Bibliographical reference

Species Identity Coding by the Song of a Rainforest Warbler: An Adaptation to Long-Range Transmission?, Thierry Aubin, Nicolas Mathevon and Maria Luisa Da Silva, Acta Acustica **vol. 100** (Number 4), 2014, pp. 748-758

DOI

https://doi.org/10.3813/AAA.918754

Acta Acustica united with Acustica
Vol. 100 (2014) 748 – 758

DOI 10.3813/AAA.918754

Species Identity Coding by the Song of a Rainforest Warbler: An Adaptation to Long-Range Transmission?

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Summary
In tropical forest, visual communication is limited by obstacles and birds use mainly the acoustic channel to communicate at long range. However, in this dense vegetation environment, sounds may be greatly altered during transmission over distance. To be effective, information transfer must rely upon parameters resistant to degradation, e.g., a slowly-modulated and low-pitched signal. Nevertheless, a common bird of the Brazilian Atlantic forest, the White-browed Warbler *Basileuterus leucoblepharus* (Oscines, Parulidae), presents a territorial song having the opposite characteristics: a wide frequency band and high-pitched signal. Thus, the aim of our study was to characterize the propagation-induced modifications of this signal, and to identify its species-specific coding parameters. According to propagation experiments performed in the field at different distances, it appears that the signal is particularly sensitive to degradation through the vegetation: the fine acoustic structures (rapid frequency and amplitude modulations) are strongly modified, and the highest pitched notes tend to disappear at a relatively short distance (about 25 m). Playback experiments show that, for species-specific recognition, birds use the only feature that is resistant to degradation, i.e., the overall slow frequency modulation of the song phrase, and ignore those parameters sensitive to propagation distance. Moreover, birds do not need to hear the whole song, a part of it being sufficient to elicit a behavioural response. Thus, in spite of its structure, the song of the White-browed Warbler succeeds in conveying, over a long range (more than 100m) and through the dense vegetation, the information required for species- specific recognition.

PACS no. 43.80.-n, 43.80.Ka, 43.80.Lb, 43.80.Nd

1. Introduction

Animals commonly use acoustic signals for long range communication as they are able to rapidly transmit a large amount of information over great distances. Sounds are especially useful in obstructed environments such as forests where visual communication is seriously impaired by the vegetation. However, in such environments, sounds suffer various propagation-induced modifications such as attenuation produced by absorption and multiple scattering, blurring of amplitude and frequency patterns due to selective frequency filtering, reverberation and atmospheric turbulences, which alter the initial characteristics of the signal and thus may impair the transmission of the information between individuals [1, 2, 3, 4, 5]. These modifications depend on both the propagation distance and the physical characteristics of the transmission environment [6, 7, 8, 9, 10, 11, 12].

These environmental constraints constitute a selective pressure on biological signalling, making acoustic communication in forest a good model to investigate the potential evolutionary influences of the environment on a biological process. In this perspective, studies in environmental acoustics predict that the structure of animal signals will differ depending on general features of the habitat, the so-called "acoustic adaptation" or "signal structure" hypothesis [13, 14]. Species that inhabit areas with dense vegetation are then expected to produce low-pitched signals with slow amplitude and frequency modulations. Such characteristics will increase the signal's "active space". Propagation experiments have shown that fast amplitude and frequency modulated sounds as well as high-pitched sounds are the most susceptible to propagation-induced degradation [4, 5]. The "signal structure" hypothesis has been primarily tested in songbirds, since communication over a large active space is partic-

Received 4 February 2014,
accepted 1 May 2014.

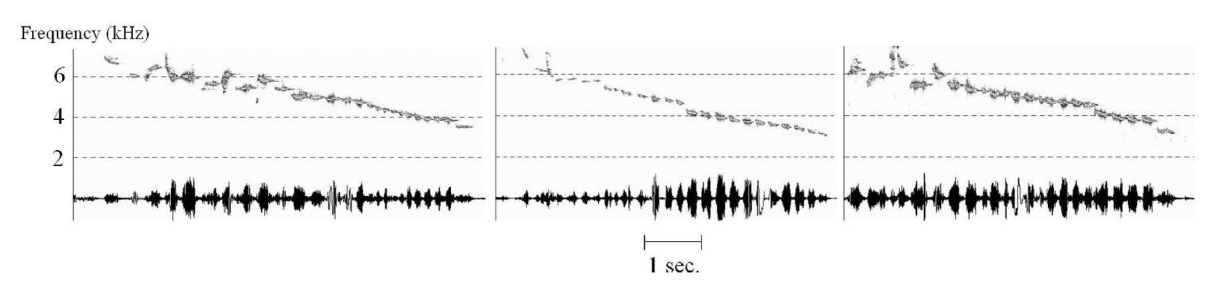

Figure 1. Original songs from three different individuals recorded in different locations.

ularly useful in the context of territorial advertising and female attraction, the two main functions of birdsong besides species-specific recognition. However, support for this prediction is somewhat mixed. Several studies have reported that the average frequencies of songs differ in forested and open habitats [5, 13, 15, 16]. Conversely, Richards and Wiley [17] found no differences in the frequencies of songs between related bird species of open and forested areas in North Carolina. Moreover, there is a number of cases showing that the structure of emitted signals is not obligatorily fitted to propagation constraints [18, 19, 20, 21, 22, 23, 24, 25].

Besides the "signal structure" hypothesis, there is an alternative, although not exclusive, possibility for the evolution of the communication processes under environmental constraints. Indeed, the emitted signal is only a part of the story. At the end of the communication chain, the receiver has to deal with the transmitted sound and the success of the communication process will depend on its ability to decode the information in the altered signal. This "information decoding" hypothesis has received a particular attention in noisy and confusing environments, like seabird colonies, where receivers have been shown to be skilled in decoding the information despite the very low signal-to-noise ratios (in penguins: [26, 27]; in gulls: [28]). Conversely, this hypothesis has been neglected for communications in cluttered environments such as forests. Although several studies have investigated the decoding process of cues for species-specific identity in avian vocal signals (see [29] for a review), only few of them have tried to relate this process to signal degradation during propagation. To our knowledge, only three species of birds, all from European temperate forests, have been investigated from this perspective: the Blackbird *Turdus merula* [6, 30, 31, 32], the Blackcap *Sylvia atricapilla* [33, 34], and the Wren *Troglodytes troglodytes* [7, 35, 36, 37, 38, 39]. The Blackcap and the Blackbird both emit a song which fits the "signal structure" hypothesis; only the Wren has a signal that is particularly susceptible to modification during propagation and playback tests showed that this species has adopted a decoding process that is highly tolerant to signal degradation [37, 39]. However, except for the Wren, there is no available study that considers both the propagation-induced modifications and the decoding processes of signals that appear to lack the adaptations predicted by the environmental constraints.

