

SOUND-BASED SPECIES-SPECIFIC RECOGNITION IN THE BLACKCAP *SYLVIA ATRICAPILLA* SHOWS HIGH TOLERANCE TO SIGNAL MODIFICATIONS

by

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Summary

The aim of the present study is to investigate the male blackcap decoding process allowing species-specific recognition in the perspective of possible adaptations for communication in dense vegetation. We played back modified and natural blackcap songs to territorial blackcap males and scored the reaction of the territory owners. We examined the response of blackcap males to artificial songs manipulated to reflect a possible environmental degradation. Territory owners respond strongly even to crude models of conspecific song. Only when frequency modulation is suppressed or the number of syllables in the song is drastically reduced do the territory owners cease to respond. The importance of frequency modulation for species recognition is further emphasised by territory owners' strong response to synthetic sounds, in which rapid frequency modulation is superimposed by a less rapid and a slow frequency modulation within the frequency range of conspecific song.

Our results have then put forward the acoustic basis for the initial perception of potential conspecifics. It appears that blackcap species-specific decoding process seems highly tolerant towards song structure modifications. May be this is an adaptation to the propagation acoustic constraints imposed by the forest environment.

Introduction

One of the most consistent and striking characteristics of bird vocalisations is species-specificity. This is related to the fact that most sounds are directed

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toward conspecifics whose reactions should be appropriate to the content of the message (Catchpole, 1982, 1986). Previous studies have shown the importance of song characteristics as species-specific parameters. They emphasised the role of song length, intervals between elements, frequency range, syntax and frequency modulation (see Becker, 1982 for a review). Because male territorial songbirds are usually spaced far apart, species-specific recognition has to be achieved then at long range through acoustic signals. Unfortunately, sounds propagating over long distances are susceptible to modifications by various processes, such as interferences, reverberations and attenuation (*e.g.* Morton, 1975; Marten & Marler, 1977; Wiley & Richards, 1982; Klump, 1996; Holland *et al.*, 1998). Despite this widespread phenomenon, only few studies have used information about how songs are affected by transmission to predict what sorts of cues should be important for recognition (Naguib, 1995, 1997).

The present study deals with the blackcap *Sylvia atricapilla*, a forest territorial bird facing with signal modifications during propagation (Fig. 1; Dabelsteen & Mathevon, 1999). We investigate the male decoding process allowing species-specific recognition, focusing on how tolerant is this process regarding song modifications or simplifications.

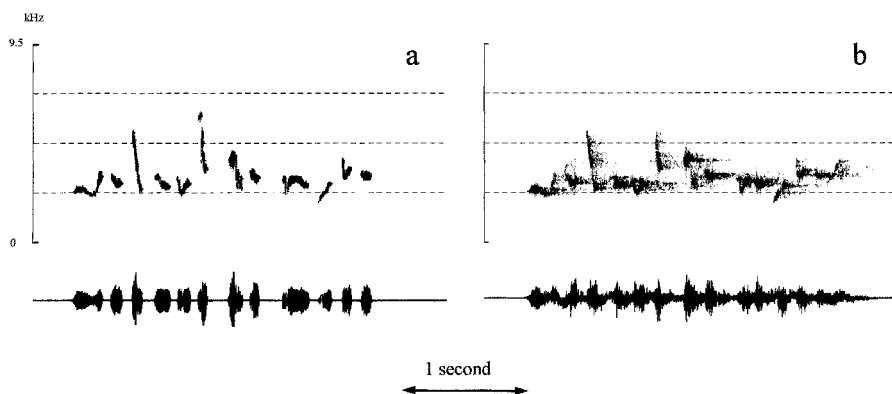


Fig. 1. Sonograms (above) and oscillograms (below) of an unpropagated song (a) and the same song after a 50 m propagation (b) (microphone height: 4 m; speaker height: 9 m). Alteration of amplitude modulation, reverberation and high-frequency filtering induce modifications of the song structure.

Material and methods

Subjects and location

Experiments were conducted from March to June 1996 and 1997, between 7h30 to 10h30 a.m., in deciduous forests of the Pilat Regional Natural Park, near Saint-Etienne, France. To avoid any effect of breeding stage, we randomised the playback trial types across the season. Deciduous forests, used for the experiments were constituted of various species of trees, especially beech *Fagus sylvatica*, and in a lesser degree, maple *Acer pseudoplatanus*, fir *Abies alba* and spruce *Picea abies*. The density of the blackcap was about 50-60 pairs per km².

