

MEMORY DOES NOT CONSTRAIN INDIVIDUAL RECOGNITION IN A BIRD WITH SONG REPERTOIRES

by

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(With 5 Figures)

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Summary

We tested the hypothesis that memory or perceptual limitations imposed by song repertoires constrain the ability of song birds to recognize their neighbours by song. Using operant conditioning procedures, we trained male song sparrows (*Melospiza melodia*) (median repertoire size = 8) to discriminate between two artificial song sparrow repertoires of 32 songs each (64 songs total). Both song sparrows learned to discriminate concurrently between all 32 song pairs. The birds learned later songs as quickly as they learned earlier songs. These results suggest that song sparrows are capable of memorizing the full song repertoire of their neighbours under natural conditions. In a second experiment we found that song sparrows readily generalize from one exemplar of a song type to other variations of that song type. We conclude that the evolution of song repertoires of song sparrows have neither constrained nor been constrained by individual recognition of neighbours by song.

Introduction

Most contemporary theories of song repertoires posit or imply strong directional selection pressure for larger repertoires (see reviews in SEARCY & ANDERSSON, 1986; KROODSMA, 1988). The small repertoire size observed in most species - almost less than 10 types, many less than 5 —

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thus presents something of a paradox: If a bird with 6 songs does better than one with 3 songs, one with 9 songs should do better yet. KREBS & KROODSMA (1980) pointed out that this paradox suggests countervailing selection against, or constraints on, large repertoires; as one possibility, they suggested that larger repertoires might interfere with individual recognition.

Numerous studies have shown that birds can discriminate the songs of neighbours from those of strangers; a few studies have shown further that birds can distinguish among the songs of different neighbours (*e.g.* FALLS & BROOKS, 1975; MCGREGOR & AVERY, 1986; BRINDLEY, 1991; GODARD, 1991; STODDARD *et al.*, 1991). Neighbour discrimination implies long-term memory for songs, and in species where males have repertoires, many songs would have to be learned. If birds are limited by how many songs they can commit to memory, then we might expect poorer neighbour recognition in repertoire species than in non-repertoire species. In fact, the few studies that do not find robust neighbour-stranger discrimination turn out to involve repertoire species (*e.g.* KROODSMA, 1976; HARRIS & LEMON, 1976; SEARCY *et al.*, 1981; FALLS & D'AGINCOURT, 1981). FALLS (1982) reviewed the evidence on neighbour-stranger discrimination and observed that the degree of neighbour-stranger discrimination was inversely related to repertoire size, with strongest discrimination found in species that have single songs. He concluded that "Whatever the benefits of repertoires, they have to be weighed against possible costs, one of which may be a reduction in neighbour-stranger discrimination. This is a possible constraint on repertoire size" (p. 264). Many have suggested that it is beneficial to a singer to be recognizable to his neighbours (*e.g.* FALLS, 1982; GETTY, 1987). Thus, the cost of degraded recognition might counter the pressure for large repertoires; hereafter we will refer to this idea as the Memory Constraint hypothesis.

Field studies provide little evidence concerning the mechanism of neighbour discrimination. In this study, we have directly examined the limits of song memory in the laboratory by training birds to learn as many songs as would be required in the field to recognize any neighbour by any song in its repertoire. The laboratory approach has major advantages over the field approach. In the field, the subject may respond equally to the songs of neighbour and stranger (or of different neighbours) for either of two reasons: 1) He may be unable to perceive the difference between the two songs, or 2) he may regard them as biologically equivalent, *e.g.* equally threatening. In the lab, the test songs are chosen to be biologically equivalent (all stranger songs), and the bird is reinforced for discrimina-

tion between them, so he will do so if he possibly can. Thus in the lab, unlike in the field, we can make a strong test of the Memory Constraint hypothesis. For a detailed discussion of the advantages of laboratory conditioning procedures for insight into this sort of question see BEECHER & STODDARD (1990).

