Alternative forms of song matching in song sparrows

JOHN M. BURT, SUSANNE C. BARD, S. ELIZABETH CAMPBELL & MICHAEL D. BEECHER

Animal Behavior Program, Departments of Psychology and Zoology, University of Washington

Song matching, replying to a song with a similar song, occurs in many songbird species. Almost all investigations of song matching have been of type matching, where one bird's reply is unambiguously similar to the other's song (i.e. the same song type). In many populations, however, neighbours do not share song types, and therefore cannot type-match. We hypothesized that a bird lacking a true type match could still song-match a stimulus song with a song from his repertoire that was similar in some way the birds recognized. We tested this hypothesis in song sparrows, *Melospiza melodia*, in two playback experiments. We played the subject a stranger song that was similar to one or more of his songs, but a type match to none of them. In the first experiment, we used playback songs that began with two buzzes ('double-buzz' songs). In the second experiment, we used songs that began with a slow trill that increased in tempo ('speed-up' songs). Birds replied at rates significantly above chance with their own double-buzz, or speed-up song match to the respective types of playback. The results suggest that birds who do not share true song types, can still song-match each other. This broad-sense form of song matching may also occur in populations with low song type sharing.

Song matching is said to occur when one songbird replies to another bird's song with a similar song. To song-match a bird must either have a similar song in his song repertoire or the ability to modify his song so that it is more similar to the stimulus song (e.g. Morton & Young 1986; Shackleton et al. 1991; Horn et al. 1992). Most studies of song matching to date have been carried out on repertoire species, and stimulus songs have been chosen for which the subject has an unambiguously similar reply song, usually classified by the investigator as being the same song 'type' (e.g. Kroodsma 1979; Krebs et al. 1981; Falls et al. 1982; Payne 1982; Schroeder & Wiley 1983; Falls 1985; Stoddard et al. 1992; Kroodsma et al. 1999). Replying with a song of the same type as the stimulus song is often described as 'type matching'.

Birds may song-match as a way of directing replies to specific individuals (Catchpole & Slater 1995; Bradbury & Vehrencamp 1998). Song theories have generally viewed the function of song matching in the context of neighbour–neighbour agonistic interactions. The best-supported hypothesis so far is the threat hypothesis, according to which song matching is a warning of a potential escalation (Krebs et al. 1981; Beecher et al.

Correspondence and present address: M. D. Beecher, Box 351525, University of Washington, Seattle, WA 98195, U.S.A. (email: beecher@u.washington.edu). J. M. Burt is now at the Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, U.S.A. (email: jmb237@cornell.edu).

2000). Recent support for the threat hypothesis comes from an interactive playback experiment with song sparrows, *Melospiza melodia*: we found that a singing song sparrow responds more aggressively when matched by his neighbour (in a playback simulation) than when replied to with a shared but nonmatching song type of the neighbour (Burt et al. 2001).