Preceding to the playback experiments, the blackcaps' territories were roughly mapped by surveying the tested birds and noting their favourite song posts. The broadcast speaker was then located inside the territory boundaries. Playbacks always began when the territory owner ceased to sing and stopped any acoustic interaction with other birds. To prevent habituation, each bird was tested only once.

Experimental signals

The original (control) signal

We chose a typical blackcap song as control signal (Fig. 2a). The recording was made at about 3 meters from a blackcap male using a Nagra type IIIB tape recorder and a Sennheiser MD211N microphone. As the recording was performed in a very distant area from our playback experiments, the tested males were not familiar with this song. The first part of this control song consists of chattering sounds (rapidly repeated fast frequency modulated elements). The second part of control song consists of louder segment of pure fluting tones (slowly amplitude and frequency modulated notes). Duration of the control signal is 6 s. This length is representative since the duration of a blackcap song is usually between 2 to 7 s (Cramp, 1992). For all parameters and features, the control signal is well within the range

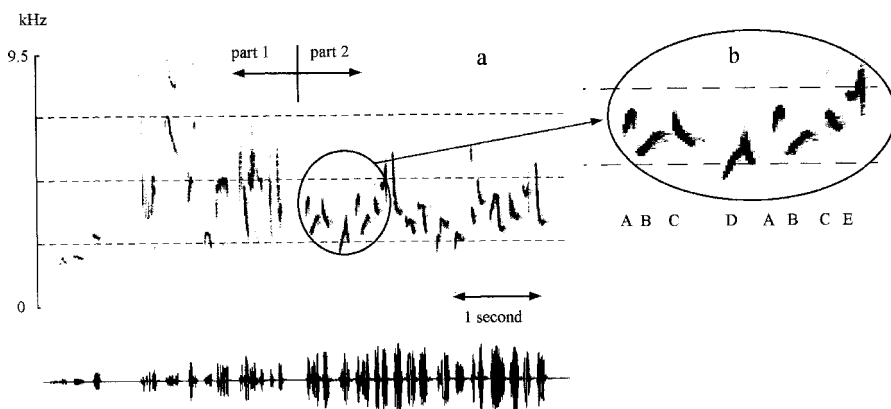


Fig. 2. a) Control signal (part 1: chattering sounds; part 2: fluting tones). b) Notes used for simplified signals.

of blackcap song (Garcia, 1981 in Cramp, 1992; Bergmann & Helb, 1982 in Cramp, 1992; Simms, 1985 in Cramp, 1992).

We built experimental signals modifying song parameters considering both temporal and frequential domains. Experimental signals were built either by destructive synthesis, *i.e.* by modifying the natural control song, or by constructive synthesis, *i.e.* by computer-synthesis of artificial signals (Aubin, 1994).

Modifications in time domain

1. Suppression of amplitude modulation. Like all bird song, blackcap song presents amplitude modulated notes. Long-range propagation alters the initial amplitude modulation (Wiley & Richards, 1982). To assess the biological importance of this phenomenon, we tested whether or not amplitude modulation is a useful parameter in species-specific recognition. We removed from the natural signal all amplitude variations of the initial song, keeping all other acoustic parameters as in the natural signal (Fig. 3a). To do so, we used the method of the analytic signal concept which allows demodulation of amplitude modulated signal using Hilbert transform (Mbu Nyamsy *et al.*, 1994).

2. Modifications of sound/silence alternations. In an environment with dense vegetation, reflected signals induced by sound reverberation modify sound/silence alternation by shortening the silences between notes (*e.g.* Wiley & Richards, 1982; Mathevon, 1998). To test if this phenomenon could affect the species-specific recognition process, we first built a synthetic reverberated song (*i.e.* stuttering effect by addition of echoes with a magnitude of 50% and a delay of 100 ms) (Fig. 3b). Second, to know if the rhythm of silences was important for the decoding process, we removed all silences. Consequently, this experimental song is shorter than the natural one (Fig. 3c).