The song sparrow is an appropriate subject for studies where we attempt to quantify the memory load required for individual recognition of neighbours. It sings with eventual variety (repeats a type 5-20 times before switching) and it cycles through its repertoire fairly regularly. Thus it is advantageous for birds to learn every song in their neighbours' repertoires. We estimate the typical memory load for the song sparrow to be approximately 32 songs, obtained by multiplying the largest expected number of neighbours (4) by the average repertoire size (8). Our field tests for neighbour discrimination support this estimate, showing that male song sparrows can recognize a randomly-selected song from the neighbour's repertoire (STODDARD *et al.*, 1990, 1991).

Briefly, our method in this lab study consisted of training the bird to discriminate between two sets of songs (artificial repertoires): the bird pecked a key when presented a song from one set, and withheld pecking when presented a song from the other set. Each set contained 32 songs, for 64 total songs. The 64 songs divided equally among two sets is equivalent to the "prototypical" field situation of 4 neighbours with 8 song types each, *i.e.* 32 songs divided equally among 4 sets. If all songs are equally likely, then the uncertainty in these two systems is equivalent, *i.e.* $2^{64} = 4^{32}$ (Hailman, 1977; BEECHER, 1989). In fact, this "prototypical" field situation is a more difficult one than birds in our population normally experience, because the bird often has fewer than 4 neighbours within audible range. Moreover, we formed our artificial repertoires from the songs of many different birds, and when we used more than a single song from a particular individual, we put them in both categories (GO and NOGO). Thus if the different songs of an individual contain any "signature" or "voice" characteristics that normally simplify the learning of a bird's repertoire, this would hinder, not help, the learner in our laboratory situation. We thus view our 64-song discrimination task as a stringent test of the Memory Constraint hypothesis.

Our procedure was to introduce songs one pair at a time, one song from each category, gradually increasing the number of songs in the daily training set. When the bird had learned one pair to criterion, the second pair was introduced. This procedure was continued until the bird had learned all 64 songs, or had reached capacity, whichever occurred first.

We presumed that if the bird were nearing capacity, this would be reflected in a increase in the learning time for later song pairs, and/or a drop in the overall performance level. It is important to note that at the end of this procedure, if a subject had learned to discriminate all 32 song pairs, it would hear each of the 64 songs only once or twice per day. Although comparisons of the laboratory and field situations are problematic, we note that in the field the bird has considerably more exposure to each of his neighbour's songs than this, and so in this sense too the laboratory situation strikes us as a stringent test of the Memory Constraint hypothesis.

We carried out a second experiment to test whether song sparrows can generalize across the variation that naturally occurs within discrete song types. A male song sparrow sings his songs in well-defined bouts of a particular type (eventual variety), but he typically varies successive versions of a type, and these variations can be quite extreme in some cases. We have shown in a field experiment that the birds are sensitive to variations at this level (STODDARD *et al.*, 1988). Thus when a bird in the laboratory is given one exemplar to represent a type class, we must ask whether he has learned the type in some broader sense, or has learned only the particular exemplar of that song type. After our subject had completed the 64-song discrimination task, we presented the birds with variants on a subsample of these song types to see if they would generalize their learning of these new exemplars.

Methods

We trained and tested two song sparrows. Both sparrows were male and were caught in the autumn of their hatching year. Birds were maintained on natural light in sheltered outside aviaries, each in its own cage (60 × 45 × 45 cm) with natural foliage, *ad lib* water and a rationed amount of commercial chick starter food. At the onset of a training session, the bird, still in his home cage, was placed in a sound attenuation chamber in the lab. An enclosed coaxial full-range speaker played sound from a PDP-11/23 computer which resynthesized natural digitized songs through a 12-bit D/A converter at 30 ksamples/s. A 7-pole elliptic lowpass filter with an 11 kHz corner frequency smoothed the DAC output signal. A 4-pole Butterworth highpass filter set at a corner frequency of 1.5 kHz reduced environmental noise from the field recordings to eliminate extraneous identification cues. A solenoid-activated feeder delivered a millet seed as a reward for a correct response. The feeder was equipped with two Fresnel-lensed LEDs mounted to piezo-electric peck detectors (STODDARD, 1988).