Playback experiments in our Seattle, Washington population have shown that song sparrows type-match to self, neighbour and stranger song (Stoddard et al. 1992; Beecher et al. 2000). Figure 1a and b give examples of neighbour and stranger type matches. In this population, a bird typically shares several songs with any neighbour, and none at all with birds four or five territories removed (i.e. 'strangers') (Hill et al. 1999). Nevertheless, strangers will occasionally have very similar songs, and we have shown that song sparrows match these stranger songs at high levels, nearly as high as they match self song (around 50% where chance level is about 12%, or one out of the typical repertoire size of eight to nine songs; (Stoddard et al. 1992). Song sparrows in our population tend to song-match their neighbours only early in the breeding season, when they are new neighbours (Beecher et al. 2000). After this time, neighbours tend to 'repertoire-match' (i.e. reply with a different song they share with their neighbour, Beecher et al. 1996), probably reflecting a 'dear enemy' pattern of de-escalation between familiar neighbours. In contrast, song sparrows will
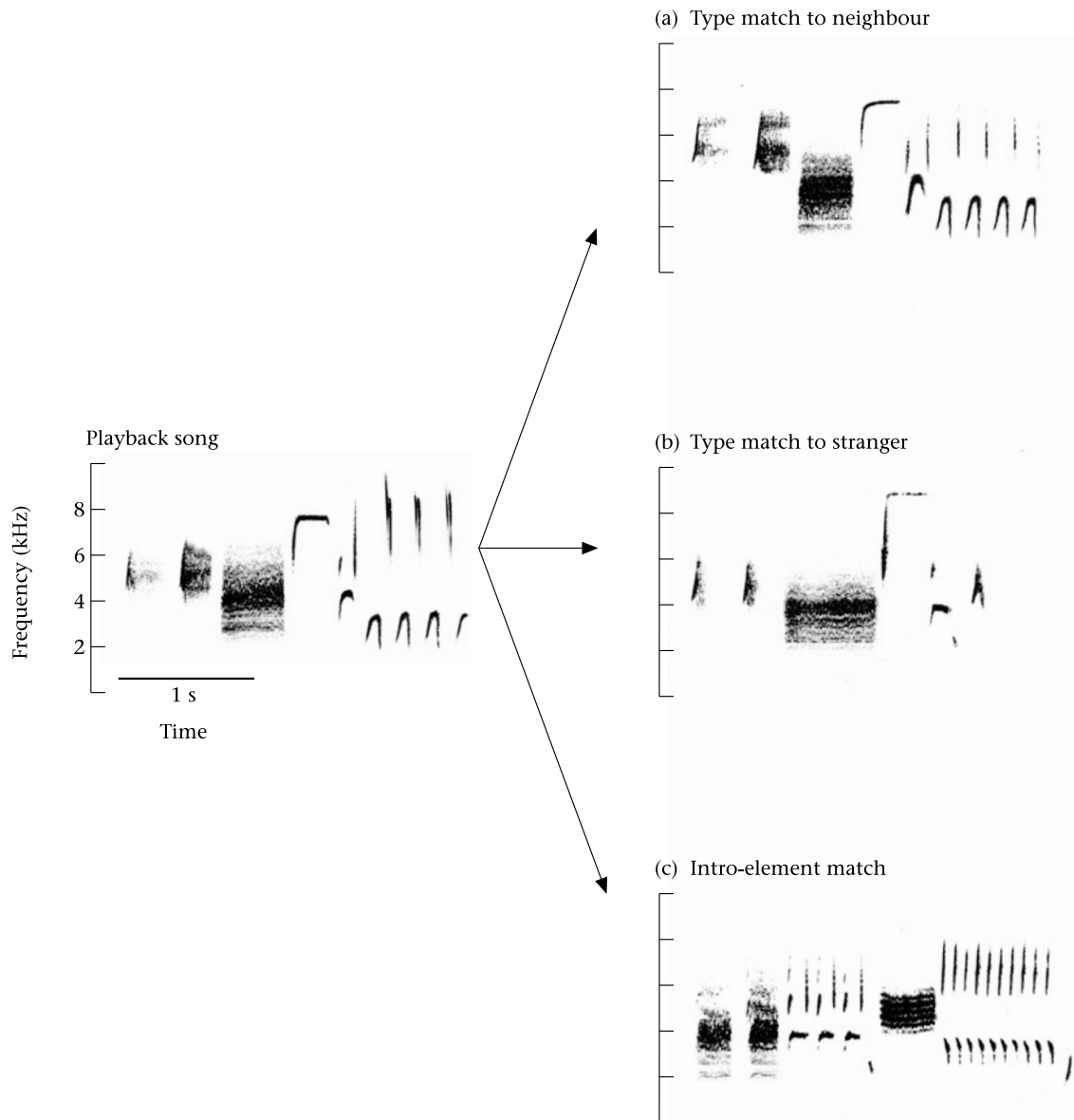
Figure 1. Different potential matching replies to a playback song. (a) Type matches to a neighbour's song are usually very similar to the playback due to a shared learning history. (b) Type matches to stranger song are often not as similar to the playback, although they are recognizable as type matches. (c) Birds may also song-match with songs that are similar in some respect (here they both begin with two buzzes) but are not similar enough to be classified as the same type.

match stranger song or self song (probably both perceived as stranger song) at high levels at any time of the year (Stoddard et al. 1992).

In our study population of song sparrows, a high degree of song sharing between neighbours arises naturally through the song-learning process (Beecher et al. 1994b; Nordby et al. 1999). Two neighbours will 'share' a song type because one of them learned the song from the other, or both learned it from a common tutor, or each learned it from different tutors who both learned from a common tutor, or some other similar pattern; the degree of similarity will generally reflect the recency of common learning ancestry. Other songs in the birds' repertoires, in contrast, can be quite dissimilar, presumably because these songs have only a remote common

learning ancestor, and these we classify as 'unshared' song types.

A problem for the scope and generality of song-matching hypotheses is the occurrence of populations in which neighbours share few or no song types. In eastern populations of song sparrows, for example, neighbours usually share no song types (Hughes et al. 1998). Even in our western population, where sharing between neighbours is high on average, there are still neighbours who share few or no songs (Hill et al. 1999). In these cases of minimal or total lack of song sharing, opportunities for type matching will accordingly be limited or nil. Nevertheless, birds not sharing song types (according to the investigators' definition) may still have song types that are similar enough to be used in song matching.

If we assume that there is selection for effective communication between neighbours, and that song matching is adaptive, it follows that birds who do not share song types should still song-match using similar songs. If birds did song-match in the broader sense, by countersinging with similar songs, song matching could occur in a wide range of songbirds and in any species/population in which the singer has a song repertoire (or the ability to modify a song so that it is more similar to the stimulus signal). Thus, two neighbours having no shared song types by the investigators' criterion, may still have songs they themselves regard as similar, and so they could song-match with these songs. We can test the hypothesis of broad-sense song matching by playing the subject a stranger song that is not the same type as any in the subject's repertoire: if subjects consistently select reply songs that resemble the playback songs in some predictable way, then they are song matching. Figure 1c gives an example of one such potential song match.

