Discrimination of redundant auditory stimuli in pigeons

SATORU ISHIKAWA¹ ², TAKUYA MIYAZAKI, and TAKASHIGE IWAMOTO³

Department of Psychology, Hokkaido University, Sapporo, 060-0010, Japan

Abstract We investigated how pigeons use auditory dimensions for discrimination of complex tunes. Six pigeons were trained to match two redundant auditory stimuli varied along two dimensions, "rhythm" and "timbre", to two colors using a cross-modal symbolic matching-to-sample task. All pigeons learned this discrimination. The subjects matched the novel stimuli having new combination of each dimension's original values and the novel stimuli having the original "rhythms" and new "timbres", based on the "rhythm" dimension. These results suggest that the pigeons are able to divide complex auditory stimuli into several dimensions, and that they paid more attention to the "rhythm" dimension. However, they matched the stimuli having the original "timbres" and new "rhythms", to the color associated with the "rhythm" combined with the preserved "timbre" in the baseline discrimination. This result suggests that a dimension combined with a more salient dimension may become a conditional, or contextual cue for the discrimination of complex auditory stimuli in pigeons.

Key words: auditory discrimination, pigeons, rhythm, timbre, cross-modal symbolic matching-to-sample task.

Avian species have sensitivity to the various auditory features and dimensions such as pitch, loudness, frequency components, and temporal components (Hulse, Takeuchi, & Braaten, 1992). They are able to use these features and dimensions to discriminate among auditory stimuli (Cynx, 1995; Hulse, Humpal, & Cynx, 1984; Shy, McGregor, & Krebs, 1986). Among these dimensions, perception and recognition of spectral and temporal components have been studied intensively, because bird songs, one form of communicative tools of avian species, have rich spectral and temporal dynamics.

For example, Cynx (1993) indicated that zebra finches (Taeniopygia guttata) were able to discriminate original conspecific songs from modified conspecific songs lacking some of harmonic or temporal structures. In another study, zebra finches were able to detect lack of the second harmonic in a conspecific song (Cynx, Williams, & Nottebohm, 1990). European starlings (Sturnus vulgaris) also discriminated two patterns of tunes (linear and random) that were different in the temporal dimension (Humpal & Cynx, 1984). These studies show that songbirds are sensitive to both spectral and temporal dimensions.

Several studies in songbirds examined which of these dimensions was more salient than the other as a cue for discrimination of complex auditory stimuli. Weary (1990) trained great tits (Parus major) to discriminate two syllables of their conspecific songs with a go/no-go procedure. Then he tested generalization of this discrimination to novel stimuli modified in each of the following five auditory properties: frequency, amplitude, duration, amplitude modulation, and frequency modulation. The change of frequency modulation affected the generalization performances, whereas the
change of duration had no effect. On the other hand, Braaten and Hulse (1993) trained European starlings to discriminate two tunes differed in the temporal structure. When novel stimuli having original timbres with novel temporal structures were presented, the subjects did not maintain the discrimination. These studies show that the relative saliency of spectral and temporal dimensions as a cue for discrimination depends on the stimuli and species.

It is adaptive for songbirds to have such an ability to utilize spectral and temporal dimensions separately as a cue for discrimination, because they use complex songs to breed. An important question is whether this ability is limited to songbirds, or common to avian species. To answer this question, we have to examine if nonsongbirds can separate spectral and temporal dimensions to discriminate complicated auditory stimuli.

Pigeons (*Columba livia*), one of nonsongbirds, show remarkable similarities to songbirds in simple discrimination of auditory intensity and frequency (Cynx, 1995; Hienz, Sinnott, & Sachs, 1980). Some reports suggest that pigeons have the ability of using spectral dimension as a cue for discrimination (Hienz, Sachs, & Sinnott, 1981; Ishikawa & Iwamoto, 1995), and at least one report suggests that pigeons may have the ability to use temporal dimension as a cue for discrimination as well (Porter & Neuringer, 1984).

In this article, we asked if pigeons were capable of using spectral and temporal dimensions as a cue for discrimination separately. We presented complex auditory stimuli to pigeons in a selective attention paradigm. In the visual modality, pigeons may pay attention to only one of the dimensions when they discriminate the stimuli having two redundant dimensions (color and shape) (Reynolds, 1961). We prepared two redundant auditory stimuli differed in spectral and temporal structures (“timbre” and “rhythm”, respectively), and trained pigeons to discriminate these stimuli. After learning to discriminate these stimuli, we presented novel auditory stimuli to examine which dimension the pigeons would mainly use as a cue for discrimination of the stimuli.

