Perceptual relevance of species-specific differences in acoustic signal structure in *Streptopelia* doves

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Acoustic signal characteristics that differ strongly between vocalizations of closely related species need not necessarily be the perceptually most important ones. In the dove genus *Streptopelia*, temporal parameters have been identified as the most distinctive species-specific differences between perch-coo vocalizations. Using synthetic coo model stimuli and an operant design, we tested the perceptual relevance of species-specific differences in temporal structure and amplitude modulation structure for two partly sympatric species, *S. decaocto* and *S. chinensis*. The majority of birds used both parameters to classify sound stimuli, although overall, amplitude modulation structure appeared somewhat more important. In an additional experiment, we tested the same birds to examine whether they predominantly used the first element in the classification of coo model stimuli. Our results show that the characteristics of the full signal, rather than the first element, determine classification.

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Sympatric bird species often use dissimilar vocal signals, even when they are closely related and phenotypically similar. One explanation for this is that misidentification of conspecific signals because of confusion with those of closely related species can reduce the fitness of both sender and receiver. Such mistakes are a driving force for divergence of vocal signals, facilitating species discrimination. As Miller (1982) has pointed out, a scenario like this is likely to have most effect on long-range, unlearned sound signals, in particular when these are used in mate attraction and territorial advertisement.

Differentiation in acoustic signal structure can involve multiple parameters, the nature and magnitude of which will reflect constraints and biases in the mechanisms of signal production (sender) as well as signal perception (receiver). Although statistical techniques can be used to identify which parameters contribute most to species differences in signal structure, they do not reveal the role these parameters play in species discrimination. A parameter contributing considerably to the description of the difference in signal structure need not necessarily be equally important for the perception of signal differences. Psychophysical experiments have shown that proportionally identical changes in separate sound parameters may differ greatly in their perceptual salience. Birds, for instance, are about 10 times more sensitive to changes in

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frequency than in duration (Dooling 1982). The integration of results from acoustic analysis and psychophysical studies, however, does not suffice to analyse which differences in various parameters between two acoustic signals are perceptually the most relevant ones. Differences in detection thresholds are usually measured in experiments using simple, arbitrary acoustic stimuli, such as short pure tones. For this reason, such experiments allow no direct conclusion about how a difference in one dimension of a more complex acoustic signal, for example in temporal structure, compares in perceptual salience to another dimension, for example frequency. Furthermore, the fact that a receiver can detect specific differences between sounds in a psychophysical experiment does not necessarily mean that it uses such differences to classify the sounds. To gain more insight into how animals perceive acoustic parameters in complex sounds such as vocalizations, we can use various psychoacoustic methods. Indeed a variety of studies have used such methods, ranging from the use of naturally occurring behavioural responses in amphibians (e.g. Gerhardt 1991; Simmons & Bean 2000) and insects (e.g. Wyttenbach et al. 1996), to operant techniques in, for example, monkeys (e.g. LePrell & Moody 1997; Sinnott & Saporita 2000), songbirds (e.g. Gentner & Hulse 2000), nonsongbirds (e.g. Dooling et al. 1987a, b) and humans (Iverson & Kuhl 1995).