3. Inversion of temporal structure. Blackcap song presents a specific temporal succession of notes and silences. During propagation through an environment with dense vegetation, this temporal pattern may be modified: for example, some notes, especially high-frequency ones, may be attenuated more than others and are no longer heard by the receiver bird. To test the importance of this temporal structure, we built a reverse song. This signal is exactly the same as the initial one except it is time reversed (Fig. 3d): notes are then played backward.

4. Simplification of syntax. Blackcap song is typically constituted by a phrase of about 30 notes (Cramp, 1992). During propagation through an environment with dense vegetation, the emitted signal may be attenuated differently at different moments, depending on the relative position of emitter and receiver birds (Mathevon *et al.*, 1996; Mathevon, 1998; Dabelsteen *et al.*, 1993). To investigate which minimal succession of notes elicits territorial response, we built several simplified signals using notes belonging to the fluting segment of the song. The first part of this fluting segment is composed of several types of notes (A to E) repeated with a defined syntax (see Fig. 2b): ABCDABCE. ABC is a succession of notes belonging to the same frequency range (around 3.5 kHz). In comparison with these three notes, D is of lower frequency (around 2.5 Hz) while E is of higher frequency (around 4.5 kHz).

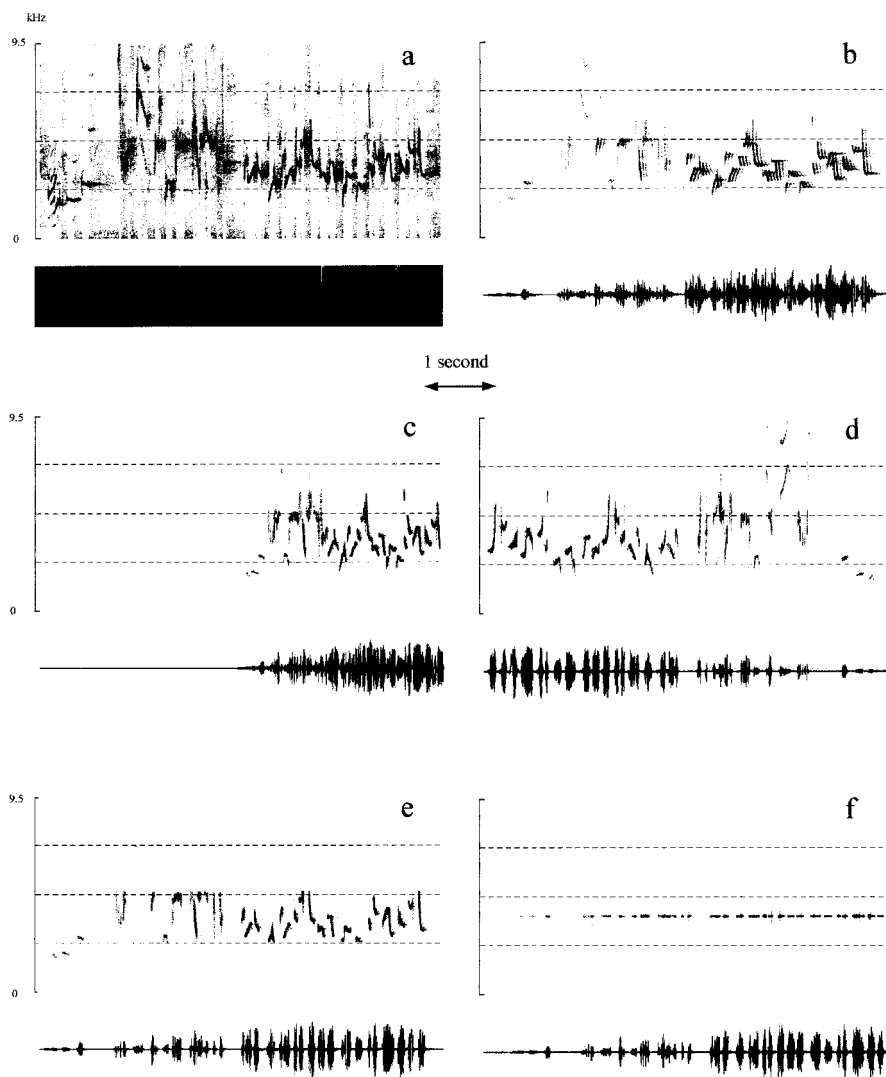


Fig. 3. Experimental signals investigating the importance of parameters modifications. Temporal parameters: a) song without amplitude modulation; b) reverberated song; c) song without silences; d) song with an inverted temporal structure. Frequency parameters: e) filtered song; f) song without frequency modulation.