In this study we asked how a subject would reply to a stranger song that was similar in a particular way to one or more of his songs, but was not classified (by us) as a type match to any of his song types. The elements that comprise song sparrow songs can be roughly divided into several categories: broad-band elements ('buzzes'), series of rapidly repeated elements ('trills'), pure tonal elements ('pure notes') and more complex combinations of notes ('note complexes'). Songs can be separated into broad classes based on the ordering within the song of these categories of song elements. For example, in Fig. 1, the song labelled 'type match to neighbour' could be characterized as being composed of two brief buzzes, a longer buzz, a note complex and a trill. Based on our field experience with song sparrow song, we chose two distinctive classes of songs, categorized by the introductory elements alone, that most birds in our population have in their repertoire (and in some cases a bird has more than one example in his repertoire).

In two separate playback experiments, we examined song matching using the two different song classes as playback stimuli. In experiment 1, we used playback songs that began with two buzzes ('double-buzz' songs). In experiment 2, we used songs that began with a long slow trill that increased in tempo ('speed-up' songs). We tested the hypothesis that birds would reply with a song of the same description. All subjects had at least one song type that could match the broad class of their playback stimulus (double-buzz, or speed-up song) but no subjects had a song type match to their playback stimulus; thus, song matching, but not true type matching was possible in these experiments.

We chose the double-buzz and speed-up categories as candidates for song matching in the present study because (1) they are very distinctive song features and we could easily identify them; (2) most birds in the population had them in their repertoires; and (3) we had gained the impression, during many years of field work, that birds will song-match with these song categories. Although we could have chosen additional song categories (e.g. songs beginning with repeated pure tones), we thought it was wiser to put our power into two song categories that we thought were good candidates for song matching. Testing more song categories would potentially have increased the generalizability of the test but would have meant testing each on fewer subjects, and thus reduced the power of the tests.

METHODS

Study Area and Subjects

Our song sparrow study site is an undeveloped 3-km² park bordering Puget Sound in Seattle, Washington. The song sparrow population is sedentary (nonmigratory) and there are approximately 150 males on territories in a given year. This population has high rates of song sharing between adjacent neighbours (about 25%, Hill et al. 1999). For the two playback experiments, we used as subjects a total of 41 banded territorial males that were at least 1 year old. The repertoires of 17 birds contained both double-buzz and speed-up categories of song so these birds were used in both experiments. An additional nine birds with double-buzz but not speed-up songs were tested in experiment 1, for a total of 26 subjects. An additional 15 birds with speed-up but not double-buzz songs were tested in experiment 2, for a total of 32 subjects.

Recording, Playback and Song Type Analysis

The complete song repertoire of each subject was recorded in the field with a Sennheiser ME88 directional microphone and a Sony TC-D5M tape recorder. We estimated a repertoire to have been completely measured (all song types) when we had recorded 20 or more consecutive song type switches (method and rationale described in Kroodsma 1982). Songs were analysed on a Kay DSP-5500 Sonagraph.

Playback songs were presented using a Dell Latitude LT laptop computer with a 16-bit sound card, attached to an amplified speaker via a 10-m cable. Playback songs were digitized in 16 bits at a 22 050 Hz sample rate. A program written by J.M.B. ('Syrinx') managed playback timing, and recorded voice notations of the subjects' behaviour and the subjects' song replies using a directional microphone as input to the computer.

Trial dates ranged from 9 April to 25 June 1999, with trials conducted in the morning between 0700 and 1000 hours. The same playback procedure was used for both experiments, and both were run concurrently. Subjects tested in both experiments were given only one trial per day. Before each trial, we set our playback speaker to broadcast towards the subject from 3 m within the subject's territorial boundary. A single playback song was selected from the set of stimuli for the particular experiment, with the requirement that it be from a bird at least five territories distant from the subject, and not be a type match to any song in the subject's repertoire. Trials lasted 3 min, starting from the first playback. Playbacks occurred at 10-s intervals for the duration of the trial and were synchronized with the subjects' singing to avoid

song overlap. If the bird had not been singing before the trial, his first song sung was considered the reply type. Otherwise, if the bird had been singing before the trial, the next song type he switched to was counted as his reply type.

Experiment 1: Double-buzz Song Matching

Buzzes are a distinct category of song element found in many song sparrow songs. The distinguishing feature of buzzes is that they are continuous and broadband in frequency, although there is considerable variation in frequency range, duration and fine structure. We selected songs that began with two buzz elements as playback stimuli for experiment 1 (i.e. double-buzz songs). Double-buzz songs were good candidates for this song-matching test because they are distinctive yet most birds in our population have at least one of them.

To create a set of double-buzz playback stimuli, we first selected a set of potential stimulus songs from a large library of song sparrow songs. Then, the four authors independently rated each song on a 0–3 scale, with 3 being a perfect example of a double-buzz song. The following rules were used to rate songs: (a) only the beginning element was considered for rating; (b) if the introductory elements were not buzzes, the song was rated 0; (c) probable buzz introductory elements were scored lower if they were too brief, had an overly narrow frequency range, or were actually composed of a buzz and another substantial nonbuzz element. The 23 songs that received an average rating of 2.0 or better were selected for use as playback stimuli. Using this rating threshold, all the selected songs had two introductory buzzes, but the buzz elements had a wide range of variation in frequency, duration and structure (Fig. 2a gives examples of double-buzz playback stimuli). Because there were more subjects than playback stimuli, some songs were used more than once: three of the 23 songs were used a second time (the repeats were chosen randomly).