We used a psychoacoustic, operant technique to examine whether the prime parameter that characterizes the difference in vocalizations between related species is also the perceptually most salient one. The model system we
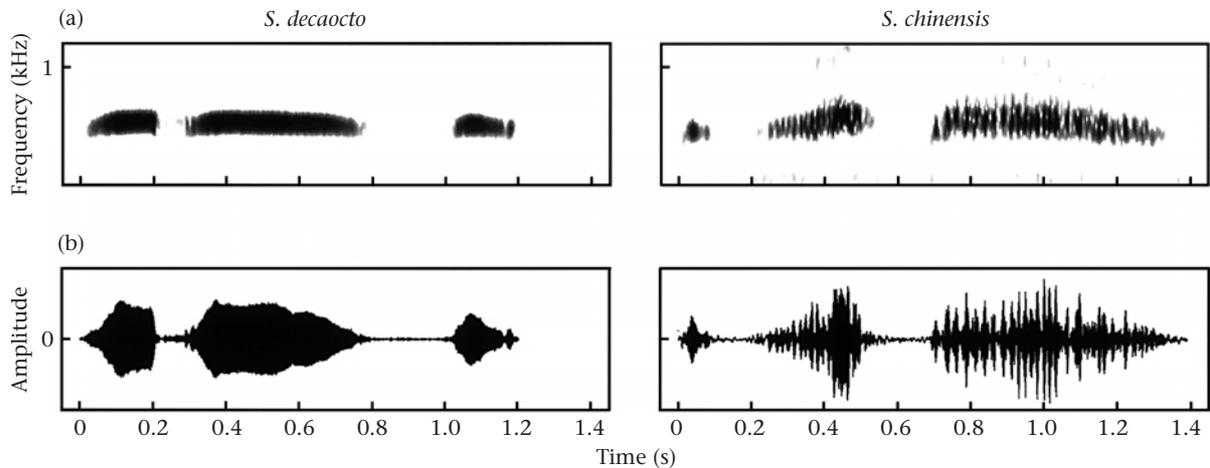
Figure 1. Perch coos of *S. decaocto* and *S. chinensis*. (a) Spectrograms (calculated with a Short Time Fourier Transform, Hamming window, time resolution 15 ms, frequency resolution 87 Hz, dynamic range 25 dB) and (b) oscillograms.

used concerns the relative importance of two features that *Streptopelia* doves (turtle-doves) may use to distinguish their own perch-coo vocalizations from those of other species in the same genus, namely temporal structure and amplitude modulation structure. The genus *Streptopelia* consists of 17 species (K. P. Johnson, S. de Kort, K. Dinwoodey, A. Mateman, C. ten Cate, C. Lessells and D. H. Clayton, unpublished data), some of which look very similar, and almost all of which live in sympatry with other congeneric species. Each species produces its species-specific perch-coo (Slabbekoorn et al. 1999), which is a relatively simple, unlearned, long-range signal, used in male–male conflict and female attraction (Goodwin 1983).

Temporal and amplitude modulation parameters vary conspicuously between these perch-coos, and playback experiments in the field have shown that territorial males of various *Streptopelia* species differentiate between conspecific and allospecific perch-coos (de Kort & ten Cate 2001). An earlier study (Slabbekoorn et al. 1999) showed temporal structure to be the most distinctive feature differing between *Streptopelia* perch-coos. It has also been shown that *Streptopelia decaocto* is sensitive to the rhythm of perch-coos (Slabbekoorn & ten Cate 1999). This may suggest that selection has operated on temporal parameters in particular and that these parameters are the most important ones for species discrimination. On the other hand, psychophysical studies suggest that differences in sound duration have to be relatively large in order to be noticed. So it can also be argued that species differences in this dimension are caused by evolutionary 'drift', which has occurred because the parameter is not perceptually relevant. The other feature, amplitude modulation structure, also differs between *Streptopelia* species, but not all species can be identified on this characteristic alone. Seven species produce perch-coos with cyclic amplitude modulation, which gives rise to a trill quality, at least to the human ear. Such vocalizations sound distinctly different from the perch-coos of the other species in the genus that lack cyclic amplitude modulation. However, the perceptual salience of this feature is unknown.

We compared the perceptual salience of interspecific differences in temporal and amplitude modulation structure. We created two synthetic sounds differing only in these parameters. These sounds resembled the species-specific perch-coos of two *Streptopelia* species, *S. decaocto* and *S. chinensis*. These species are sympatric in part of their geographical range (Baptista 1997) and their perch-coos differ mainly in temporal structure and amplitude modulation structure (Fig. 1). We trained birds of both species to discriminate between the sound stimuli, with a Go/No-go design (Hulse 1995). In such a design, a bird is trained to respond differentially to, and thus classify, different complex acoustic stimuli. By presenting hybrid probe sounds, varying one parameter at the time, we can examine which parameters the animal uses to make the classification (Weary 1990). This set-up allows precise control over the nature and degree to which parameters differ between the two signals. We can also measure differences in response strength, expressed as differences in number of operant responses, between species. We predicted that if species differences in temporal aspects of the perch-coo structure were due to selection on temporal structure, then this should also show up as the main parameter used for classification in our experiments. If, however, evolutionary 'drift' caused differentiation in temporal structure, then we do not expect this parameter to be perceptually important. In this case, the amplitude modulation structure is expected to be the perceptually most salient one and used as a basis for classification of coo model stimuli in our experiments.