To investigate this problem, we chose to work on a warbler (Passeriformes Oscines, Emberizidae, Parulinae) of the Brazilian Atlantic forest, the White-browed warbler (hereafter WBW) *Basileuteurus leucoblepharus*. This typical and widespread bird presents a territorial song whose characteristics - a wide frequency band, high-pitched signal consisting of a succession of notes produced at a fast tempo - are opposite to what the "signal structure" hypothesis predicts. This species lives in the dense vegetation of the Atlantic rainforest, an environment in which song is rapidly degraded. However, long range communication is effective as males defend acoustically their territory and succeed in attracting females by their song. In previous studies, we showed that the WBW can extract various information from a received song: species-specific identity, individual identity and location of the sender [40]. Individual identity appears to be coded by acoustic parameters highly susceptible to long range propagation [41] whereas species identity seems to be supported by simpler features that propagate well through the forest. Using both sound transmission experiments and playback tests, here we present a detailed investigation of how the WBW's song codes for species identity.

2. Methods

2.1. Subject and location

The experiments were performed in a typical habitat of the WBW, at Morro Grande State Reserve (latitude 46.57, 32 W, longitude 23.40,15 S) in the Atlantic forest of Southeastern Brazil, during November 2000 and 2001, i.e. at the beginning of the wet season (summer). At this period of the year, the weather conditions were characterized by rather cool temperature (16–22 °C), high relative humidity (85% to 100%), almost no wind, and frequent rains.

The species was chosen for its high abundance and regular singing activity. In the Morro Grande reserve, the WBW shows a very high IPA-Index of Point Abundance [42]. The species was also chosen for its song characteristics. No geographical variation in the song structure has been evidenced so far (148 songs of 25 individuals analysed, Figure 1). The song has a mean ± SD duration of 2.70 ± 0.52 s and consists of a regular, rapid succession of 15–18 similar notes that slowly and continuously decreases in frequency. These notes are pure tones with a fast FM, a duration of 0.132 ± 0.023 s (mean ± SD) and a silent interval of 0.057 ± 0.012 s. The frequency of the whole song decreases from 7.98 ± 0.23 to 3.74 ± 0.48 kHz, making the WBW song a wide-band signal.

2.2. Recording and playback material

Natural songs were first recorded using an ultra-directional Sennheiser MKH 816 microphone connected to a Sony TCD-D10 DAT recorder (sampling frequency: 48 kHz; frequency response: flat within the range 20–20000 Hz) and subsequently digitised at a sampling frequency of 22 kHz.

Songs were played back on a Sony TCD-7 DAT recorder connected to a self powered 10W amplifier equipped with an Audax loudspeaker (frequency response 100–8600 Hz +2.5 dB). Recordings during propagation experiments were made with an omni-directional Beyer Dynamic M-69 microphone (150–15000 Hz ±2 dB) connected to a Sony TCD-D10 DAT recorder. Intensity level measurements in dBSPL were performed using a Brüel & Kjær sound level meter type 2235 equipped with a 1/2 inch 4126 microphone (slow setting, linear scale).

2.3. Analysis and synthesis material

The analysis and synthesis of signals were done using Syntana [43] and Avisoft SASLab Pro [44] software.

2.4. Propagation experiments

2.4.1. Propagated signal

To eliminate propagation-induced modifications existing in recorded songs, we built a synthetic copy of a representative natural song of a WBW (Figure 2, control) chosen after analysis of signals recorded from 15 individuals. The duration of notes and inter-notes silent periods was representative of the natural variation and the signal covered the frequency range typically used by the species.

2.4.2. Propagation procedure

To assess the modifications of signals during propagation through the natural habitat, the synthetic song was broadcast repetitively (10 signals separated by 3.5 s of silence) and recorded at different heights and distances. The SPL of the broadcast signal was ca. 90 dB at 1 m from the loudspeaker.

The test sequence was transmitted along two 100 m transects through an area representative of the natural habitat of the WBW. Two speaker and microphone heights (0.20 m, 6 m) were chosen as representative song perches and receiver locations. For each transect and each height, 3 propagation distances were tested: 25 m, 50 m and 100 m. These distances were chosen so as to correspond to the usual distances between interacting neighbours (Vielliard, pers.obs.), with the longest distance representing the maximum diameter of a territory. During propagation experiments, the SPL of the broadcast signal was measured at the position of the microphone for each distance and each height. All propagation measurements were made during calm weather, without wind, with a mean relative humidity of 94% and a mean temperature of 18 °C.

2.5. Signal analysis

All propagated signals were compared to a non-propagated signal. This reference signal was the synthetic song broadcast and recorded at 2 m high and 1.50 m distance, in a quiet open field area. The series of recorded signals were examined in the amplitude-versus-frequency, the amplitude-versus-time and the frequency-versus-time domains. Among the ten propagated signals, recorded songs with overlapping foreign signals in the vicinity of the microphone were eliminated. Then, among the remaining signals, only 6 (3 by transect) were chosen at random for subsequent analysis. Each signal was first aligned in time with the others by maximizing the successive cross-correlations between them.

We used an envelope calculation to compare the amplitude fluctuations of the signal before and after propagation. The envelope was digitally filtered using FFTs (band-pass: 0–150 Hz) as we wanted to focus only on the main amplitude modulations of the notes. To minimize the influence of accidental events occurring in the environment, the 6 envelopes corresponding to each test condition were averaged. Bravais-Pearson product–moment correlations were used to compare the averaged envelopes of the propagated signal with the one of the non-propagated signal. To analyse the modification of the spectral content of the call during propagation, we computed a FFT of the whole song by splitting short term overlapping FFTs (FFT size 512, overlap 50%). As for envelope analysis, the 6 spectra corresponding to each test condition were averaged and each averaged spectrum was compared with that of the non-propagated signal by a Bravais-Pearson product–moment correlation.