### Method

#### Subjects

Six experimentally naive pigeons (*Columba livia*) were used as subjects. They were kept in individual cages in a room in which the lights were turned on at 7 a.m. and off at 9 p.m. daily. All birds were maintained at 80% of their normal body weights throughout the experimental period. Grit and water were freely accessible in their home cages. The pigeons were served most daily diet in the experimental sessions. Supplementary food was given to them after daily session if necessary.

#### Apparatus

A standard operant box (BRS/LVE, PIP-013, 35.0 cm long × 30.0 cm wide × 35.0 cm high) with three response keys (2.5 cm in diameter) at 24 cm above the floor on the front panel, was used. A houselight was put on the top of the front panel. A food hopper was mounted behind the center of the front panel at 9 cm above the floor, and a small loudspeaker (Foster, 80A04DIA77) was placed on the left of the food hopper. Auditory stimuli were presented by this loudspeaker. A personal computer (NEC, PC9801RA) was used to control the experimental box, to generate auditory stimuli with an FM-sound board (NEC, PC9801-26K), and to collect the data.

#### Stimuli

The auditory stimuli were used as sample stimuli for the symbolic matching-to-sample (MTS) task. The stimuli were sequential sounds consisting of 20 tones and 20 rests. The duration of each tone was 0.5 sec and the each rest was also 0.5 sec, hence the overall length of these stimuli was 10 sec. The intensity of the stimuli was about 70 dB at the center of the experimental box and the fundamental frequency of the stimuli was 1046 Hz. These stimuli were readily audible to pigeons (Necker, 1983).

Auditory stimuli were controlled experimentally along the two dimensions. There were “rhythm” and “timbre” dimensions in these stimuli, and each dimension had four values. We followed two previous studies (Braaten & Hulse, 1993; Ishikawa & Iwamoto, 1995) for selection of
Ishikawa et al.: Discrimination of redundant auditory stimuli in pigeons

the values in each dimension. The values of the “timbre” dimension were glockenspiel, piccolo, zither, and oboe prepared by the FM-sound board, and the values of the “rhythm” dimension were alternation “OXMXOXMXO→→→→XOXMXOXMXO” (“O” indicated one note and “X” indicated one rest), long-intermittent “OOOXXXXXOO→→→→XX OOOXXXXX”, short-intermittent “OOXXOOXX O→→→→XOOXXOOXX”, and random “OXXOOX OOO→→→→XXXOOOOXX”. Therefore, sixteen auditory stimuli were produced from the combinations of the four values on the two dimensions. In this experiment, we used only twelve stimuli out of 16 combinations; two were used in discrimination training, and the remaining ten were used for tests. The stimuli actually used in this experiment are listed in Table 1.

Red and green colors were used as comparison stimuli for the symbolic MTS task. These colors were back-projected on the response keys by in-line projectors (BRS/LVE, IC-900) mounted behind the response keys.

Procedure

Training Each bird was first trained to eat food through the opening of the food hopper, and to peck at the response keys. Then, the subjects were trained on the symbolic MTS task to discriminate the two auditory stimuli mentioned above. Trials started with illuminating the houselight and the center key. After the fifth peck at the center key (FR 5), one of the two auditory stimuli was presented as the sample stimulus from the loudspeaker, and the two colors, red and green, appeared on the side keys simultaneously as the comparison stimuli. The relationships between the two sample stimuli and the comparison stimuli were determined arbitrarily, and the relations were counterbalanced across the subjects. If the first choice of the comparison after 10 sec from the onset of the sample was correct, the comparison stimuli disappeared and the subjects were allowed to eat the mixed grain from the food hopper for 3 sec as reinforcement (FI 10 sec). Then the houselight was turned off, and the next trial was started after a 15-sec intertrial interval (ITI). If the first choice after 10 sec from the onset of the sample was incorrect, or if there is no response during 5 sec (LH 5 sec) after 10 sec, the houselight was turned off, and a 10-sec blackout period were inserted before the ITI began. After the 15-sec ITI, the same trial was repeated until a correct choice occurred (a correction method). A schematic diagram of this symbolic MTS task is shown in Figure 1.