We employed a variant of the standard "GO-NOGO" psychophysical presentation/reward paradigm (Fig. 1). When the program started, the observing key was illuminated. At any time, the bird could initiate a trial by pecking this key. The computer then selected and played the bird one song from the training set. When the song was completed, the response key was illuminated. The bird could either peck the response key (GO response) or not

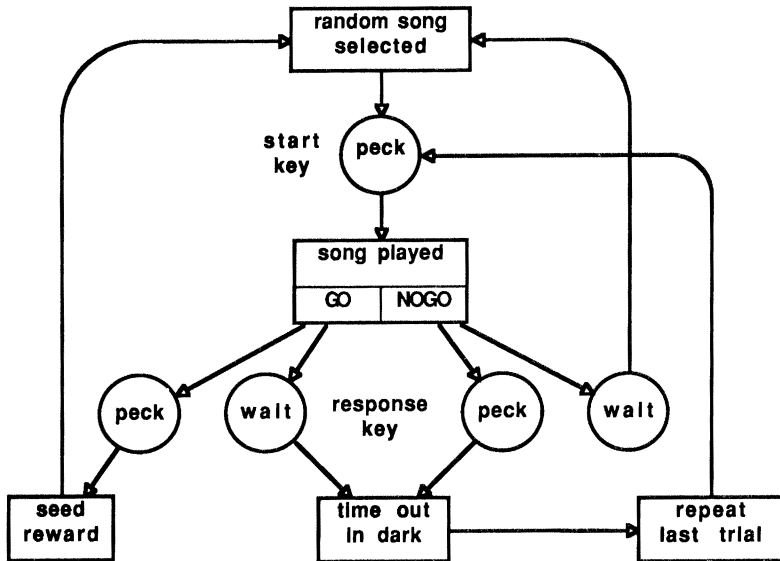


Fig. 1. Flow chart of the GO-NOGO forced choice training paradigm. Actions performed by the computer are enclosed in rectangles. The bird's actions are indicated as circles.

(NOGO response). If the presented song belonged to the GO set and the bird pecked (correct response), it was immediately rewarded with a seed. The bird was then able to initiate a new trial by pecking the observing key. If the bird did not peck to a GO song (incorrect), the bird spent a 4-sec timeout period in the dark. At the end of the timeout the chamber lights came back on and the bird could initiate a new trial. If the presented song belonged to the NOGO set and the bird did not peck (correct), there was no reward, but the bird was immediately able to initiate a new trial. A response peck following a NOGO stimulus (incorrect) produced an 8-sec timeout. For any stimulus, a peck before the song had completed playing (2-3 sec) produced a timeout. Pecks during a timeout reset the timeout clock. An error on a stimulus was followed by a correction procedure in which the song was repeated on 2-5 consecutive trials or until the bird made a correct response. Correction trials did not enter into computation of daily performance. The computer randomized the presentation order of GO and NOGO trials and song stimuli within the two sets. Daily training sessions consisted of 100 trials 6 days per week except during the moult when the birds were not trained.

Birds were taught new songs two at a time, one GO song and one NOGO song. Once the bird had learned a song pair, a new pair was added to the set, and so on, until the bird had learned to discriminate concurrently all 64 songs, or had reached its capacity. The newest song pair was always presented at a higher daily rate than were old song pairs. For the first 3 pairs, each of the two new songs was presented on approximately 25 of the 100 trials in a session. As more pairs were added, the presentation coefficients were reduced to 15-20 trials each of the two new songs. The rationale for this presentation schedule was to present the new songs relatively often (15-25 trials per session), while guaranteeing that each old song would be presented at least once in a session.

Criteria for advancement to the next pair of songs were that the bird had to 1) classify the most recent GO-NOGO song pair at a combined accuracy of at least 85%, and 2) retain an average overall performance level of 85% on all songs in the sets. Several days after a bird reached criterion performance, we added the next two songs to the set of training songs. Results below are presented in terms of sessions to criterion; analysis in terms of trials to criterion gives essentially the same results.