Finally, we analyzed the modification of the frequency modulations during propagation using digital spectrographic cross-correlation (SPCC). This technique, described in detail by Clark *et al.* [45] and Khanna *et al.* [46], simultaneously analyses the frequency, amplitude and time components of a signal by sliding the averaged spectrograms (FFT size 128, overlap 50%) of the propagated signal along the time axis of the averaged spectrogram of the non-propagated signal. Due to the chosen FFT size and spectral resolution value, this procedure only allowed us to detect possible changes in the overall frequency modulation (i.e. mainly the slow decreasing FM) during propagation.

For each specific analysis (envelopes, spectra, sonagrams), the axis of the propagated and non-propagated signal had been normalised before computation of correlations.

The r values of the correlations and their significance were calculated using Statistica V5.1 software [47].

2.6. Playback experiments

2.6.1. Experimental signals

As model songs, we chose three typical WBW songs from three different individuals coming from different locations in Brazil (Figure 1). For all parameters and features, these

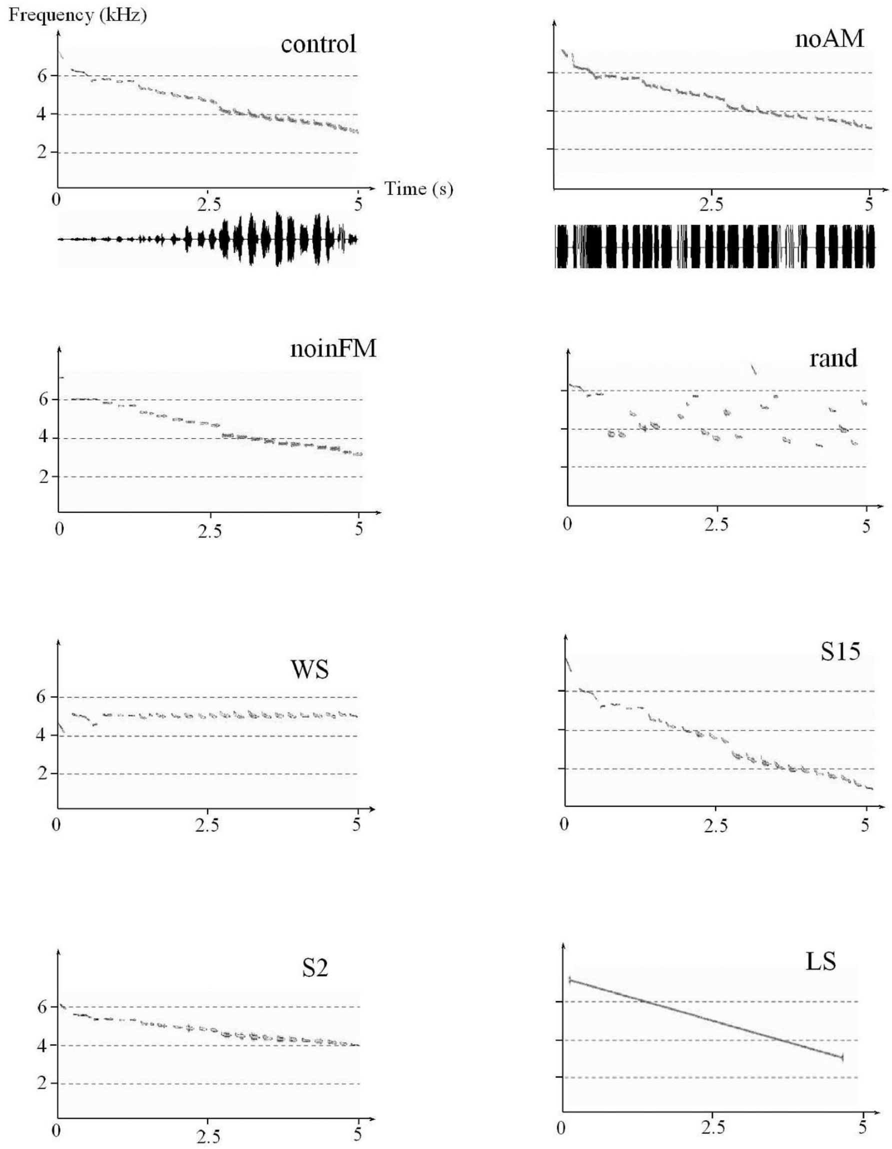

Figure 2. Synthetic signals used for playback (control: copy of the original song; noAM: without amplitude modulation; noinFM: without intra-note frequency modulation; rand: notes distributed at random; WS: without downward sloping frequency modulation (FM); S15: FM slope multiplied by 1.5; S2: FM slope divided by 2; LS: continuous linear frequency slope).

model songs were well within the range of the species song structure.

As control songs, we used synthetic songs copying the natural models. We created signals without propagation-induced modification, using Avisoft package to digitally synthesize signals matching the acoustic features of natural songs. We also built experimental signals to explore the different song parameters that were likely to carry the species-specific message. Modifications of the control songs were performed using the Avisoft and Syntana packages.

– Question 1: is amplitude pattern important?

We built a synthetic signal that matched all the features of the control songs except that amplitude modulation was lacking (noAM, Figure 2). To demodulate the amplitude, we used the analytical signal concept [48, 49].