The pigeons were given one training session consisting of 64 trials per day. When either the proportion of the correct choice was higher than 80% during three consecutive training sessions, or 75 training sessions were given, the subjects were over-trained under a condition in which 16

| Table 1. Auditory stimuli used for training and tests |

<table>
<thead>
<tr>
<th>Values of “timbre” dimension</th>
<th>Values of “rhythm” dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Glockenspiel</td>
</tr>
<tr>
<td>Alternation</td>
<td>a*</td>
</tr>
<tr>
<td>Long-intermittent</td>
<td>C</td>
</tr>
<tr>
<td>Short-intermittent</td>
<td>E</td>
</tr>
<tr>
<td>Random</td>
<td>G</td>
</tr>
</tbody>
</table>

*: The stimuli written in small letters are used in the training sessions, and the stimuli written in capitals are used in the three tests.
unreinforced probe trials were randomly inserted among 48 training trials. The probe trials simply ended after 10 sec from the onset of the sample, no matter whether the pigeons' choice was correct or not. A 3-sec blackout period followed the probe trials, and the next trial started after the 15-sec ITI. The pigeons were over-trained until the proportion of the correct choice was higher than 90% during five consecutive sessions, or higher than 80% during five consecutive sessions after 75 training sessions.

Test Three series of test sessions were given to the subjects; Test 1 was the new combination test, Test 2 was the new “rhythm” pattern test, Test 3 was the new “timbre” test. In these test sessions, novel auditory stimuli were presented as the sample of probe test trials in place of the training probe trials of the over-training sessions. First, the pigeons were given Test 1. Two novel stimuli having the same value as the training stimuli in the two dimensions (“timbre” and “rhythm”), but rearranged these combinations, were presented. These stimuli were presented 64 times in a random order across eight test sessions.

Second, the pigeons were given Test 2 (“rhythm” pattern test) with the four novel stimuli having one of the four new values in the “rhythm” dimension and the same value in the “timbre” dimension as the training stimuli. These were presented 32 times in a random order across eight test sessions. Finally, the subjects received Test 3 (“timbre” test), with the remaining four novel stimuli having one of the four new values in the “timbre” dimension and the same value in the “rhythm” dimension as the training stimuli. These were also presented 32 times in a random order across eight test sessions.

Results

Training
All six pigeons learned this training task. Table 2 shows mean accuracy of the MTS task during the last 3 training sessions and the last 5 over-training sessions, and the number of sessions until the subjects reached the learning criterion in the training and the over-training sessions. The final accuracy differed little among the subjects, though the number of training sessions greatly varied.

Test
We analyzed the number of responses to each of the two comparison stimuli during presentations of novel sample stimuli. Trials in which no response was made during 3 sec after 10 sec from the onset of the trial, were not used for the analysis. The novel stimuli had at least one value of either of the two dimensions used in the training. Therefore, there were four cases of pigeons’ responses depending on the novel stimuli presented. 1) The pigeons pecked at the color associated with the training sample stimuli having the same value in the “timbre” dimension with the test stimuli. 2) The pigeons pecked at the color other than the one associated with the training sample stimuli having the same value in the “timbre” dimension with the test stimuli. 3) The pigeons pecked at the color associated with the training sample stimuli having the same value in the “rhythm” dimension with the test stimuli.
The pigeons pecked at the color other than the one associated with the training sample stimuli having the same value in the "rhythm" dimension with the test stimuli. We classify the cases of 1) and 4) as type "T" response and the cases of 2) and 3) as type "R" response respectively. Figure 2 shows the response ratio of type "R" responses to type "T" responses for the novel test stimuli.

In Test 1, the subjects showed more type "R" responses than type "T" for the two novel stimuli having new combinations of each dimensions' value of the training stimuli. The result of a three-way ANOVA (subjects \( \times \) stimuli \( \times \) response type) showed significant main effects of subjects and response type in the number of responses \( [F(5, 42)=111.97, p<.001; F(1, 42)=44.40, p<.001; \) respectively], and significant interactions of subjects \( \times \) stimuli and subjects \( \times \) response type \( [F(5, 42)=6.94, p<.001; F(5, 42)=4.74, p<.01; \) respectively]. Post-hoc comparisons using Tukey's honestly significant difference (HSD) test revealed that more "R" responses occurred for both test stimuli \( (p<.05 \) for stimulus "C" and "D").