We used the following natural successions of notes for the playback experiments:

ABC (3 notes around 3.5 kHz)

ABCD (3 notes around 3.5 kHz followed by a note of low frequency)

ABCE (3 notes around 3.5 kHz followed by notes of higher frequency)

DABCE (3 notes around 3.5 kHz surrounded by notes of respectively lower and higher frequency)

Each succession of notes was repeated so often that each experimental signal had the same duration as the initial one (*i.e.* about 6 s).

Modifications of frequency domain

1. Filtration of frequency bands. During propagation at long range in a forest, acoustic signals are affected by frequency-dependent attenuation (*e.g.* Wiley & Richards, 1982). After long range propagation, frequencies higher than 5 kHz are particularly attenuated. Also if signals propagate near the ground, frequencies below 2.5 kHz are severely attenuated (ground effect, *e.g.* Michelsen, 1983). To test the tolerance of blackcaps in regard to frequency-dependent attenuation, we filtered the initial signal with a 2.5-5 kHz bandpass, all frequencies respectively above 5 kHz and below 2.5 kHz being removed by a numerical filter (Fig. 3e).

2. Suppression of frequency modulations. After propagation through the forest, the received signal results from a summation of direct and reflected sound waves. These waves have different phase displacements and their summation gives a complex result. Notes of blackcap song are strongly modulated in frequency. Then, the frequency modulation rate may be degraded by long-range transmission in a close environment (*e.g.* Mathevon *et al.*, 1996).

To test the importance of the frequency modulation in species-specific recognition, we made a signal keeping the natural amplitude envelope but with notes not modulated in frequency. The unmodulated frequency represents the average frequency of blackcap song (Fig. 3f).

3. Modifications of the modulation of the carrier frequency. During the fluting part of blackcap song, the carrier frequency is doubly modulated in frequency. First, the carrier follows linear variations, increasing and decreasing from approximately 2000-3000 Hz to 4000-5200 Hz. Each progression between extreme frequencies takes approximately 0.25 s. Second, this carrier is modulated in frequency with a sinusoidal modulation rate of about 7 Hz and a frequency excursion of about 1200 Hz (Mathevon, unpublished data). Creating synthetic signals by constructive synthesis, we investigated the simplest frequency modulation of the carrier allowing species-specific recognition. The design of experimental signals was as follows:

a. Slow linear variations of a carrier frequency. To test if species-specific decoding process relies on the slow linear variations of the carrier frequency, we made a synthetic signal as follow: a carrier increasing and decreasing from 2000 to 4000 Hz with a period of 0.5 s (Fig. 4a).

b. Sinusoidal modulations of a carrier frequency. First, we made a synthetic signal without slow linear variations of the carrier frequency but presenting a sinusoidal frequency modulation (modulation rate: 7 Hz; frequency excursion: 1200 Hz) (Fig. 4b).

Second, we made a synthetic signal imitating the natural double frequency modulation: a carrier frequency increasing and decreasing linearly from 2000 to 5200 Hz with a period of 0.5 s, and with a sinusoidal frequency modulation (modulation rate: 7 Hz; frequency excursion: 1200 Hz) (Fig. 4c).

Finally, we made a similar synthetic signal as the previous one, except that the monotony of linear variations of the carrier frequency were less important: extreme values of carrier frequency were successively 5200, 3000, 4000, 2000, 4000, 3000 and 5200 Hz (Fig. 4d).