– Question 2: to what extent do birds rely on frequency modulation?

a) Suppression of the intra-note frequency modulation (noinFM, Figure 2). In the WBW song, the carrier frequency of each note is modulated in frequency (so called “intra-note FM”). We built an experimental signal where the natural intra-note FMs were lacking. Each note was replaced by a pure tone whose frequency corresponded to the mean carrier frequency of the natural note. The duration of the notes and all the other acoustic features of the song remained identical to those of the control signal.

b) Modifications of the FM slope (Figure 2). To test whether the descending FM slope carries information for species-specific recognition, we built the following experimental signals:

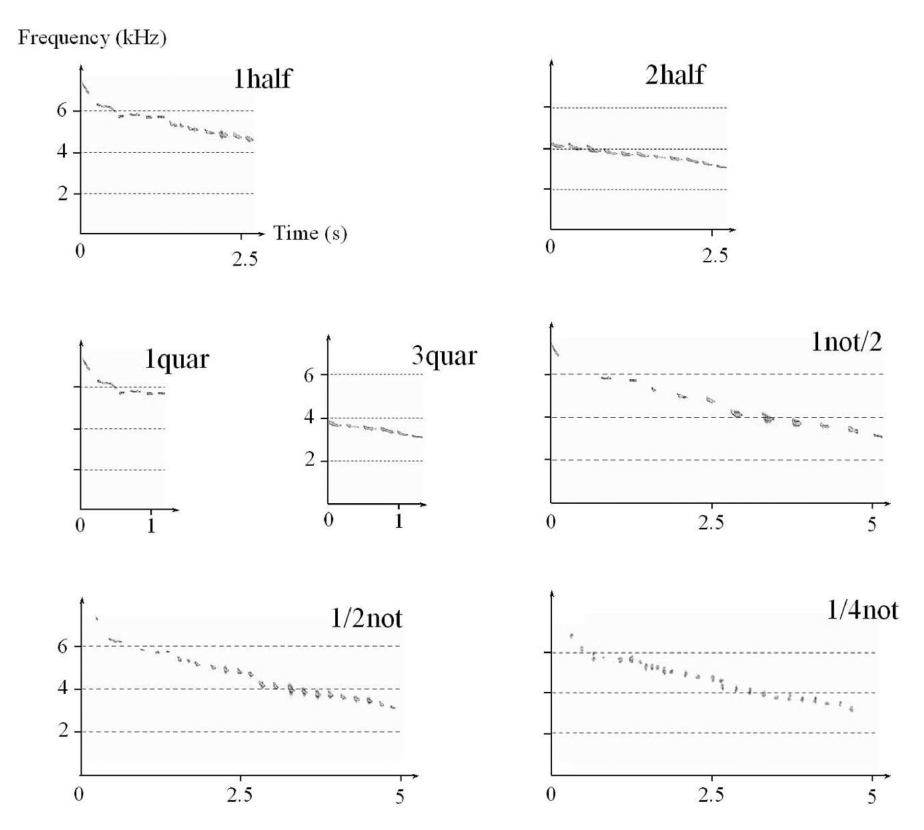

Figure 3. Synthetic signals used for playback (1half: first half of the song; 2half: second half of the song; 1quar: first quarter of the song; 3quar: third quarter of the song; 1not/2: song with every other note deleted and replaced by silence; 1/2not: second half of each note deleted and replaced by silence; 1/4not: only the first quarter of each note is preserved, the deleted portion being replaced by a silence).

- Notes in any order (rand): notes and corresponding silences following them were distributed at random along the time axis. The FM descending slope was no longer present.
- Without FM slope (WS): Each note was centred on the average frequency of the control song.
- The slope of the descending FM was multiplied by a factor 1.5 (slope*1.5 = S15; start frequency = 8500 Hz, end frequency= 2000 Hz) or divided by a factor 2 (slope/2 = S2; start frequency = 6200 Hz, end frequency= 4100 Hz).
- Linear frequency slope (LS). The slope of this FM was the averaged slope of the control song. This signal contained no silences and no notes: it was a single continuous sound with the same duration than of the control song.

– Question 3: is the whole song necessary for species recognition?

We built four experimental signals in which respectively only the first half (1half), second half (2half), first quarter (1quar), or third quarter (3quar) of the song was kept (Figure 3).

– Question 4: is the sound/silence ratio a coding parameter?

To answer to this question, three experimental signals were built (Figure 3). In ‘1not/2’, every other note was kept. In ‘1/2not’, the duration of each note has been divided by two, only the first half of each note being preserved. Finally, in ‘1/4not’, only the first quarter of each note was conserved. In these last three signals the notes or part of them that was removed were replaced by an equivalent duration of silence. The overall duration and the FM slope of the song were thus preserved by stretching the silences between the notes.

– Question 5: is the frequency bandwidth of the signal important ?

To assess the importance of the absolute frequency, the control song was linearly shifted in frequency by +1000 Hz (shift+) or −500 Hz (shift-).

2.6.2. Playback procedure

Playback experiments were performed between 06h15 and 10h30. This time of the day represents the period of most intense spontaneous territorial activity of the WBW (Vielliard, pers.obs.). Each tested individual only received one playback treatment to avoid habituation. Moreover, neighbours were tested with different experimental songs. To minimize the effect of possible eavesdropping, neighbours were subjected to playback on different days. Before playback, male territories were mapped. The broadcast loudspeaker was then located inside the territory boundaries, at approximately 2 meters high (i.e., well within the range of perch heights used by this species, Vielliard, pers.obs.). During the experiments, the observers remained at 10 meters from the loudspeaker.

Each playback treatment contained five repetitions of a given song each separated by 6 seconds of silence, similar to the natural song rate. Experimental signals were emitted at the natural intensity level of 90 dB SPL (measured at 1.5 m from the loudspeaker).

2.6.3. Analysis of behavioural responses

Each tested bird was observed for three minutes before the playback trial, during playback, and for three minutes following the emission. The movements of the bird relative to the location of the loudspeaker, the rate of emission of contact calls and of songs were noted during the whole observation period. These signal emission rates (number of calls or of songs /minute) during the playback trial and the three minutes following playback were compared with the rates during the three minutes before the playback. From these data, the following four response measures were extracted and scored:

- latency of response (score 0: no response or response after more than 3 minutes after the end of the playback session; score 1: response within the 2- 3 minutes after the playback session; score 2: response during playback or within 1 minute after the playback session);
- approach to the speaker (score 0: no approach; score 1: approach at a distance to the loudspeaker not closer than 10 m; score 2: approach at less than 10 m);
- variation of calls emission rate (score 0: no variation; score 1: weak variation, i.e. until 3 times the initial calling rate; score 2: strong variation, i.e. more than 3 times the initial calling rate);
- variation of songs emission rate (score 0: no variation; score 1: weak variation, i.e. until 3 times the initial singing rate; score 2: strong variation, i.e. more than 3 times the initial singing rate).