Songs stimuli (Fig. 2) were chosen from clean field recordings of song sparrows, obtained 10 km from the trapping location. A song was randomly placed into one of the two response categories. In selecting songs we avoided songs from the same bird and songs that were clearly the same song type (neighbours in our population often share the same song types). Songs of the same type were avoided because we wished to distinguish between song confusions due to type similarity (which we are investigating separately) and song confusions due to limited memory capacity (the hypothesis being tested). Although we avoided closely matching songs, the songs we used often resembled one another in particular ways; we placed such similar songs into opposite response categories to maximize the difficulty of the classification. When we used two or more songs from a particular singer, we placed them in opposite categories so that if the songs shared common "voice" or "signature" features, this too would work to maximize the difficulty of the classification.

Two different sets of songs were used for the two sparrows. The two song sets had 39 songs in common; each song set had 25 songs not shared with the other set. Of the shared songs, approximately half were in a different category in the two sets.

Results

Memory experiment.

The cumulative number of sessions to criterion for both male song sparrows are shown in Fig. 3. Both birds performed similarly, learning to discriminate concurrently all 32 song pairs (64 songs). The sparrows learned later songs as readily as they learned earlier songs. Finally, overall post-criterion performance was as high at the end (about 90% correct) for 64 songs as it was earlier in training.

As mentioned before, if we added a song to the training set that was similar to one already learned (*i.e.* similar sonograms), we placed it in the opposite category where it would be expected to slow learning. Although we specifically avoided exemplars of the same song type, we did make two exceptions: We included in the song set learned by song sparrow 1 two exemplars of the same type from one singer, *i.e.* "variations" (Fig. 2: GO7-NOGO5) and two exemplars of the same type sung by two neighbours (Fig. 2: GO8-NOGO9). As expected, these similar songs caused the bird initial confusion on the first session after their introduction: for instance, in the session in which we introduced GO7, song sparrow 1 dropped from above criterion (86% correct) to 50% correct on NOGO5; however, the similar songs were mastered at the same overall rate as the other stimuli. Song sparrow 1 took 9 sessions to reach criterion on GO7-

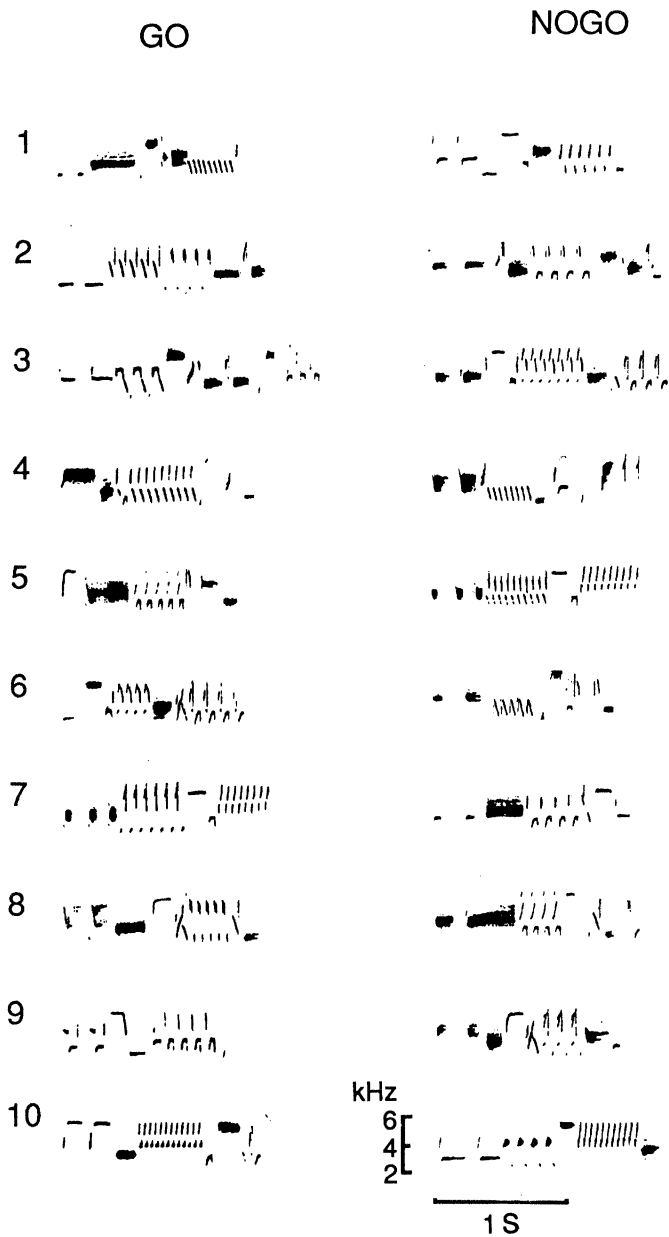


Fig. 2. Sonograms of the first 10 pairs of song sparrow songs used as stimuli for song sparrow 1. Note that GO #7 and NOGO #5 are variations on the same type from one singer and that GO #8 and NOGO #9 are shared types from different singers.