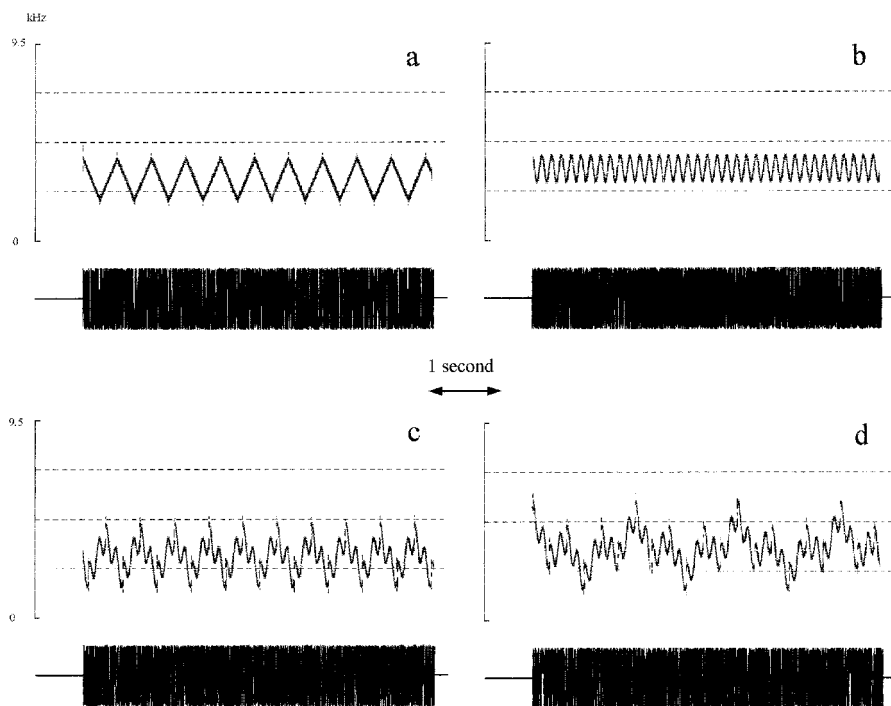


Fig. 4. Synthetic signals investigating the frequency modulation used for encoding species-specific information: a) carrier frequency with linear variations; b) rapid sinusoidal frequency modulation; c) carrier frequency with linear variations and sinusoidal modulation; d) idem to c with linear variations less monotonous.

Playback procedure and behavioural response

Signals were broadcast through an Uher tape recorder and a 10 W amplifier connected to an Audax loudspeaker (frequency response varied less than ± 4 dB within the 1–9 kHz range). The signals were emitted at an acoustic level similar to a natural signal, *i.e.* 90 dB measured at 1 m in front of the loudspeaker (2235 Bruel and Kjaer decibel-meter set in A-weighting with a 4176 microphone). Each *experimental tape* consisted of 10 experimental signals, separated by 6 s of silence. As the duration of an experimental signal was the same as the one of the control song, *i.e.* 6 s, the total duration of an *experimental tape* was about 114 s. For the signal where the inter-notes silences had been removed, which is consequently shorter than the control song (about 3 s), the total duration of the *experimental tape* was 84 s. One minute after the end of the playback of an *experimental tape*, we played a *control tape* (10 consecutive control songs separated by 6 s of silence) to assess the presence and the reactivity of the territory owner. As all modified signals were built from the same natural call, a problem of pseudoreplication should occur (McGregor *et al.*, 1992). Nevertheless, in our playback experiments, the presentation of signals was paired: a series of modified signals and then a series of control (natural) songs.

For each reconstruction, the natural song was modified according to only one dimension; a temporal or a frequency parameter. When using a simple dimension as an independent variable, the levels of the variable can be under direct control of the experimenters, and thereby be less likely to be affected by external variables (Hopp & Morton, 1998). The use of artificially modified or made stimuli allows us to control over the differences between our stimuli, minimizing greatly the problem of pseudoreplication (McGregor *et al.*, 1992).

During playback, we remained motionless 15-20 m from the loudspeaker which was fixed 1.5-2 m above ground level to a tree branch. Behavioural response of tested birds was estimated during the playback of both the *experimental tape*, giving the *experimental response*, and the following *control tape*, giving the *control response*. We did not take into account the behaviour observed during the 1 minute of silence separating the experimental and the control playbacks. We assessed the behaviour of a tested bird according three degrees of increasing intensity:

R0-No answer.

R1-Moderate territorial response: the bird starts singing, but remains more than 10 m away from the loudspeaker.

R2-Strong territorial response: the bird perches and sings at less than 10 m from the loudspeaker.