For each response measure, the effects of the playback of experimental stimuli were assessed using a Kruskall-Wallis ANOVA. The behavioural response to each experimental signal was compared to the control response using a Mann-Whitney U post-hoc test. As we performed a multiple significance testing, we made a Bonferroni adjustment by multiplying the P value by the number of tests carried out (16 tests). To assess the significance of the tests, the Bonferroni-corrected P values were compared against the level of 0.05. Computations were carried out with Statistica software.

3. Results

3.1. Propagation experiments

3.1.1. SPL measurements

The measurements (mean ?SD, n=10 for each case) of the SPL of the signal broadcast and recorded at different distances give the following results:

- for the non-propagated signal (1.5 m): 90.01 dB ± 0.67.
- for the 0.20 m height propagation: 61.50 dB ± 1.22 at 25 m; 52.70 ± 1.62 at 50 m. The SPL at 100 m was below the background noise and not measurable.
- for the 6 m height propagation: 63.05 dB ± 1.77 at 25 m; 55.27 dB ± 0.98 at 50 m; 47.40 dB ± 4.72 at 100 m.

According to these results, it appears that the intensity level of the signal decreases regularly with the distance and this decrease is greater close to the ground (0.20 m) than at a higher elevation (6 m). For all distances and heights, the forest environment generates an excess attenuation (EA) since the observed attenuations exceed those expected (6dB per doubling of distance) in a theoretical free field with a spherical spreading. Thus, for example, for the signal broadcast at a SPL of 90 dB and a height of 6 m, after 100 m of propagation, the EA is 6.6 dB (54–47.4, with 54 corresponding to the theoretical value).

Table I. Pearson product moment correlations (r values) between a non propagated signal and signals propagated at different distances and heights for averaged envelopes (n=6, 5450 data points), averaged spectra (n=6, 1024 data points) and averaged spectrograms (frequency versus time representation, n=6). To assess the reliability of each correlation, a significance level has been calculated, and in each case the value obtained was p<0.01. n.c.: not calculable (below the background noise).

Height 0.20 m, Distances:	25 m	50 m	100 m
Envelopes	0.64	0.49	n.c.
Spectra	0.86	0.84	n.c.
Spectrograms	0.84	0.78	n.c.
Height 6m, Distances:	25 m	50 m	100 m
Envelopes	0.84	0.56	0.36
Spectra	0.95	0.94	0.80
Spectrograms	0.93	0.91	0.68

3.1.2. Amplitude vs time measurements

Correlation values of averaged envelopes between the propagated and the non- propagated signals decrease with increasing distance (Table I) and are greater for propagation at a 6 m height than for propagation at a 0.2 m height. Values of correlations are weak (r<0.7) at distances of 50 m and 25 m for propagation heights of 6 m and 0.2 m, respectively. An examination of the envelopes (Figure 4a, only the 6m height represented) shows that, as the distance increases, the first half of the signal progressively disappears into the background noise. In addition, the depth of the amplitude modulation is linked to the silent intervals between notes, such that these intervals decrease in duration with increasing distance, resulting in a progressive blurring of inter-notes silences.

3.1.3. Amplitude vs frequency measurements

The correlations between averaged spectra of propagated and non-propagated signals slightly decrease with distance and their values are greater for propagation at a 6m height than for propagations at a 0.2 m height. Nevertheless, the values of correlations remain high even after propagating

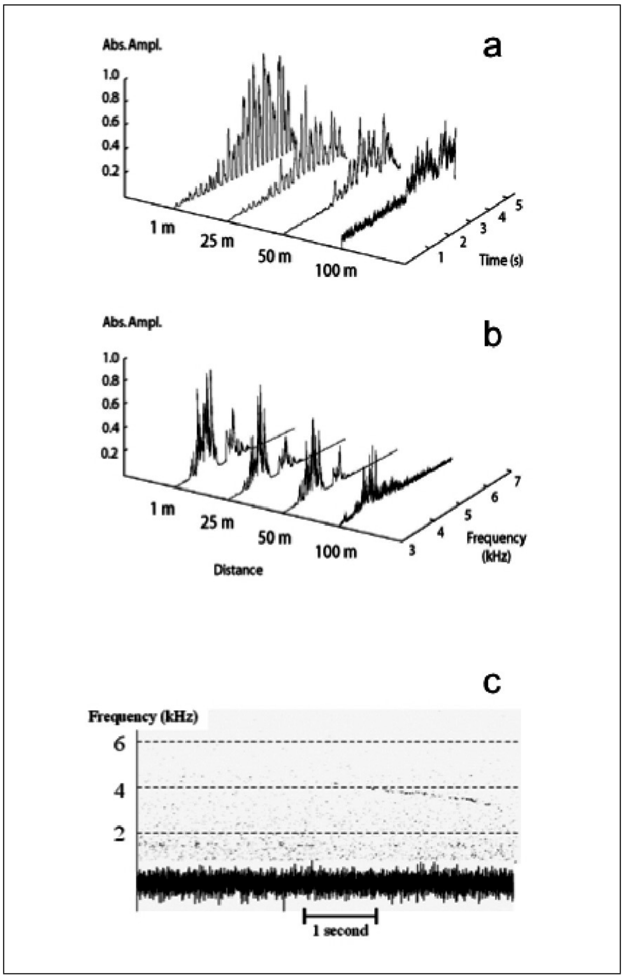

Figure 4. Comparison between control and 25, 50, 100 m propagated signals (only the 6 m height represented): a) envelopes, b) spectra, c) sonagrams (only the 100 m propagated signal is represented). A striking feature is that the first part of the song corresponding to the higher frequencies is embedded in the background noise after a propagation at long range (>50 m).

100 m (r = 0.80 for a 6 m height). Figure 4b (only the 6m height represented) shows that it is mainly the higher frequencies (> 4.5 kHz) of the song that are attenuated as distance increases.

3.1.4. Frequency vs time measurements (SPCC)

As observed previously for the sound envelopes, the correlations between averaged sonagrams of propagated and non-propagated signals decrease with distance, with lower values obtained for the 0.2 m height condition. But, as observed for the spectra, the values of correlations between sonagrams remain high. At 100 m propagation and a height of 6 m r is only slightly less than 0.70. The sonagram in Figure 4c shows that only the lower pitched second half of the song is still above the background noise after propagating 100 m.