Experiment 2: Speed-up Song Matching

As with double-buzz songs, songs that begin with speed-up trills (i.e. speed-up songs) are relatively infrequent in the repertoires of most birds, yet most birds have at least one of them. When compared with other song sparrow songs, speed-up songs have a distinctive cadence because they usually begin with a particularly long trill, half or more of the total song duration, with trill elements repeated at an increasing tempo (they are also described as 'Type 2' songs in Borror 1965). Although the elements comprising the trill are usually identical throughout (e.g. Fig. 2b, third song), sometimes the trill is constructed from two slightly different trills (e.g. Fig. 2b, second song). The speed-up trill is followed by a relatively brief series of other song elements such that the total duration of speed-up songs is about the same as for other songs.

We selected a set of speed-up song playback stimuli for experiment 2 the same way we selected double-buzz

songs for experiment 1, using the following rating rules: (a) songs that did not begin with a trill (four or more repeated elements) were rated 0, (b) songs that began with trills were scored lower if they made up less than about half the total duration of the song, or did not change from slow to fast tempo during the trill. We did not consider the finer structural detail of the trill, or the portion of the song following the trill when assigning ratings to songs. The 27 songs that received an average rating of 2.0 or better were selected for use as playback stimuli (Fig. 2b gives examples of speed-up songs used as playback stimuli). The speed-up stimulus songs we selected all contained introductory trills that were half or more of the total song duration and all increased in tempo. Because there were more subjects than playback stimuli, some songs were used more than once: five of the 27 songs were used a second time (the repeats were chosen randomly).

Analysis

The analysis had two parts. First, and most important, we tested the hypothesis that when presented with a stranger stimulus song containing a double-buzz introduction (experiment 1) or a speed-up introduction (experiment 2), subjects would tend to reply with a similar song of their own, specifically one containing a double-buzz (experiment 1) or a speed-up (experiment 2) introduction (i.e. 'introduction category matching'). Second, we tested the hypothesis that finer details of similarity beyond the simple equivalence of the introduction category might affect song matching. Therefore, we planned a second, post hoc analysis to determine whether the fine structure of the songs was relevant to song matching (i.e. 'fine structure matching').

Introduction Category Matching

Prior to the experiment, every song in the repertoire of every subject, along with the potential playback stimuli, was classified as a double-buzz song or a speed-up song or neither with the same rules we used for choosing playback stimuli. Hence the decision as to whether or not a subject song constituted a 'match' to a playback song was made without reference to the results. A reply song rated 2.0 or higher in the same introduction category as the playback stimulus was considered a song match (e.g. a reply song with a double-buzz rating of 2.5 was a match to a double-buzz playback, while a reply song with a 1.5 rating was not). Figure 2c gives an example of the repertoire of one subject containing one double-buzz, and one speed-up song (first and second songs, respectively).