The results were apparently conflicting between Test 2 and Test 3. In Test 2, pigeons heard the novel stimuli having two new values on the "rhythm" dimension with the original "timbre" values. There were many type "R" responses, despite that neither stimulus had preserved the original value in the "rhythm" dimension. In Test 3, pigeons heard the novel stimuli having two new values on the "rhythm" dimension with the original "timbre" values. There were many type "R" responses, despite that neither stimulus had preserved the original value in the "rhythm" dimension.

---

Table 2. Results of training for each pigeon

<table>
<thead>
<tr>
<th>Subjects</th>
<th>MTS task Condition</th>
<th>Mean correct % of the last 3 training sessions</th>
<th>Number of training sessions</th>
<th>Mean correct % of the last 5 over-training sessions</th>
<th>Number of over-training sessions</th>
</tr>
</thead>
<tbody>
<tr>
<td>#701</td>
<td>a - Green* b - Red</td>
<td>85.9</td>
<td>22</td>
<td>90.9</td>
<td>20</td>
</tr>
<tr>
<td>#702</td>
<td>a - Green b - Red</td>
<td>84.4</td>
<td>43</td>
<td>90.9</td>
<td>20</td>
</tr>
<tr>
<td>#703</td>
<td>a - Green b - Red</td>
<td>84.9</td>
<td>19</td>
<td>91.9</td>
<td>20</td>
</tr>
<tr>
<td>#704</td>
<td>a - Red b - Green</td>
<td>84.4</td>
<td>73</td>
<td>87.8</td>
<td>6</td>
</tr>
<tr>
<td>#705</td>
<td>a - Red b - Green</td>
<td>83.3</td>
<td>52</td>
<td>80.9</td>
<td>31</td>
</tr>
<tr>
<td>#706</td>
<td>a - Red b - Green</td>
<td>83.3</td>
<td>53</td>
<td>84.4</td>
<td>26</td>
</tr>
</tbody>
</table>

*a" and "b" are training stimuli in Table 1.

---

Figure 2. Performance of the pigeons for novel test stimuli in the three tests. Y-axis indicates the ratio of type "R" responses to type "T" responses. White bars show the results of Test 1, striped bars show the results of Test 2, and gray bars show the results of Test 3 (see text for details). "C"~"L" are test stimuli shown in Table 1.
A three-way ANOVA (subjects x stimuli x response type) showed significant main effects of subjects, stimuli and response type in the number of responses [F(5, 18)=206.29, p<.001; F(3, 54)=16.42, p<.001; F(1, 18)=53.41, p<.001; respectively], and significant interaction of subjects x stimuli [F(15, 54)=8.78, p<.001]. Post-hoc Tukey's HSD comparisons revealed that more "R" responses occurred when the "short-intermittent" was presented with the training "timbre" (p<.05 for stimulus “E”; n.s. for stimulus “F”), and the "random" pattern was presented with the training "timbre" (p<.01 for stimulus “G”; p<.05 for stimulus “H”).

In Test 3, there were weak tendencies in the pigeons’ responses. The same three-way ANOVA (subjects x stimuli x response type) showed significant main effects of subjects and stimuli in the number of responses [F(5, 18)=26.37, p<.001; F(3, 54)=19.09, p<.001; respectively], and significant interactions of subjects x stimuli and stimuli x response type [F(15, 54)=6.40, p<.001; F(3, 54)=4.24, p<.01; respectively]. Post-hoc Tukey’s HSD comparisons did not show any significant differences, but Fisher’s least significant difference (LSD) test indicated two significant differences. When the “zither” was presented with the “alternation” which is one of the training “rhythm”, the subjects showed more type “R” responses (p<.05 for stimulus “I”). However, when the “zither” was presented with the “long-intermittent” which is the other training “rhythm”, the subjects showed more type “T” responses (p<.05 for stimulus “J”). When the “oboe” was presented with the training “rhythm”, the pigeons showed comparable type “R” and type “T” responses (n.s. for stimulus “K” and “L”).