3.2. Playback experiments

A total of 153 different individuals were tested. In the following results, $N1$ (=19) represents the number of individuals tested with the control signals and $N2$ (ranging from 6 to 12) the number of individuals tested with the experimental signals.

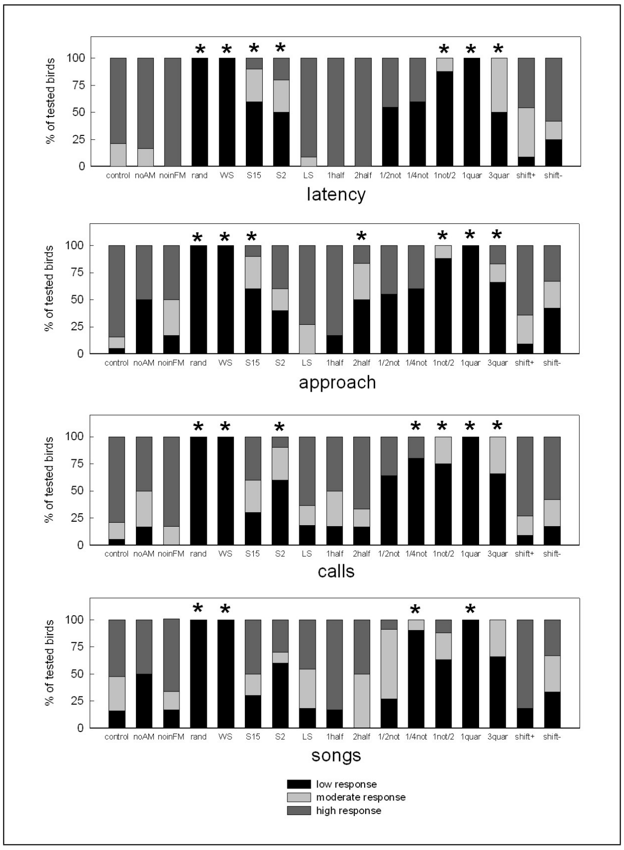

Figure 5. Behavioural responses to experimental signals (abbreviations: see legends of figures 2 and 3). For species-specific recognition, birds use the only feature that is resistant to propagation at some distance, i.e. the overall slow frequency modulation of the song phrase.

The behavioural responses to the whole played-back signals differ in terms of latency (Kruskal-Wallis test: H_{17} = 94.9, $P < 0.05$), approach (H_{17} = 68.4, $P < 0.05$), call rate (H_{17} = 78.1, $P < 0.05$), and song rate (H_{17} = 65.7, $P < 0.05$).

3.2.1. The amplitude pattern is not a species-specific recognition parameter

The response to the signal without amplitude modulation (Figure 5, noAM) does not differ from the control with regard to the latency of response (U = 54.5, $N1$ = 19, $N2$ = 6, P = 1.000), the calling rate (U = 40.0, $N1$ = 19, $N2$ = 6, P = 1.000), or the singing rate (U = 46.5, $N1$ = 19, $N2$ = 6, P = 1.000). Half of the birds did not approach the loudspeaker whereas the other half exhibited a strong approach (U = 34.5, $N1$ = 19, $N2$ = 6, P = 0.882). Overall, the response to the no-AM signal shows no strong difference from that to unmodified signals.

3.2.2. Birds rely on a species-specific slow frequency modulation (the "song slope")

The suppression of intra-note frequency modulations has no effect on the bird response (Figure 5, noinFM, comparison with control: latency: $U = 45$, $N1 = 19$, $N2 = 6$, $P = 1.000$, approach: $U = 37.5$, $N1 = 19$, $N2 = 6$, $P = 1.000$, calls: $U = 54$, $N1 = 19$, $N2 = 6$, $P = 1.000$, songs: $U = 50.5$, $N1 = 19$, $N2 = 6$, $P = 1.000$). Conversely, a change in the slope of the descending frequency modulation has a great impact on the responses. When notes are at random, the signal triggered no response (Figure 5, rand, comparison with control: latency: $U = 0$, $N1 = 19$, $N2 = 9$, $P < 0.05$, approach: $U = 4.5$, $N1 = 19$, $N2 = 9$, $P < 0.05$, calls: $U = 4.5$, $N1 = 19$, $N2 = 9$, $P < 0.05$, songs: $U = 13.5$, $N1 = 19$, $N2 = 9$, $P < 0.05$). More interestingly, when the slope of the FM is modified, the response is also abolished (Figure 5, WS, FM slope = 0, comparison with control: latency: $U = 0$, $N1 = 19$, $N2 = 6$, $P < 0.05$, approach: $U = 3$, $N1 = 19$, $N2 = = 6$, $P < 0.05$, calls: $U = 3$, $N1 = 19$, $N2 = 6$, $P < 0.05$, songs: $U = 9$, $N1 = = 19$, $N2 = 6$, $P < 0.05$) or severely diminished (Figure 5, S15 and S2, FM slope respectively multiplied by 1.5 or divided by 2, S15 compared with control: latency: $U = 17.5$, $N1 = 19$, $N2 = 10$, $P < 0.05$, approach: $U = 20$, $N1 = 19$, $N2 = 10$, $P < 0.05$, calls: $U = 55$, $N1 = 19$, $N2 = 10$, $P = 0.467$, songs: $U = 86.5$, $N1 = 19$, $N2 = 10$, $P = 1.000$, S2 compared with control: latency: $U = 29$, $N1 = 19$, $N2 = 10$, $P < 0.05$, approach: $U = 50$, $N1 = 19$, $N2 = 10$, $P = 0.182$, calls: $U = 22$, $N1 = 19$, $N2 = 10$, $P < 0.05$, songs: $U = 57$, $N1 = 19$, $N2 = 10$, $P = 0.978$). Finally, a synthetic signal characterized by a simple linear frequency modulation reproducing the natural FM slope triggers the same behavioural responses as the control signal (Figure 5, LS, comparison with control: latency: $U = 92$, $N1 = 19$, $N2 = 11$, $P = 1.000$, approach: $U = 4.5$, $N1 = 19$, $N2 = 11$, $P = 1.000$, calls: $U = 4.5$, $N1 = 19$, $N2 = 11$, $P = 1.000$, songs: $U = 13.5$, $N1 = 19$, $N2 = 11$, $P = 1.000$).