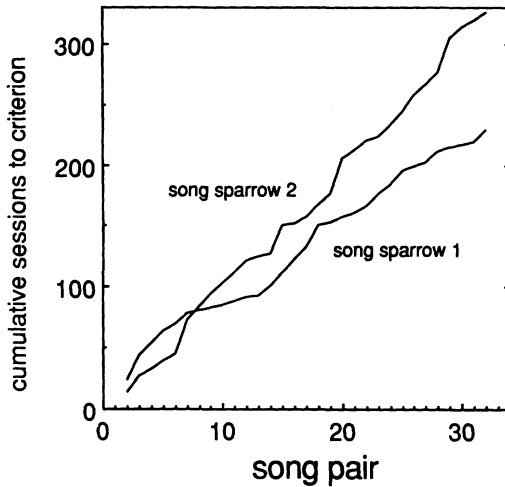


Fig. 3. Learning curves for sparrows discriminating increasingly large repertoires. Values shown are the cumulative number of sessions. A shallow slope indicates rapid learning of new types, a steep slope indicates difficulty. Inspection of the slopes shows that the learning rates for both birds were steady throughout the experiment. In particular, both subjects learned later songs as quickly as the earlier songs.

NOGO7 and 2 sessions for GO8-NOGO9. His mean for all song pairs was 8 sessions to criterion.

Variation experiment.

This experiment was designed to show whether, in learning to classify 64 songs, the subjects had learned something general about the song types, or only something about the particular 64 song exemplars that were used. This question is crucial to the broader context in which we wish to place our results, since in nature, song sparrows normally vary successive presentations of a song type. This use of immediate variety in the stimuli raises the question of whether the birds would generalize their learning of particular song types to new, slightly different versions of those types. We tested whether the birds had extrapolated their knowledge of the trained exemplars to general song type classes by presenting unfamiliar variations on a subsample of the types presented to our two song sparrow subjects. For song sparrow 1, we chose 15 GO and 15 NOGO variations, and for song sparrow 2 we chose 10 different pairs of GO and NOGO variations (one variation per type). Examples are shown in Fig. 4. Data collection

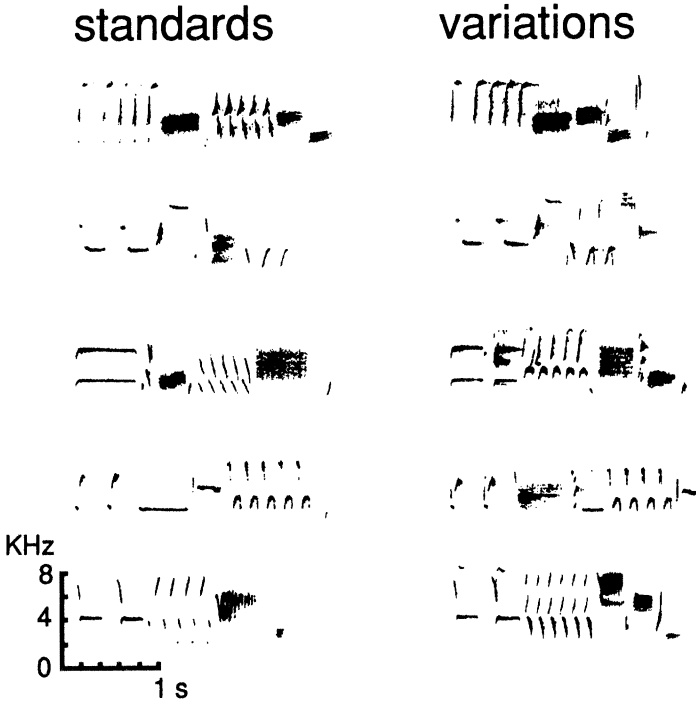


Fig. 4. "Standard" song types and their variations used as stimuli in the experiment on generalization across song variations. Each variation is from the same singer as the matching standard.

