simple auditory discrimination should produce either a diminution or reversal of the asymmetry found on the complex task. Experiment 2 was designed to examine this question using a simple, high-low tone discrimination task.
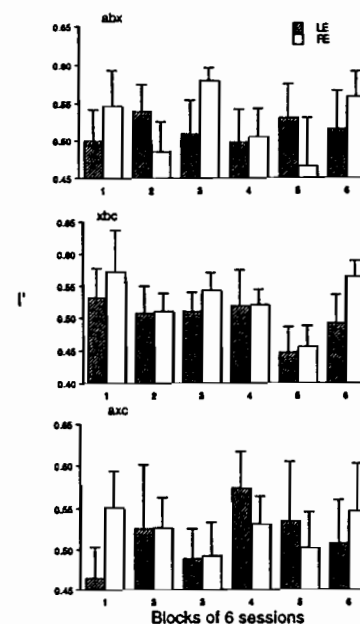
Figure 13.4. $I'$ values calculated over subjects for individual negative sequences containing two matching elements are shown.

Figure 13.2 shows that performance on this task was quite good relative to that in Experiment 1. There was no apparent difference in mean performance between the ears in the first or second half of the experiment: On 8 of the first 15 sessions, performance is superior for RE presentations (sign test, $p > .05$), and on 10 out of the second 15 sessions performance is better for LE presentations (sign test, $p > .05$). Neither did individual performance show a clear ear bias. Six out of eight rats exhibited better performance for RE presentations (one subject showed no difference) during the first half of the experiment, but the magnitude of these differences was not large (one-tailed $t = 6$, $p > .05$).

The strongest support for congruence of the findings from Experiment 2 with results from human studies would be a significant difference in favor of LE presentations, implying better RH performance. It is difficult to make a case when no clear differences are found, even though such a result is not uncommon in humans. In lieu of a strong LE bias, it seems reasonable to ask whether the asymmetries found on the sequence discrimination task in Experiment 1 were larger that those found in Experiment 2. The first 18 sessions were chosen for this comparison, because of the consistent ear bias found in Experiment 1 during this period. In Experiment 1, 14 out of the first 18 sessions showed larger $l'$ values for the RE (Sign test, $p < .05$), differences which were significant [$t(18) = 21.3$, $p < .01$]. In Experiment 2, 10 out of 18 did and the differences were not significant [$t(18) = 70$, $p > .05$]. A comparison of the first 18 sessions of the two experiments revealed the ear differences by session on the three tone task to be significantly larger than those from the single tone task [$t(18) = 16.5$, $p < .05$].

If this relationship holds, we would expect training on a 2-element tone sequence to result in an RE bias greater than that found on a single tone discrimination, but smaller than the bias previously demonstrated using a three element sequence. We decided to examine this question with the rats having undergone training in Experiment 2. Six of these rats successfully adapted to the modified chamber and were transferred to a two tone discrimination employing tones of the same frequency. Transfer from a 1- to 2-tone task in these subjects permitted comparison of asymmetries for two types of negative sequence of interest during acquisition: (a) sequences closely resembling the previously positive and negative stimuli in form (doublets or sequences with a single repeating element, AA or BB), and (b) a novel sequence composed of two different elements (BA). Responses made to doublets early in training should reflect the strategy used for single tone discrimination in Experiment 2, resulting in little or no asymmetry. The negative sequence composed of two different tones should be handled as a novel case. Discrimination of this type, then, should result in a greater degree of asymmetry early in training with a bias in favor of RE presentations.

Not surprisingly, overall performance on this task was better than that of Experiment 1, but poorer than that in Experiment 2, as Figure 13.2 reveals. An examination of performance by session though, revealed little difference dependent on ear: Ten out of 18 sessions were better for the RE, in both the first and second half of the experiment. Individual performance also did not show a large difference. As in the previous two experiments, there is a bias in favor of RE presentations for performance early in training, though the differences are
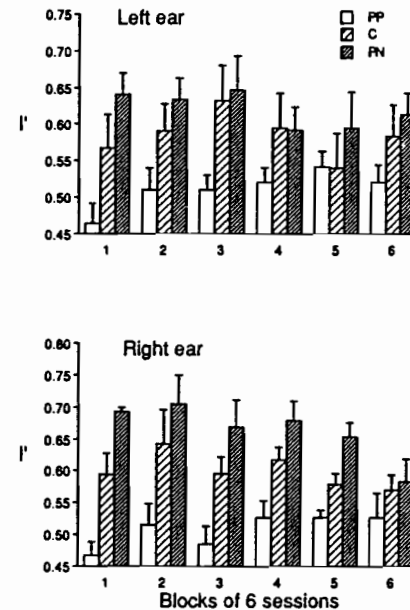
Figure 13.5. $l'$ values calculated for each of the negative cases over subjects are displayed. PP = previously positive, PN = previously negative, C = combination.

not large as in Experiment 1. Four out of six rats show superior performance for RE presentations during the first half of the experiment, though the magnitude of these differences was not significant [$t(6) = 5$, $p > .05$].