Different parts of a song can have different perceptual relevance (e.g. Johnsrude et al. 1994). For *S. decaocto*, field studies (Slabbekoorn & ten Cate 1999) showed that the first element of the three-element perch-coo is the most important one in eliciting territorial responses. Without it, playback stimuli did not evoke a significant response, whereas stimuli lacking the second or third element elicited normal responses. We carried out an additional

experiment to test whether *Streptopelia* doves also classify coo model stimuli predominantly on the first element.

METHODS

Subjects

We used four adult *S. decaocto* (Eurasian collared doves; female number 45 and males number 15, 31, 47) and four adult *S. chinensis* (spotted doves; males number 138, 139, 152, 154) as subjects. The *S. decaocto* doves were originally captured from the wild in the Netherlands, and had been kept in our laboratory for more than 2 years. The *S. chinensis* doves originated from the wild in Indonesia, and had been kept for 1.5 years in our laboratory after we obtained them from a bird dealer in the Netherlands. All of the birds were naïve to operant experimental procedures. In spite of extensive training, two of the subjects, *S. chinensis* 152 and 154, did not acquire the operant task (see Results). Therefore, these birds could not be used for experimental tests.

On nonexperimental days the animals were housed in individual cages (80 × 60 cm and 60 cm high) in a room (maintained at ca. 22 °C) containing other *Streptopelia* doves. Illumination was provided by high-frequency fluorescent lights, and the light:dark cycle was always 12:12 h. The diet of both species consisted of commercially available dry seed mix for turtle-doves, which was available ad libitum on nonexperimental days. On experimental days the same food was used as reinforcer. As subjects could initiate trials whenever they were motivated to do so, they could regulate their food supply according to their own needs. Every day we monitored the amount of food each bird had eaten, and, if necessary, a supplementary quantity was given. The birds were weighed twice a week. None of the birds showed weight loss below 90% of their free-feeding weight. After the experiments were completed, all subjects remained in our laboratory for other behavioural studies. We obtained permission for this study from the Animal Experiments Committee of Leiden University.

Operant Test Cages

We used four identical operant test cages, each placed in a separate sound-attenuating chamber, for shaping, training and testing procedures. The test cages (60 × 50 cm and 60 cm high) were built of an open wooden frame, the top and three sides of which were covered with wire mesh. The fourth side was of plywood and held the control panel. On the top side, the control panel held a loudspeaker from which sound stimuli were presented. In the centre, two microswitch keys (diameter 1 cm) with built-in, red light-emitting diodes (LEDs) were placed 16 cm apart. The left key functioned as the 'observation key', and the right as the 'report key'. In between the keys a food dispenser was mounted. Keys and food dispenser were accessible to the bird via a perch. Illumination was provided by a high-frequency fluorescent light on top of the cage. We could observe the birds through one-way glass windows in the doors of the sound-attenuating chambers.

Each operant test cage was controlled by a small, custom-built computer device that was developed at the workshop of our institute. This device can be set up to function as a stand-alone machine, but we used it as an interface between the operant test cage and a personal computer. This allowed for faster and easier programming of more complex procedures. The device was also used to digitally store and play back sound stimuli.

Stimuli

For baseline discrimination training, we designed two artificial sound stimuli, Train A and Train B (Fig. 2), which were modelled after the natural perch-coo vocalizations of *S. decaocto* and *S. chinensis* (Fig. 1), respectively. We constructed the sounds in such a way that they differed only in the two most important differences of the natural signals. The first difference concerned temporal structure. Both stimuli had three sound elements separated by two silent intervals, but the length of these structures, and thus the rhythm of the sounds, differed. The second difference concerned amplitude modulation structure. Train A had no amplitude modulation, while Train B was amplitude modulated. For details of sound parameters see Fig. 2. Signals were created digitally (10 kilosamples/s) with GoldWave software (version 4, GoldWave Inc., St. John's, Newfoundland, Canada). Although our training stimuli were simplified versions of their natural counterparts and sounded artificial to human observers, the values chosen for temporal, amplitude modulation and frequency parameters fall within their natural ranges (Slabbekoorn et al. 1999).