3.2.3. Modifications of song duration and of sound/silence ratio barely impair recognition

Eliminating the first or second half of the song does not significantly modify the behavioural responses compared to those elicited by the control songs, except that birds tested with only the second part of the song do not approach close to the loudspeaker (Figure 5, 1half compared with control: latency: $U = 45$, $N1 = 19$, $N2 = 6$, $P = 1.000$, approach: $U = 55.5$, $N1 = 19$, $N2 = 6$, $P = 1.000$, calls: $U = 40$, $N1 = 19$, $N2 = 6$, $P = 1.000$, songs: $U = 42.5$, $N1 = 19$, $N2 = 6$, $P = 1.000$, 2half compared with control: latency: $U = 45$, $N1 = 19$, $N2 = 6$, $P = 1.000$, approach: $U = 16.5$, $N1 = 19$, $N2 = 6$, $P < 0.05$, calls: $U = 49$, $N1 = 19$, $N2 = 6$, $P = 1.000$, songs: $U = 54$, $N1 = 19$, $N2 = 6$, $P = 1.000$).

When the duration of the notes is divided by two (Figure 5, 1/2not), or when only the first quarter of each note is conserved (Figure 5, 1/4not), the response differs strongly from one bird to another: some individuals may not respond at all and others may respond quite strongly (1/2not compared with control: latency: $U = 57.5$, $N1 = 19$, $N2 = 11$, $P = 0.243$, approach: $U = 58$, $N1 = 19$, $N2 = 11$, $P = 0.203$, calls: $U = 49.5$, $N1 = 19$, $N2 = 11$, $P = 0.088$, songs: $U = 60.5$, $N1 = 19$, $N2 = 11$, $P = 0.663$, 1/4not compared with control: latency: $U = 46$, $N1 = 19$, $N2 = 10$, $P = 0.121$, approach: $U = 47$, $N1 = 19$, $N2 = 10$, $P = 0.106$, calls: $U = 27$, $N1 = 19$, $N2 = 10$, $P < 0.05$, songs: $U = 19.5$, $N1 = 19$, $N2 = 10$, $P < 0.05$). When every other note is deleted, the response is less intense than to the control in terms of latency, calling rate and approach to the loudspeaker, but the singing rate is not significantly different (Figure 5, 1not/2, comparison with control: latency: $U = 2$, $N1 = 19$, $N2 = = 8$, $P < 0.05$, approach: $U = 5.5$, $N1 = 19$, $N2 = 8$, $P < 0.05$, calls: $U = 8$, $N1 = 19$, $N2 = 8$, $P < 0.05$, songs: $U = 33.5$, $N1 = 19$, $N2 = 8$, $P = 0.260$).

When the last three quarters of the song are removed, birds do not respond to playback (Figure 5, 1quar, comparison with control: latency: $U = 0$, $N1 = 19$, $N2 = 6$, $P < 0.05$, approach: $U = 3$, $N1 = 19$, $N2 = 6$, $P < 0.05$, calls: $U = 3$, $N1 = 19$, $N2 = 6$, $P < 0.05$, songs: $U = 9$, $N1 = 19$, $N2 = = 6$, $P < 0.05$). When only the third quartile of the song remains, the singing rate does not differ significantly from the control, whereas the responses in terms of latency, approach and calling rate are very weak compared with the control (Figure 5, 3quar, comparison with control: latency: $U = 6$, $N1 = 19$, $N2 = 6$, $P < 0.05$, approach: $U = 15$, $N1 = 19$, $N2 = = 6$, $P < 0.05$, calls: $U = 7$, $N1 = 19$, $N2 = 6$, $P < 0.05$, songs: $U = 18$, $N1 = 19$, $N2 = 6$, $P = 0.132$).

3.2.4. The absolute frequency range is not an important parameter for species-specific recognition

The behavioural responses to shifted signals do not differ significantly from those elicited by the control song (Figure 5, shift+ compared with control: latency: $U = 67.5$, $N1 = 19$, $N2 = 11$, $P = 0.848$, approach: $U = 83.5$, $N1 = 19$, $N2 = 11$, $P = 1.000$, calls: $U = 97.5$, $N1 = 19$, $N2 = 11$, P = 1.000, songs: $U = 80$, $N1 = 19$, $N2 = 11$, $P = 1.000$, shift- compared with control: latency: $U = 84.5$, $N1 = 19$, $N2 = 12$, $P = 1.000$, approach: $U = 52.5$, $N1 = 19$, $N2 = 12$, $P = 0.053$, calls: $U = 89$, $N1 = 19$, $N2 = 12$, $P = 1.000$, songs: $U = 86$, $N1 = 19$, $N2 = 12$, $P = 1.000$).

4. Discussion

An "unadapted" signal in the constraining environment of tropical forest?

The humid and cluttered environment of the tropical forest imposes significant constraints on the transmission of acoustic signals. To convey information at long range, signals may be expected to emphasize parameters that are maximally transmitted in the habitat in which they are used [50, 51]. In a dense forest, it has been hypothesized that degradation could be minimized by concentrating the signal into a narrow frequency range, and by the use of low frequencies, slow frequency modulations and slow temporal structures [24]. In contrast to these predictions, WBW song contains a rapid succession of short notes distributed over a wide frequency range, about half of them being high-pitched (5 to 8 kHz). Since these features are the opposite of those optimized for transmission through a forest habitat, the song of WBW should be particularly susceptible to degradation. Indeed, our propagation experiments show that the signal is strongly modified at a relatively close range. After a transmission distance of only 25m, examination of the propagated sound envelopes reveals significant changes in the amplitude modulation and inter-note pauses that are filled by "tails" of energy. This blurring of amplitude and the elongation of song elements by a tail are mainly due to the reverberations generated by the dense vegetation. The propagated spectra and sonagrams also indicate that higher frequencies, corresponding to the first half part of the song, progressively disappear as the distance increases. This attenuation of high frequencies is principally due to the obstacles (trunks, stems and leaves) and to the high humidity, both these factors engendering a selective frequency filtering. After travelling 100m through this habitat, the WBW song is degraded into a continuous sound at a low, slowly decreasing frequency with duration much shorter than the original emitted signal.