We used a binomial test to determine whether birds matched the playback above chance level, with the N representing the number of stimuli used, which was slightly less than the number of subjects. The chance matching probability, the probability of randomly selecting a song with the same introduction category as the playback, was separately calculated for each experiment with the formula: mean number of introduction matching songs/adjusted mean repertoire size. The bird's computed repertoire size was reduced by one for trials where
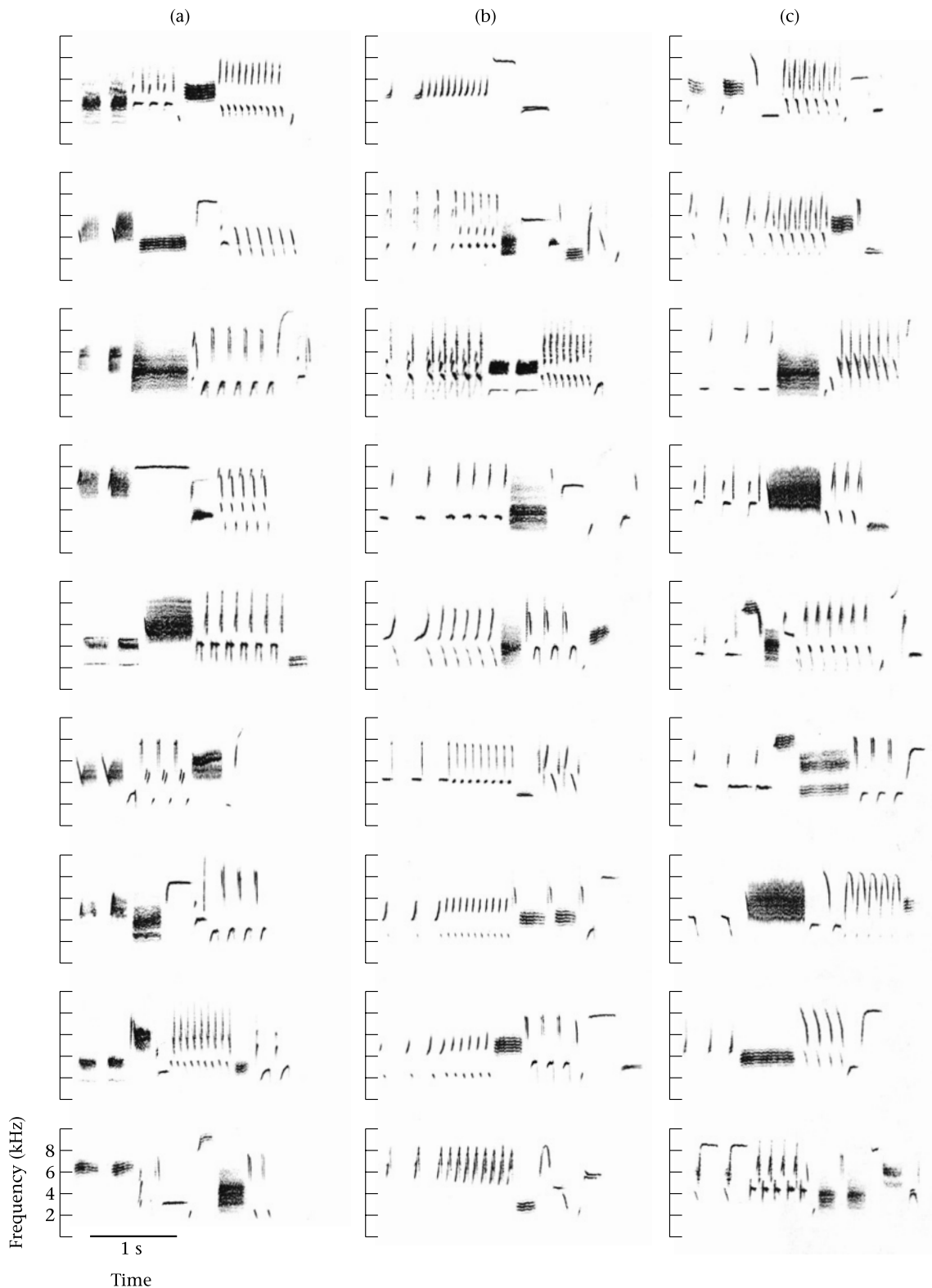
Figure 2. Examples of double-buzz (a) and speed-up (b) playback stimuli, and the repertoire of one subject with a potential match for each category of playback song (c). Spectrograms made with Syrinx software.

the bird was singing before the trial, because that song could not be counted as a reply type (the next song type he switched to was counted as his reply type; experiment 1 had three trials with pretrial song, experiment 2 had six trials). For experiment 1, the probability of a bird replying with a double-buzz by chance was estimated at 21.4%. For experiment 2, the probability of a bird replying with a speed-up by chance was estimated at 17.5%. The
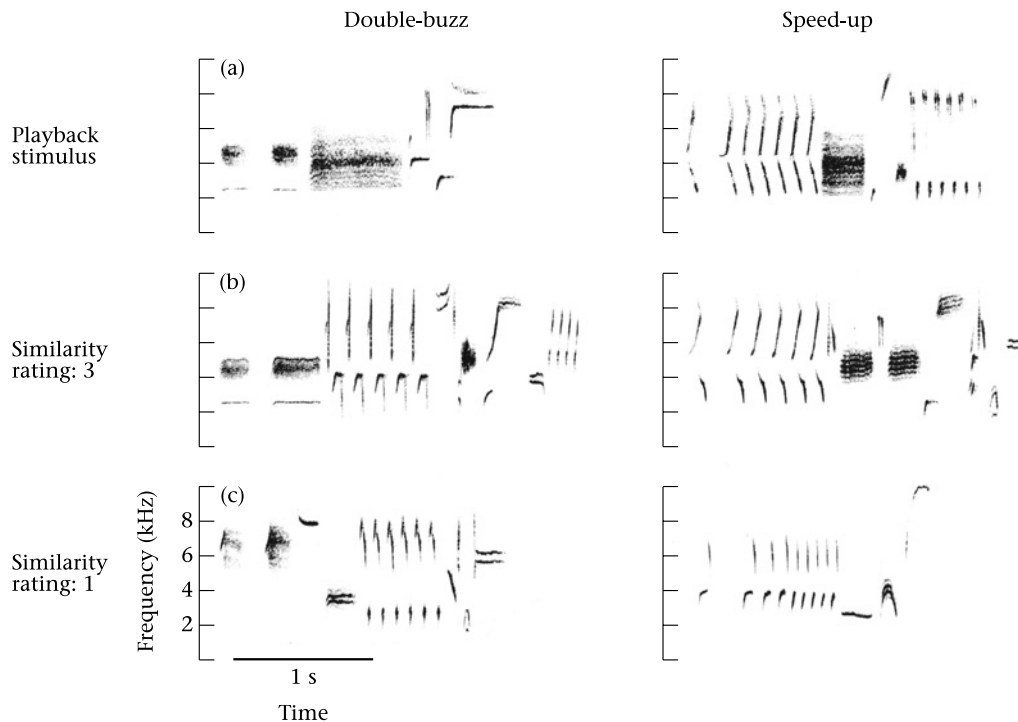
Figure 3. Examples of subjects' songs with different similarity ratings of introductory element detail to the playback stimuli. (a) Double-buzz and speed-up songs playback stimuli; (b) subject song introductory elements rated similar to the playback song (rating 3); and (c) subject song introduction elements rated dissimilar to the playback (rating 1). Spectrograms made with Syrinx software.