**Discussion**

The Pigeons learned to discriminate the two complex auditory stimuli with the symbolic cross-modal MTS task. This result was consistent with our previous study in which pigeons discriminated four timbres using the same symbolic cross-modal MTS task (Ishikawa & Iwamoto, 1995). Several studies showed similar results in pigeons and other avian species with different kinds of learning tasks (Braaten & Hulse, 1993; Porter & Neuringer, 1984). All of these results convergingly indicate that many avian species have an ability to discriminate complex auditory stimuli.

In Test 1, our pigeons showed more type “R” responses than type “T” for the novel stimuli having new combinations of the two dimensional values. This suggests that the pigeons may have paid attention selectively to the “rhythm” dimension for this discrimination. If this was the case, we should expect that the pigeons would show fewer type “R” responses in Test 2 where the “rhythm” dimension’s value was varied, and more type “R” responses in Test 3 where the original “rhythm” dimension’s value was preserved.

When the test stimuli having novel values in the “timbre” dimension were presented in Test 3, there were more type “R” responses than type “T”, though the differences between type “R” responses and type “T” in Test 3 were smaller than those in Test 1. This is consistent with the selective attention hypothesis raised above.

On the other hand, when the test stimuli having novel values in the “rhythm” dimension were presented in Test 2, the pigeons again showed more type “R” responses than type “T”. This puzzling result is not explained by the simple selective attention hypothesis, because this discrimination is impossible without referring to the “timbre” value. How can we explain these conflicting results in the three tests? We suggest one plausible learned rule that the pigeons could have followed. First, when the pigeons do not detect the original “rhythm” value, they look at the other dimension, the “timbre” value, in the novel stimuli. Then they determine which “rhythm” value is lacking in reference to the “timbre”. That is, if the “timbre” is the one which has been combined with one of the “rhythm” in the original training, they determine this “rhythm” as lacking, hence match the novel stimulus to the color associated with the other “rhythm”. This
explains why there are more "R" responses in Test 2.

This interpretation suggests that the pigeons may spontaneously have afforded to the "timbre" dimension a function as a conditional discriminative stimulus or a contextual cue to control the judgement depending on the "rhythm" dimension. A related phenomenon in which stimuli constructing an environment other than the immediate discriminative stimuli may come to control discriminative responding is known as the "context effect" in learning (e.g.; Domjan & Best, 1980; Lubow, Rifkin, & Alec, 1976). In these studies, animals are not able to choose the context stimuli; subjects learn the contextual cue passively. We suggest that, in such tasks as was used in our study, the pigeons may separate the redundant auditory stimuli into two dimensions, and then afford such a role to one of the dimensions actively.

These findings in the present study are comparable to songbirds in following two points. First, these results show that the pigeons share the ability with songbirds to use spectral and temporal dimensions to discriminate complex auditory stimuli. In the previous study, we had already found that pigeons used spectral dimensions to discriminate complex sounds (Ishikawa & Iwamoto, 1995). In the present study, we have shown that pigeons may use temporal dimensions to discriminate complex tunes as well.

Secondly, the pigeons used spectral and temporal dimensions separately. The pigeons seem to have given different roles to these dimensions for discrimination spontaneously. Namely, the "rhythm" dimension was treated as an immediate discriminative cue, and the "timbre" dimension was treated as a conditional stimulus or context when they discriminated the redundant auditory stimuli based on the "rhythm" dimension. Temporal dimension seems more salient than spectral dimension as a cue for discrimination of complex stimuli in pigeons. However, songbirds did not show such conditional using of any dimensions for discrimination of auditory stimuli. When several dimensions were available simultaneously as a cue for discrimination, they seemed to attend and use particular dimension alone (Braaten & Hulse, 1993; Weary, 1990). However, it is possible that this difference has resulted from differences in experimental conditions, we should study the generality of the spontaneous conditional learning in other avian species, especially in songbirds, and in other dimensions such as fundamental frequency and sound intensity.

In summary, this study shows that at least one species of nonsongbirds (i.e. pigeons) is able to use spectral and temporal dimensions to discriminate complex auditory stimuli, and also use these dimensions conditionally for discrimination. So, it is likely that the use of these dimensions has evolved in common to avian species.

Acknowledgement

We gratefully acknowledge K. Fujita for his helpful comments and discussions on the manuscript.

References


Cynx, J. 1995 Similarities in absolute and relative pitch perception in songbirds (starling and zebra finch) and a nonsongbird (pigeon). Journal of Comparative Psychology, 109, 261–267.