An examination of negative cases revealed a stronger RE bias. The results for each negative case are presented in Figure 13.5. Before discussing ear differences some remarks regarding general performance dependent on negative sequence type should be made. First, there was a large and significant difference in discrimination depending on stimulus type [$F(2,10) = 9.58$, $p < .005$]. The smallest value of $l'$ emerged for the repetition (doublet) of the single tone that had been positive in the first experiment. The best performance, not

surprisingly, is reserved for the doublet comprising the single tone that had previously been negative. Values of $\Gamma$ for the negative sequence comprising the combination of both tones are intermediate to these other two. Second, the differences in the degree to which the negative cases are discriminated decline over the course of the experiment; there is a significant interaction between block of training and stimulus type [$F(10,50) = 3.18, p < .005$]. These results indicate that training in Experiment 2 influenced responding primarily during early sessions, but had a declining effect as the experiment progressed.

Inspection of Figure 13.5 reveals overall better performance when stimuli were presented to the RE. Thirteen out of a total of 18 blocks show better performance for RE presentations (sign test, one-tailed $p < .05$), and the magnitude of these differences was significant [$t(18) = 43$, one-tailed $p < .05$]. Though there is no main effect of ear of presentation ($F(1,5) = 1.95, p > .05$), the interaction between ear and stimulus type approaches significance [$F(2,10) = 3.75, p < .10$].

Recall that the largest ear difference was predicted for the negative sequence bearing the least resemblance to the stimuli in Experiment 2, that is, the sequence composed of two different elements. The largest ear difference, however, occurs with the doublet of the tone that was previously negative; for every block except the last one, performance is better for RE presentations [$t(6) = 1$, one-tailed $p < .05$]. There is also a bias in favor of the RE for discrimination of the doublet that was previously positive (five out of six blocks) and for the sequence composed of two different elements (four out of six blocks), but these differences are not significant.

Examination of individual performance once again reveals an RE bias during the first half of the experiment, which is also dependent on stimulus type, and again is largest for the doublet that was previously negative. Five out of six subjects show superior discrimination of this stimulus for RE presentations during sessions 1 through 18, and the magnitude of these differences is significant [$t(6) = 1$, one-tailed $p < .05$]. The magnitude of ear differences during the first block of six sessions is also biased in favor of the RE. For the sequence composed of two different elements, and the previously positive and previously negative doublets, five, four and five of the rats, respectively, demonstrated better discrimination for RE presentations. Regardless of stimulus type, then, in a total of 14 out of 18 cases (six subjects × three negative cases), subject performance was better for RE presentations (Sign test, $p < .05$), and these differences were large [$t(18) = 37.5, p < .05$].

Table 13.1.
$\Gamma$ (RE - LE)

| Experiment | Rat | First 18 | Total Sessions |
|---|---|---|---|
| 1 (3 tones) | 2 | .045 | .003 |
| | 3 | .053 | .025 |
| | 4 | .017 | -.001 |
| | 7 | .053 | .035 |
| | L | -.039 | -.005 |
| | C | .011 | -.018 |
| | G | .034 | .014 |
| | M | .035 | .030 |
| Mean | | .026 | .011 |
| SE | | .011 | .007 |
| 2 (1 tone) | 19 | .080 | .059 |
| | 13 | .001 | -.008 |
| | 20 | .028 | .029 |
| | 11 | .012 | .011 |
| | 16 | -.011 | -.014 |
| | 12 | -.034 | .029 |
| | 17 | -.009 | -.034 |
| | 15 | -.007 | .001 |
| Mean | | .008 | .009 |
| SE | | .012 | .010 |
| 3 (2 tones) | 19 | .030 | -.005 |
| | 13 | .059 | .049 |
| | 20 | -.032 | .019 |
| | 11 | .048 | .050 |
| | 16 | .016 | -.022 |
| | 12 | .004 | .040 |
| Mean | | .021 | .022 |
| SE | | .012 | .012 |

The analysis for individual negative cases reveals a RE, and therefore, probable LH advantage for discrimination of an auditory sequence comprising two tones. If hemispheric asymmetry is dependent on sequence complexity, increasing with complexity as seems to be the case in humans, then we should find the greatest asymmetry in Experiment 1 and the smallest in Experiment 2. Differences in $l'$ between ear presentations are listed for each subject in Table 13.1, both for the first 18 sessions and over each of the entire three experiments, together with the mean and standard error of the differences. Inspection of the mean differences for the first half of each experiment, those in which the most consistent ear bias was found, shows that they lie in the right direction. It is also apparent from looking at Table 13.1 that there is an overall bias in favor of the apparent RE. Questions of the precise relationship between complexity and hemispheric asymmetry aside, the point should be made that the LH of the rat may be generally superior to the right hemisphere at auditory processing .

