

How grouping improves the categorisation of frequency in song birds and humans and why song birds do it better.

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There is evidence that song bird species produce, recognize, and discriminate song notes on the basis of frequency within a range. How song birds do this is unknown. One hypothesis is that song birds represent individual frequencies separately, somehow knowing which identify conspecifics. This hypothesis suggests that song birds memorise individual song frequencies as a list without underlying rules (see Herrnstein, 1990). Because of natural continuous variability in song frequency within and among individuals (Borror, 1961; Weisman et al. 1990) song birds might need to memorize a number of individual frequencies to discriminate conspecifics from heterospecifics. A second hypothesis is that song birds categorise song notes into frequency ranges, forming large open-ended categories (see Herrnstein, 1990), and use knowledge about these ranges in song. Here, song birds treat exemplars of a frequency range collectively as suggested by theories of category learning (Keller & Schoenfeld, 1950).

To decide between these hypotheses we trained zebra finches and, for comparison, humans in a (distributed S+) discrimination that required memorisation of individual frequencies and in a (compact S+) discrimination that could be acquired by classifying frequencies into ranges. If acquisition of the compact S+ discrimination is faster and more accurate then both species can use frequencies in a common range as a category. We examined transfer to novel frequencies to test whether the compact S+ groups form open-ended frequency range categories. The frequency range hypothesis predicts more control over responses to transfer tones following compact than distributed discrimination, because category learning causes subjects to treat tones within each frequency range collectively.

Method

We assigned 4 birds and 4 humans each to the

compact and distributed S+ discrimination groups.

Discrimination Training

Subjects heard 27 tones, beginning at 2000 Hz separated by 120 Hz. In the compact S+ groups, 9 tones in the frequency range 3080-4040 Hz were positive: approach to the feeder produced food (zebra finches), breaking a photo-beam by hand produced visual and auditory feedback (humans); 9 tones each in the ranges 2000-2960 Hz and 4160-5120 Hz were negative: approach to the feeder produced lights out. In the distributed S+ groups, 9 tones spread across the 3 ranges (2000-5120 Hz) were positive and the remaining 18 tones were negative.

Transfer

Training continued for several days before the transfer test. The procedure alternated daily between discrimination and transfer sessions, which substituted 9 test tones for training tones. Over 3 transfer days, both groups heard 27 test tones, 9 per day, beginning at 2060 Hz spaced 120 Hz apart, and 18 training tones. The consequences for responding to training tones were unchanged, but responding to test tones ended the trial without food or feedback.

Results and Discussion

Acquisition to Day 15

In both species (Fig. 1), the compact group learned significantly ($p < .001$) more quickly and to a higher asymptote than the distributed group, whose discrimination ratios rose only slightly above chance. In comparison to zebra finches, humans learned the compact discrimination more slowly and less completely, and did not learn the distributed discrimination.

Transfer tests

Training tones. Percent responding in the compact groups increased significantly after all positive tones in zebra finches ($F(2,6) = 993.75, p < .001$), and humans ($F(2,4) = 18.94, p < .01$). In the distributed groups, the percent response to S-s just above and below S+s did not differ significantly in humans, ($F(2,6) = 2.68, ns$), but after 20 days of training (in addition to that in Fig. 1) zebra finches discriminated all S+s from all S-s ($F(2,6) = 22.48, p < .01$) (Fig. 2).

Transfer tones. The compact group had a significantly higher percent response to transfer tones in the middle (positive) range than in the lower and upper (negative) ranges in both zebra finches ($F(2,6) = 394.22, p < .001$) and humans ($F(2,4) = 28.74, p < .01$), showing that both species categorised transfer tones within each range. The distributed groups showed no evidence of transfer of discrimination: percent response to

tones similar and different from training S+s did not differ, $F < 1$, (Fig. 2).

General Discussion

Both zebra finches and humans can sort tones into frequency ranges. The compact groups learned quickly to categorise training tones in the middle range as S+s and tones in the lower and upper ranges as S-s. By contrast, zebra finches discriminated distributed S+s very slowly (about 40k trials) and humans discriminated them not at all. Discrimination of compact S+s transferred to other tones in the three frequency ranges, but discrimination of distributed S+s did not transfer to adjacent tones.

Because of natural variability in song (Borror, 1961; Weisman et al. 1990) the ability of song birds to identify conspecifics by individual frequencies would require an enormous amount of memory capacity. We found song birds have difficulty with this kind of memorisation, acquiring a distributed S+ discrimination very slowly. Given their facility in compact discrimination and their difficulties in distributed discrimination, it is likely that song birds identify the frequency of conspecific song using open-ended categorisation rather than rote memorisation. This level of categorisation effectively reduces memory capacity. Humans, too, can use frequency range to categorise tones, but their performance lacks the crisp accuracy of zebra finches. Interestingly, humans, unlike zebra finches, can not memorise 9 distributed tones.

The frequency range hypothesis helps to explain why song birds produce the frequencies in song notes over narrow ranges and why the territorial responses of song birds decline abruptly when playback songs are transposed outside their normal frequency range (Falls, 1962; Emlen, 1972; Nelson, 1988).

References

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