began with each bird's last 6 sessions on the full set of 64 standards. We then substituted the variations for the standards for several more sessions. The birds were switched back to the standards for another set of sessions, then placed once again on the variations. Finally, to see if birds might generalize according to singer rather than type, song sparrow 1 received 10 new song types (5 GO, 5 NOGO) from 10 singers who had each contributed a single song to the experiment. The singer's new song type was placed in the same category as the singer's previous song type; if the subject were to generalize according to singer, he would show better than random performance on this task.

The results are shown in Fig. 5. The two song sparrows transferred from their trained song types to the type variations with minimal decline in performance. For both birds there was a small initial drop in performance and then an immediate recovery. Contrast the performance on

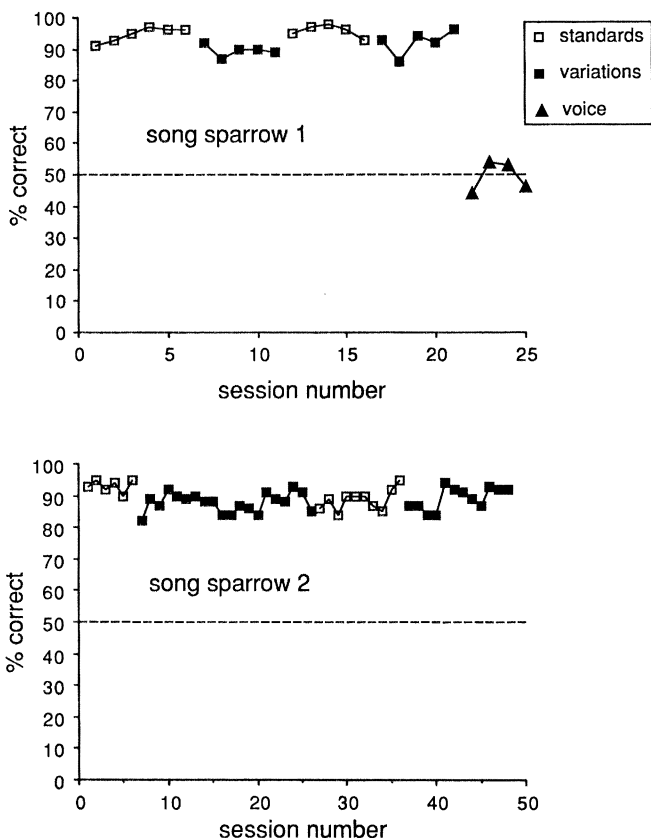


Fig. 5. Performance on natural variations of song types already learned (standards) was virtually the same as for the standards. Song sparrow 1 was also run on a set of 5 GO and 5 NOGO new song types from familiar singers, preserving classification category. Performance was random on unfamiliar types. Data shown are the average performance on all song types, GO and NOGO, for each session.

variations within familiar song types with the performance on new types from the repertoires of familiar singers. Song sparrow 1 dropped from over 90% correct on variations to random performance on new types, indicating that his high transfer rate on variations was due to their structural similarity to the standards, and not to a vocal similarity that is common to all songs of a given singer. Note that this test does not exclude the possibility that vocal traits may be perceived by birds in the field. In the present experiment, birds were trained to disregard such traits, since

the artificial repertoires of songs were assembled from many singers, and different types of particular singers were placed in both categories.

Discussion

If song sparrows are limited in how many songs they can discriminate, we should have seen a gradual increase in the learning time for each song pair added to the set and a cumulative decline in overall performance. Ultimately a subject should have reached a point where he could no longer learn new songs (or retain old ones). For our two subjects, there was no decline in learning rate or overall performance as the number of songs learned approached the number of songs a song sparrow would have to know to make accurate discriminations among neighbours. Thus the present experiment provides evidence against the hypothesis that repertoire size is constrained by a song sparrow's memory for songs.