# SUMMARY AND DISCUSSION

Three experiments examined ear differences on single-, two- and three-tone monaural sequence discriminations in rats. Performance was evaluated using signal detection theory and revealed: (a) superior overall performance for RE presentations, particularly early in training; (b) the greatest degree of asymmetry emerging on the three tone discrimination—performance was better early in training for RE presentations; (c) ear differences were significantly greater on the three tone than the one tone task early in training; and (d) the average of the ear differences early in training was positively related to sequence length and task difficulty.

Degree of asymmetry, then, was found to increase with sequence complexity and was biased in favor of the RE. The trend of increasing asymmetry with task complexity is found in humans, but the assignment of lateral superiority, particularly for tasks involving complex auditory information, has been more problematic and may depend on the experience and information a subject brings to the task. In the case of music, early work demonstrated skills a subject brings to the task. In the case of music, early work demonstrated a LE advantage for identification of melodic sequences (Kimura, 1973), but the subjects of the studies were not musically sophisticated. Later work showed an RE superiority for musically sophisticated subjects, while less skilled subjects showed an overall LE superiority (Bever & Chiarello, 1974; Gordon, 1975). The few studies that show an overall LE superiority for musicians use familiar and short melodies (see Bever, 1975, for review). The inferred hemispheric differences are thought to depend on differences in processing strategy that reflect the relative strengths of each hemisphere. Musically unsophisticated

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subjects may depend on a simple process, perhaps Gestalt in nature, which does little in the way of sequential structural analysis, and so show right-hemisphere (RH) superiority. The inferred LH superiority in the case of musically skilled subjects may reflect an analysis of the structural relations between the sequential elements.

These results suggest that humans would perform better on the same three-tone discrimination when the stimuli are presented to the LE, implying better RH performance, and they do (O'Connor, 1990). A three-tone discrimination is evidently handled better by the LH in humans, but the RH in rats. One might conclude that these results imply a different hemispheric organization for the two species, but the data are interpretable in terms of different processing strategies, on the basis of unitary versus relational processing (Bever, 1980). It may be that humans are able to treat this discrimination as a unitary task, involving a single perceptual unit, without analysis of the elements comprising the sequence. Rats on the other hand, may have to handle the discrimination relationally—that is, they may be unable to match the elements as a unit, but be forced to treat the stimulus as three discrete elements in sequential or relational comparison.

This species difference may be based on differences in short-term memory. Humans may be able to hold the tonal sequence in short-term store with sufficient fidelity, or convert the tonal information to a symbolic and less volatile form, in order to perform a unitary or matching operation. It is likely that rats are unable to do so given their relatively poor performance on the three tone discrimination, a task posing little difficulty for humans. Further evidence for a species difference in auditory short-term or sensory store comes from recent work showing strong retroactive interference of rats' memory for single brief tones when followed by white noise having overlapping spectral energy while to human ears, the tones are clearly distinguishable (O'Connor & Ison, 1991). Short-term memory must be critically involved in the processing of sequential information, and hemispheric differences in memory dynamics when under the load of such processing may account for the species differences we find on these tasks.

In view of the differences between rats and humans, as well as between musically sophisticated and nonsophisticated subjects, it is interesting that the RE bias declined with training in Experiment 1, perhaps to some extent undergoing a reversal in favor of the LE. Extended training may produce similar effects in both rats and humans, perhaps as a result of the shift in processing strategy discussed earlier. Longitudinal experiments using human

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subjects, and sequences of varying complexity, are clearly needed for a proper comparison of the effects of training on processing strategy.

The present study supports the notion that hemispheric processing differences may be general across mammals. Along with other demonstrations of functional asymmetry in the auditory system of nonhuman species (Heffner & Heffner, 1984; Morrel-Samuels, Herman, & Bever, 1989; Nottebohm, 1970, 1977; Peterson, Beecher, Zoloth, Moody, & Stebbins, 1977), these results help to establish the contiguity of brain mechanisms involved in the processing of temporal information in general, and perhaps crucially involved with human language.

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