calculation of the 'chance' expectation assumes that song sparrows use their different song types equally, which in fact is true when measured over a reasonably long time window versus, for example, just taking a short sequence where he is singing to one particular neighbour (C. R. Wilkerson, J. C. Nordby, S. E. Campbell & M. D. Beecher, unpublished data). As indicated earlier, a song sparrow will deviate from this pattern of equal usage when repertoire matching and type matching in a song interaction with another bird. Our hypothesis in the present study was that a song sparrow would deviate from the equal usage pattern when challenged with a song to which he has a general match.

Introduction Fine Structure Matching

Birds might match using introductory elements similar in fine structural detail to the playback introductions. To test for this possibility, during post hoc analyses, the four authors gave an additional score on a scale of 0–3 to every song in every subject's repertoire, rating the similarity in element fine structure only between the introductory portions of each song to the playback song. Elements with the same frequency range and duration, and very similar fine structure were rated at 3, while elements differing in any of these dimensions were rated lower (Fig. 3 gives examples). To avoid possible biases from knowing the subject's response songs, this rating was scored after the playback trials were complete, but before the subjects' song type responses had been scanned from the trial recordings.

RESULTS

Matching by Introduction Category

Birds replied to playback of double-buzz songs with their own double-buzz song in 12 out of the 26 trials in experiment 1, significantly more frequently than predicted by chance (two-tailed binomial test: observed matching 46.2% versus chance matching level 21.4%, $P<0.005$). In experiment 2, birds replied to playback of speed-up songs with their own speed-up song in 11 out of the 32 trials, a significantly higher rate than would be expected by chance (two-tailed binomial test: observed matching 34.4% versus chance matching 17.5%, $P=0.01$).

Matching by Similarities in Introduction Element Detail

To test for the possibility that birds were matching in terms of the detailed similarity of the introductory elements, we identified the song in each bird's repertoire with the highest introductory element similarity rating and asked whether birds responded with this song more often than would be expected by chance. To do this, we examined the subsample of birds who had more than one possible match to the playback song in their repertoires (i.e. with two or more double-buzz or two or more speed-up songs). For this subsample, we asked whether these birds were more likely to choose their song with the greatest structural similarity to the playback song from

among their several possible matches. The chance probability of selecting the most similar match was 1/mean number of matching songs for each subsample. In experiment 1, birds replied with their most similar double-buzz in four out of the 10 subsample trials, a rate not significantly above chance (two-tailed binomial test: observed 40.0% versus chance matching 38.5%, NS). In experiment 2, birds matched with the most similar speed-up in four out of the seven subsample trials (two-tailed binomial test: observed 57.1% versus chance matching 40.0%, NS).

DISCUSSION

In experiment 1, song sparrows replied with double-buzz matches to the playback of double-buzz songs significantly more often than would be expected by chance. Similarly, in experiment 2, song sparrows replied at significantly high rates with speed-up matches to the playback of speed-up songs. The fact that significant matching occurred in both experiments with two different categories of playback stimuli supports the notion that a bird may song-match with a similar song, even if he does not possess the same song type as the stimulus song. If song matching functions as a directed signal, then birds should benefit from being able to song-match in the absence of song type sharing with their neighbours. The results of this study may have important implications for situations where neighbours do not share song types, since broad-sense song matching of the sort demonstrated in these experiments might still be possible for these neighbours. Although we cannot easily generalize the type of song matching observed in these experiments beyond the particular song categories used, we hope that other investigators will pursue this hypothesis and test whether birds use other classes of songs for generalized song matching.

Our subjects tended to respond to songs with double-buzz or speed-up introductions with songs that had double-buzz or speed-up introductions, respectively. However, our post hoc analysis yielded no evidence to suggest that birds song-matched on the basis of more detailed similarity than this. To the contrary, when birds matched the playback, the songs they selected often had introductory elements that were quite different in fine structure, frequency range and duration from those of the playback. It would appear from these results that, although song sparrows are capable of much finer acoustic structural discrimination (Horning et al. 1993; Beecher et al. 1994a; O'Loghlen & Beecher 1997, 1999), they might nevertheless tend to 'lump' introductory elements into broad categories such as 'buzzes' or 'trills'. Thus, a bird may well perceive the beginning elements of two different song types as being very dissimilar, and yet classify them both as buzzes because they share the features that define that category of song element (i.e. both elements are broadband, continuous sounds, etc.). Further research, perhaps using operant conditioning methods, will be needed to determine how many different element categories song sparrows use, and what acoustic features they use to categorize song elements.