Test sounds (Probes C, D, E and F) consisted of different combinations of the parameters of Train A and Train B (see Fig. 2).

Digital signals were transferred to the playback device with a 2821 Data Translation D/A board and a Frequency Devices 900 anti-imaging filter. The device subsequently resampled (26.8 kilosamples/s) the analogue signal by using its OKI MSM6388 sound processor. During the experiments, sound stimuli were generated by the same sound processor, which has a built-in filter to prevent imaging effects, and a Blaupunkt CB 4500 loudspeaker. All stimuli were matched for average sound level, which was 70 dB (A) SPL at the point where the bird's head was during tests (as measured by a Cel-231 sound level meter, time weighting 125 ms).

Baseline Discrimination Training Procedure

To train birds to discriminate between the training stimuli Train A and Train B we used a Go/No-go procedure, in which they learned to peck a key in response to one stimulus and to withhold pecking in response to the other (Hulse 1995).

Initially, the birds were autoshaped to peck the lit observation key for the presentation of a Go-stimulus,
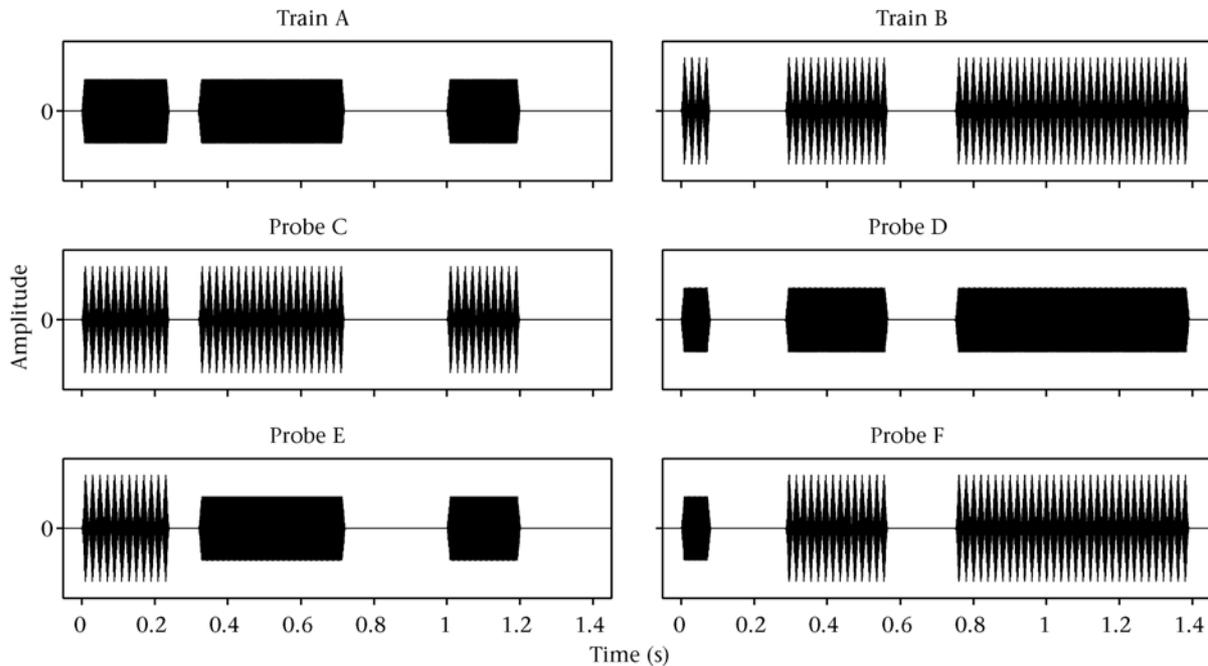
Figure 2. Oscillograms of sound stimuli. Train A and Train B were used for discrimination training, Probes C and D for tests in experiment 1, and Probes E and F for tests in experiment 2. If E_i designates the ith sound element and I_i the ith silent interval of a stimulus, then the temporal structure of Train A, Probe C and Probe E is E_1 240 ms, I_1 80 ms, E_2 400 ms, I_2 280 ms, E_3 200 ms, and that of Train B, Probe D and Probe F E_1 80 ms, I_1 200 ms, E_2 280 ms, I_2 180 ms, E_3 640 ms. Amplitude-modulated sound elements were created with a symmetric triangular modulating signal with a period of 20 ms. The carrier signal of all stimuli was a 600 Hz pure tone (sine wave), and all elements had linear rise and fall times of 15 ms.