We are aware of only one study, on great tits, which suggests memory constraints on song recognition (MCGREGOR & AVERY, 1986). Great tits have small repertoires (mean 3) and frequently share song types with neighbours. In their field experiment, MCGREGOR & AVERY concluded that the songs of neighbours that a great tit learns early in life interfere with the songs of newer neighbours that he learns later in life. Birds only confused shared songs of different neighbours. It is not clear whether repertoires contributed to this effect or whether it was due exclusively to song sharing. For instance, this sort of limitation could equally be present for non-repertoire species, such as the white-crowned sparrow (*Zonotrichia leucophrys*) or indigo bunting (*Passerina cyanea*), where neighbours sing extremely similar songs. This intriguing finding, which came out of a *post hoc* analysis of the data, deserves further investigation.

The 64 distinct song types learned by our subjects, although mathematically equivalent in difficulty to 32 types in a 4-category classification task, are probably more than they would normally have to learn to recognize their neighbours. Moreover, they learned these songs despite the potential distraction of "voice" or "signature" cues that might be present in natural repertoires (WEARY *et al.*, 1990), since we placed two songs from a given singer in opposite categories. It is possible, of course, that a song sparrow in the wild may recognize more than 32 songs at any one time, since there is variance in both the number of neighbours and the repertoire size of those neighbours. Male song sparrows occasionally make forays to territories beyond their immediate neighbours, so they may learn the songs of their neighbours' neighbours as well. A 32 song

discrimination repertoire, however, is adequate to account for the observed behaviour of neighbour recognition by song, and that is the point we wished to demonstrate.

In attempting to generalize from our lab observations to learning in the field, we have focused on relative rather than absolute rates of learning. While it is tempting to compare learning in the lab and the field in terms of the absolute number of song presentations required to learn a song, the differing conditions may render such comparisons meaningless. On the one hand, the general findings that animals are "prepared" (by natural selection) to learn natural tasks under natural conditions (*e.g.* BOLLES & BEECHER, 1989) suggests that learning should proceed more rapidly (per song presentation) in the field. But if so, how much more rapidly? On the other hand, learning might actually proceed more quickly in the lab since each and every song presentation in the lab is a) directly triggered by the animal's observing response, b) is presented under ideal acoustic conditions, and c) is followed by immediate feedback as to correct classification. But again, if so, how much more rapidly? For these and other reasons, we think it is fruitless to focus on the absolute numbers of song presentations needed for learning, except to note that the learning success of the birds in the lab cannot be attributed to excessive song exposure. In the lab, it took the sparrows, on average, 74 independent trials per song to reach the 85% criterion or about 120 trials including correction trials. In the peak singing period in the spring, an unmated male song sparrow sings each of his 8 or so song types about 185 times per day (NICE, 1943). Thus one day of intense vocal interaction in the field could potentially provide about the same number of song exposures as was required by our lab sparrows to learn 8 songs and thus, two weeks of listening in the field would give roughly the same number of song exposures as our birds received throughout the experiment.

In conclusion, we feel that our experiment rules out the strongest version of the Memory Constraint hypothesis, the idea that song repertoires degrade individual recognition because the bird cannot hold in his memory all the song types of his several neighbours. Our subjects 1) learned more song types (64) than the approximately 32 types a song sparrow normally requires to discriminate between neighbours, 2) learned later song discriminations as readily as they learned earlier ones, and 3) classified songs as accurately (around 90%) at the end of Experiment 1, when they had to classify each of the 64 songs heard once or twice per session, as they did in the beginning, when they had to classify only a few song types. These results imply that if a song sparrow can learn any of the

song types of this neighbours he can learn all of them. This conclusion parallels that of our field playback experiment in neighbour discrimination (STODDARD *et al.*, 1991). Finally, if song repertoires and individual recognition are mutually constraining in any way, the constraint may arise not from limited memory capacity for songs, but from the simple fact that it takes more time to learn more song types. While such a constraint, if it exists, does not prevent neighbour recognition in song sparrows, it might increase the time it takes to learn new neighbours; we are presently investigating this possibility in the field.

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