R2 represents the natural reaction to territorial aggression when a territory owner is threatened inside his territory (Cramp, 1992). During our experiments, the number of males that did not show a R2 response to the *control tape* following the *experimental tape* was either 0 (signals 3, 5-7, 11, 13 in Table 1), 1 (signals 1, 9: R0 response; signals 2, 8, 14: R1 response) or 2 (signal 4: one bird showing a R0 response and one bird reacting by a R1 response; signals 10, 12: two birds reacting by a R1 response). The number of non-R2 responses is not significantly different from a type of test to another, and then can be considered as independent from the nature of the *experimental tape*. This eleven birds that did not show a typical R2-response to the control song (may be because of being less reactive) have not been included in our data set. In other words, we took the *experimental response* only into account if the subsequent *control response* was R2 type. We tested a total of 151 birds; as 11 of them showed a non R2-response to the *control tape*, only 140 birds have been included in our data set.

Statistical analysis

The results of playback of experimental signals were compared with the results of playback of a control signal, using a Fisher's exact test of independence (Sokal & Rohlf, 1995). To perform this test, we combined R1 and R2 responses to obtain a 2×2 table, considering that either there was a territorial response (R1 or R2) or there was a non-territorial response (R0). This response/non-response approach is an appropriate strategy for our study since the question we asked to the birds was dichotomous: does the male respond or not, without measuring the level of discrimination among treatments.

TABLE 1. *Blackcaps responses to experimental signals*

Experimental signals	No territorial response (R0)	Territorial response		Comparison R0/R1&R2
		moderate (R1)	strong (R2)	
1. Suppression of amplitude modulation	0	1	9	NS
2. Reverberated song	0	0	10	NS
3. Suppression of silences	0	0	10	NS
4. Time reversed song	0	2	8	NS
Simplification of syntax:				
5. ABC	10	0	0	*
6. ABCD	10	0	0	*
7. ABCE	9	1	0	*
8. DABCE	0	2	8	NS
9. Filtered song	0	2	8	NS
10. Suppression of frequency modulation	10	0	0	*
11. Carrier frequency with slow linear variations	10	0	0	*
12. Carrier frequency with sinusoidal modulation	10	0	0	*
13. Carrier frequency with linear variations and sinusoidal modulation	10	0	0	*
14. Idem to 13 with linear variations less monotonous	0	0	10	NS

NS: non-significant difference with response to the control signal.

*: significant difference with response to the control signal (<0.05).

Results

Modifications in time domain

Signal without amplitude modulation elicits a strong territorial response (R2) in 9 of the 10 tested birds (signal 1 in Table 1, Fig. 3a). Playback tests show that blackcaps recognise reverberated song without any difficulty (signal 2 in Table 1, Fig. 3b). The broadcast of a song without silences between notes also elicits strong territorial reaction in each tested blackcap (signal 3 in Table 1, Fig. 3c). Most of the tested birds respond by a strong territorial reaction to the reverse song (signal 4 in Table 1, Fig. 3d). The DABCE signal triggers a response in blackcaps (signal 8 in Table 1, Fig. 1b) while birds did hardly respond to stimuli with other notes succession (signals 5-7 in Table 1).

Modifications in frequency domain

All blackcaps tested with filtered signal responded by territorial behaviour (signal 9 in Table 1, Fig. 3e). None of the birds tested reacted to the signal without frequency modulation (signal 10 in Table 1, Fig. 3f). Blackcap did not respond to the signals presenting only slow linear variations of a carrier frequency or only sinusoidal modulation (signals 11-12 in Table 1, Figs 4a and 4b). The synthetic signal imitating natural double frequency modulation did not elicit any behaviour too (signal 13 in Table 1, Fig. 4c). On the contrary, the same last signal with variations of extreme values of the carrier elicited a strong territorial reaction from blackcap males (signal 14 in Table 1, Fig. 4d).

Discussion

In this study, we analysed the decoding process used by male blackcap for the species-specific recognition of the song. Our results show that, for species-specific recognition, blackcaps are highly tolerant towards song structure modifications. The two domains of sound signals, the Time and the Frequency ones, have been taken into account.

Time domain

Blackcap disregards amplitude modulation to perform species-specific recognition. Amplitude modulation may not be a reliable parameter in any case since it is strongly modified by a long distance propagation (Wiley & Richards, 1982). Disregarding amplitude modulation for species-specific recognition appears to be an adaptation to communication in an environment with dense vegetation.