Unlike most song sparrow songs, which usually begin with one to three repeated elements, speed-up songs have a distinctly different temporal rhythm. Not only are speed-up songs found in the repertoires of many birds in our population, they can be found in many other North American song sparrow populations as well, as evidenced by their occurrence in song figures from a number of papers (e.g. Maine: Borror 1965; California: Eberhardt & Baptista 1977; Pennsylvania: Searcy et al. 1995; Washington Cascades: Hill et al. 1999), and from our own personal observations and recordings of speed-up songs in other populations (e.g. California, British Columbia, Pennsylvania and New York state). Song sparrows reared in isolation also learn to produce speed-up songs (Kroodsma 1977). The widespread occurrence of speed-up songs in different populations and among isolate birds suggests there may be a bias towards having one or two speed-up songs in a repertoire. This may also be the case for double-buzz songs, as well as other possible categories of song. The categorical level of song matching that occurred in the present experiment for speed-up and double-buzz songs suggests that birds might perceive these and other categories of song as distinct classes, which they can match. It may be advantageous for birds to have a variety of such song classes in their repertoire to ensure that they can song-match other individuals who may not share the same exact song types.

This experiment tested song sparrows in a population with high rates of neighbour song sharing. Despite the high overall sharing rate, there are still many neighbours who share few or no songs (Hill et al. 1999), and these birds could benefit from the kind of song matching described here. Another interesting population to study would be one with very low rates of song sharing overall. Presumably, birds in populations with little or no sharing could gain some of the same signalling benefits of song matching that birds in our population do for type matching. It is even possible that in low-sharing populations, birds will use the general types of song categories described here (e.g. double-buzz, speed-up songs, etc.) for song matching, perhaps at even higher rates due to their inability to use type matching. Populations in the eastern U.S.A. have much lower neighbour song type sharing (Borror 1965; Harris & Lemon 1972; Kramer & Lemon 1983; Hughes et al. 1998) and therefore would be good candidates for a study of song matching with similar but nonshared song types.

We have distinguished between songs of two birds being the same song type, they contain the same elements in the same order (probably reflecting common learning ancestry), or nearly so, and songs merely being in the same general song category, having only partial, generic (if distinctive) similarities. We do not know whether the birds themselves make this distinction. In a playback experiment, birds indicate that they perceive a stimulus song to be a 'match' to one of their own songs by replying to the former with the latter. In the present study, birds song-matched at somewhat lower levels to songs that were generically similar to their own (double-buzz matching 46% versus chance matching 21%, speed-up matching 34% versus chance matching 17%),

compared with subjects in our earlier studies of true type matching (generally 50% or better with a chance rate of about 12%). This may indicate that song sparrows regard true type matches as 'better' matches to their songs than the more generic song matches of the present study. Future studies comparing both types of matching in the same subjects will be needed to support this conclusion.

To take this argument further, when comparing the song matching observed in studies done by different investigators on different populations, it may be difficult to apply the distinction between song type matching and song matching based on more generic similarities. For example, in the population of western meadowlarks, *Sturnella neglecta*, studied by Falls and his colleagues, neighbouring birds shared no more songs with neighbours than they did with distant birds (Falls 1985; Horn & Falls 1988). In this respect, this western meadowlark population is like the eastern song sparrow population studied by Hughes et al. (1998). The western meadowlark population differed from the song sparrow population, however, in that meadowlark neighbours (or any two meadowlarks in the population) still shared about 25% of their songs on average, whereas for song sparrows, sharing was close to zero (Falls 1985; Horn & Falls 1988; Hughes et al. 1998). The difference between these two populations suggests that the level of sharing may depend on the investigators' 'sharing' criteria. Falls and colleagues based their sharing classification of songs on a catalogue they had developed for their population, whereas Hughes et al., like we, used a purely internal criterion, based on identity and order of song elements in each pair of songs. In any case, the validity of the song type criteria of Falls et al. is demonstrated by the fact that their subjects matched stranger songs as predicted. The song-matching rate to stranger song was about 50%, similar to that observed in song sparrows, and, like in song sparrows, meadowlarks did not song-match songs of their neighbours (Falls 1985). Because examples of shared songs are not illustrated in the western meadowlark papers (nor in most song-matching studies of the past), it is hard to know whether these shared songs would meet the criteria for sharing used by us or by Hughes et al. (1998). So again, we conclude that criteria defining song sharing or song similarity must ultimately be based on direct tests of the birds' perceptions of these songs. Among the candidates for such tests are song-matching playback tests, other types of playback assessments, such as the habituation paradigm (e.g. Searcy et al. 1999) and laboratory conditioning tests (e.g. Horning et al. 1993; Beecher et al. 1994a).

Acknowledgments

References

Beecher, M. D., Campbell, S. E. & Burt, J. M. 1994a. Song perception in the song sparrow: birds classify by song type but not by singer. *Animal Behaviour*, **47**, 1343–1351.

Beecher, M. D., Campbell, S. E. & Stoddard, P. K. 1994b. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences, U.S.A.*, **91**, 1450–1454.

Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. L. 1996. Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, **51**, 917–923.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000. Song type matching between neighbouring song sparrows. *Animal Behaviour*, **59**, 21–27.

Borror, D. J. 1965. Song variation in Maine song sparrows. *Wilson Bulletin*, **77**, 5–37.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.

Burt, J. M., Beecher, M. D. & Campbell, S. E. 2001. Song type matching as threat: a test using interactive playback. *Animal Behaviour*, **62**, 1163–1170.

Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. New York: Cambridge University Press.

Eberhardt, C. & Baptista, L. F. 1977. Intraspecific and interspecific song mimesis in California song sparrows. *Bird Banding*, **48**, 193–300.

Falls, J. B. 1985. Song matching in western meadowlarks. *Canadian Journal of Zoology*, **63**, 2520–2524.

Falls, J. B., Krebs, J. R. & McGregor, P. 1982. Song matching in the great tit (*Parus major*): the effect of similarity and familiarity. *Animal Behaviour*, **30**, 997–1009.

Harris, M. A. & Lemon, R. E. 1972. Songs of song sparrows (*Melospiza melodia*): individual variation and dialects. *Canadian Journal of Zoology*, **50**, 301–309.

Hill, C. E., Campbell, S. E., Nordby, J. C., Burt, J. M. & Beecher, M. D. 1999. Song sharing in two populations of song sparrows. *Behavioral Ecology and Sociobiology*, **46**, 341–349.

Horn, A. & Falls, J. B. 1988. Structure of western meadowlark (*Sturnella neglecta*) song repertoires. *Canadian Journal of Zoology*, **66**, 284–288.

Horn, A. G., Leonard, M. L., Ratcliffe, L., Shackleton, S. A. & Weisman, R. G. 1992. Frequency variation in the songs of black-capped chickadees (*Parus atricapillus*). *Auk*, **109**, 847–852.

Horning, C. L., Beecher, M. D., Stoddard, P. K. & Campbell, S. E. 1993. Song perception in the song sparrow: importance of different parts of the song in song type classification. *Ethology*, **94**, 46–58.

Hughes, M., Nowicki, S., Searcy, W. A. & Peters, S. 1998. Song type sharing in song sparrows: implication for repertoire function and song learning. *Behavioral Ecology and Sociobiology*, **42**, 437–446.

Kramer, H. G. & Lemon, R. E. 1983. Dynamics of territorial singing between neighboring song sparrows (*Melospiza melodia*). *Behaviour*, **85**, 198–223.

Krebs, J. R., Ashcroft, R. & Van Orsdol, K. 1981. Song matching in the great tit *Parus major* L. *Animal Behaviour*, **29**, 918–923.

Kroodsma, D. E. 1977. A re-evaluation of song development in the song sparrow. *Animal Behaviour*, **25**, 390–399.

Kroodsma, D. E. 1979. Vocal dueling among male marsh wrens: evidence for ritualized expressions of dominance/subordinance. *Auk*, **96**, 506–515.

Kroodsma, D. E. 1982. Song repertoires: problems in their definition and use. In: *Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 125–146. New York: Academic Press.

Kroodsma, D. E., Sanchez, J., Stemple, D. W., Goodwin, E., da Silva, M. L. & Vielliard, J. M. E. 1999. Sedentary life style of Neotropical sedge wrens promotes song imitation. *Animal Behaviour*, **57**, 855–863.

Morton, E. S. & Young, K. 1986. A previously undescribed method of song matching in a species with a single song 'type', the Kentucky warbler (*Oporornis formosus*). *Ethology*, **73**, 334–342.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 1999. Ecological correlates of song learning in song sparrows. *Behavioral Ecology*, **10**, 287–297.

O'Loghlen, A. L. & Beecher, M. D. 1997. Sexual preferences for mate song types in female song sparrows. *Animal Behaviour*, **53**, 835–841.

O'Loghlen, A. L. & Beecher, M. D. 1999. Mate, neighbour and stranger songs: a female song sparrow perspective. *Animal Behaviour*, **58**, 13–20.

Payne, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings. *Ecology*, **63**, 401–411.

Schroeder, D. J. & Wiley, R. H. 1983. Communication with repertoires of shared song themes in tufted titmice. *Auk*, **100**, 414–424.

Searcy, W. A., Podos, J., Peters, S. & Nowicki, S. 1995. Discrimination of song types and variants in song sparrows. *Animal Behaviour*, **49**, 1219–1226.

Searcy, W. A., Nowicki, S. & Peters, S. 1999. Song types as fundamental units in vocal repertoires. *Animal Behaviour*, **58**, 37–44.

Shackleton, S. A., Ratcliffe, L., Horn, A. G. & Naugler, C. T. 1991. Song repertoires of Harris' sparrows (*Zonotrichia querula*). *Canadian Journal of Zoology*, **69**, 1867–1874.

Stoddard, P. K., Beecher, M. D., Campbell, S. E. & Horning, C. L. 1992. Song-type matching in the song sparrow. *Canadian Journal of Zoology*, **70**, 1440–1444.