Our propagation experiments indicate also that the song is better transmitted from a high perch (6m) than from one at ground level. This phenomenon does not seem to be due to a "ground effect", a term used by Embleton [52] to describe the attenuation of frequencies below 1 kHz close to the ground. The low frequency notes of WBW song are well above this frequency range. More probably, the increased attenuation of WBW song from low, as opposed to high perches, is linked to the fact that, in the rainforest, the ground level is more obstructed by dense vegetation than the 6m layer.

A robust parameter to encode acoustic species-specific identity.

Playback experiments show that the species-specific recognition process of the WBW relies on the slope of the overall frequency modulation. Indeed, this recognition process is effective with a synthetic signal consisting of a simple linear frequency modulation reproducing the natural FM slope. In this experimental signal, the sound is continuous and uninterrupted by the silent intervals that separate the notes of normal song. Modifying the slope impairs the territorial response of the tested birds. Conversely, as long as the slope of the continuous FM signal matches that of a WBW song, it is equally effective as the normal song in eliciting a territorial response. Thus, the elimination of amplitude modulation or of intra-note frequency modulations does not impair species-specific recognition and the tested birds respond strongly to these experimental signals. Another interesting fact is that, if birds are tested with an experimental song in which the duration of the original notes is reduced, some birds respond strongly whereas some others do not respond at all. It seems that we face here a problem of sound perception rather than a problem of information decoding. Indeed, when reducing the note duration and consequently increasing the interval between notes, this leads to a poorer signal-to-noise ratio of the whole song. The signal becomes more sensitive to sound degradation during propagation and its "active space" is diminished. The density of the vegetation between the loudspeaker and the tested bird varied somewhat between different playback tests. In some cases, where the forest was particularly thick, it is possible that the tested birds were unable to hear the duration- reduced notes and/or to locate the sound source.

What is the perceptual basis for recognition of the FM slope? Some experiments may provide information about this process. First, when alternate notes were eliminated, birds never respond to playback, whereas signals with half of each note suppressed still elicit a territorial response. It appears then that birds need to hear sound elements at regular time intervals to perceive the slope information: when too many notes are eliminated, the remaining ones may be perceived as isolated sounds rather than forming downward sweep. If the intervals are too long - which may be the case in the signal with one note out of two - the recognition process is impaired. At the opposite extreme, if these intervals do not exist - as with the continuous FM slope signal - the recognition remains. A minimal duration of the signal appears also as an important factor for the recognition process. A half-song (either the first part or the second part of the song) still elicits a territorial response. Conversely, when only the first quartile of the song remains, birds do not respond to playback. If only the third quartile remains, some tested birds may respond. Maybe this difference between the first quartile and the third one is due to the fact that when only the high-pitched notes remain, the song is less likely to be clearly audible. It is still the case that such shortened signals are obviously less effective than the control. At last, it can be pointed out that the signals that are upward or downward-shifted in frequency but that kept the natural decreasing FM slope, still elicit a territorial response.

To summarize, the species-specific recognition in the WBW relies on the perception of a slowly decreasing FM slope, a constant characteristic of the song of this species. The succession of notes at regular time intervals supports the perceptual process of FM slope recognition.

"Signal structure" versus "information decoding" hypotheses.

Due to its acoustic characteristics, the song of the WBW is strongly modified during its propagation through the dense vegetation of the tropical forest. The "signal structure" hypothesis, which predicts that the active space of songs is optimised by an environment-adapted acoustic structure, is thus not supported here. Indeed, severe propagation-induced modifications such as amplitude fluctuations, frequency blurring, tails of echoes and disappearance of high-pitched notes due to frequency-dependent attenuations impair the reliability of song propagation in this species. In spite of this strong constraint, the species-specific recognition process nevertheless remains effective at a long range (about 100 m). The receiving bird fully exploits the remaining part of the propagated signal. As a result, a simple song that continuously decreases in frequency, and is even greatly shortened, is sufficient to support species-specific recognition. The "unadapted" structure of the emitted signal is thus compensated for by an adaptive decoding process at the receiver level.

The use of a song perch to emit and/or to receive sound signals provides an additional means of improving the efficiency of communication [6, 38, 41, 53]. Our propagation experiments show that, for any distance, perching at 6 m high results in less propagation-induced degradation in this habitat.

Besides species-specific recognition, territorial songs may bring other information of interest to potential receivers. Since selection presumably works on a variety of different kinds of information including species recognition, mate attraction, range determination etc, the resulting song may be some kind of balance that meets all of these needs. For example, in the context of territorial signalling, the localization of the emitter is crucial. A number of previous studies have shown that birds are able to estimate their distance from the emitter by relying on propagation-sensitive acoustic cues, a process called "ranging" [54, 55]. To be useful, these cues must vary predictably with transmission distance. The structure of the WBW song may be well adapted for ranging since, due to its frequency-dependent attenuation, the number of notes reaching the receiver is proportional to the transmission distance and may constitute a reliable distance cue for a receiving bird. Indeed, the results obtained with the playback experiments suggest that the absence of the high-pitched part of the song, such as it occurs when the emitter is relatively far away, results in a weaker territorial response, especially in terms of approaching the sound source. This idea needs further research to assess the effectiveness of ranging in this species and to determine the acoustic cues actually used in the ranging process.

To conclude, our results do not support the expectation that the structure of communication signals is always finely tuned to the physical constraints of the environment, despite the fact that tropical species are supposed to be highly adapted to a narrow ecological niche. What we have shown here, however, is that a vital function such as species-specific recognition may be effectively fulfilled by a coding-decoding process that fully exploits the information remaining in the portion of the signal that is most resistant to degradation.

Acknowledgement

This study is dedicated to the late Jacques Vielliard who introduced the authors to the white-browed warbler's life. Financial and logistic supports were provided by the BIOTA-FAPESP program and FMB/FUNCAMP fund in Brazil and the CNRS in France. Special thanks to Danilo Boscolo, Jean-Paul Metzger and Alexandre Uezu for their help.

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