Duration of notes or silences and sounds/silences alternation are not used by a receiving blackcap to decode species-specific information. Reflection of sound waves on numerous obstacles like trunks of trees, branches and leaves induced reverberated sounds. The resulting echo enhances the duration of notes and modifies the respective duration of sounds and silences. Disregarding duration of sounds and silences during species-specific recognition is, thus, advantageous in an environment with dense vegetation.

A blackcap requires only a succession of five different notes to recognise specifically the received signal. 5 successive notes may represent the song

minimal duration allowing species-specific recognition. A full blackcap song contains a minimum of about 30 different notes. Even if a great part of the song is altered during propagation, acoustic communication stays effective. This redundancy of information is useful for long-range signalling in a dense vegetation environment.

Blackcaps appear highly flexible in regards to modifications of temporal structure: a reversed signal induced the same behavioural response as the control song. This is advantageous in a sound scattering environment inducing modifications of sound/silence distribution.

Frequency domain

To perform species-specific recognition, blackcap relies on the modulation of the carrier frequency of conspecific song, *i.e.* a carrier frequency varying slowly up and down between 5200 and 2000 Hz, modulated in frequency at a mean rate of 7 Hz and with a mean frequency excursion of 1200 Hz. The slow variation of the carrier frequency between 5200 and 2000 Hz has to be not linear: Blackcaps respond only if the carrier frequency reaches successively 5, 2-3-4-2-4-3-5, 2 kHz as represented on Fig. 4d (signal 14 in Table 1); these variations can be considered as an added modulation. Blackcaps do not respond to the stimulus represented on Fig. 4c (signal 13 in Table 1) where these variations are lacking. The modulation of the carrier is symmetrical: may be that is why decoding process does not suffer from the presence of reversed notes structure in the reversed signal (Fig. 3d, signal 4 in Table 1). No significance is given to the carrier frequency alone. Blackcaps appear to recognize song by frequency changes over time, using the characteristics of frequency modulation (FM), and not the averaged value of the carrier frequency. However, it is probable that the carrier value must be comprised in a certain interval to allow normal decoding (Brémond, 1986). We have seen above that a succession of 5 notes is the minimum indispensable to elicit species-specific recognition. These successive notes (DABCE, see results) correspond to the minimal combination to gain sufficient information concerning the modulation of the carrier frequency. A succession of only 3 or 4 notes would not be sufficient for a receiving bird to assess all the species-specific characteristics of this modulation: the signal might be too short.

It seems to our ears that the synthetic stimulus with the frequency modulation such as this represented in Fig. 4d is unsong-like. Its structure

is quite simple, without the presence of any silence. Nevertheless, blackcap male responds to this crude sound. Why then the natural blackcap signal looks so varied? We can suppose that, in natural situations, males might be stimulated initially by a crude songster within the territory, but that as the interchange proceeded, crude songsters would be at a competitive disadvantage. So, even if the basic decoding process relies on the perception of a quite simple modulation of a carrier frequency, we must keep in mind that our study may have put forward the initial perception of potential conspecifics that is to say only one aspect of sexual selection on song perception and processing.

FM is a reliable parameter since a given sound frequency can not be transformed into another one by propagation phenomenon in the atmosphere. However, acoustic constraints imposed on FM transmission by the environment cause two problems. The first is linked with reverberation phenomenon: the receiver bird receives direct and reflected sound waves at the same time which may interfere, and so modify, the perception of the FM. We showed that blackcap identifies artificially reverberated song as a conspecific one; birds seem not to be hampered by interference between direct and reflected sound waves. The second problem is frequency dependent attenuation; high frequencies are rapidly attenuated during propagation. Blackcap song ranges from 2000 Hz to 8500 Hz and the upper part is susceptible to frequency dependent attenuation. We showed that blackcap can decode conspecific song using only the 2500-5000 Hz frequency band.

Coding versus decoding processes

Our study focuses on male decoding process for species-specific recognition and does not contain data on the encoding process. One might imagine that the two processes do not necessarily coevolve in exact synchronisation. The decoding process might lack behind the encoding process, or the information encoded in the song might be decoded differently by males and females. Indeed, females may not use exactly the same acoustic parameters for decoding. This kind of result has been shown in blackbird (Dabelsteen & Pedersen, 1988, 1993). A possibility is that females are in a position to listen at closer range than territorial males, and therefore might be capable of using amplitude modulations and other parameters which are disregarded by males.

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