which was immediately followed by a food reward. In the next stage they had to peck the lit observation key to get a Go-stimulus, and when this sound had finished they had to peck the lit report key to get the food reward. When they performed this task well, key lights were gradually dimmed and finally turned off to prevent the LED light from overshadowing the auditory stimulus (Cynx & Clark 1998).

After the shaping stage had finished, we started base-line discrimination training. A peck on the observation key initiated a trial with the random (without replacement) presentation of either a Go-stimulus or a No-go-stimulus ($P=0.5$). Pecks at the report key in response to a Go-stimulus resulted in 3 s of access to food, and pecks in response to a No-go-stimulus resulted in 20 s 'time-out', during which the cage light was turned off. Pecks at either key during the presentation of a stimulus had no effect. If no peck on the report key had occurred within 2 s after the stimulus had finished, the trial ended and the bird could initiate a new trial by pecking the observation key. The assignment of Train A or Train B as Go-stimulus or No-go-stimulus was counterbalanced across birds of both species. However, the two *S. chinensis* that could not be trained to perform their complete operant task were in the same group. Therefore, counterbalancing was no longer possible for this species.

Training took place for 5 consecutive days a week, during which the birds remained in their operant test cages. Data of trials were collected every 24 h, and we defined each day as a separate 'session'. For the remaining 2 resting days the birds were transferred to their home cage.

When the birds reached a level of 75% correct responses, reinforcement of trials was reduced to a random 90%, that is 10% of the correct responses were not followed by a reward and 10% of the incorrect responses were not followed by a punishment. We considered birds ready for testing if their discrimination level under this regime was 75% or more correct in three consecutive sessions.

Experiment 1: Use of Temporal and Amplitude Modulation Structure

Our objective in the first experiment was to determine which of the two acoustic features that differed between Train A and Train B, that is, temporal structure and amplitude modulation structure, the birds used for classification. Test sessions were the same as training sessions, except that the proportion of unreinforced training trials was reduced to a random 5%, while in the remaining 5% Probe C or Probe D ($P=0.5$) was given instead of the baseline training stimuli. Probe trials were never reinforced. Probe C had the temporal structure of Train A and the amplitude modulation structure of Train B, while Probe D had the temporal structure of Train B and the amplitude modulation structure of Train A (Fig. 2). By comparing the frequencies of Go-response of the probes to that of the training stimuli, we deduced which sound

parameters the bird used. We finished a test when both probe stimuli had been given at least 50 times.

Experiment 2: Importance of First Element

After the birds had completed experiment 1, we used them for a second experiment. Our objective was to determine if the stimuli's first element alone had caused the pattern of probe classification obtained in experiment 1, or if the second and third elements also played a role. The procedure was the same as in experiment 1, except that instead of Probes C and D we used Probes E and F as test stimuli. The first elements of Probes E and F were identical to those of Probes C and D, respectively, while the second and third elements were identical to those of Trains A and B, respectively (Fig. 2). If the birds used only the first element to classify probe stimuli, then we expected their Go-response to Probes E and F of experiment 2 to be the same as their Go-response to Probes C and D of experiment 1, respectively.

Although all sound stimuli had been matched for root-mean-square sound pressure, we wanted to rule out the possibility that potential differences in perceived loudness had played a role in the discrimination of Trains A and B. Therefore, all birds underwent a post hoc test in which louder and softer versions of the training stimuli were used as probes (135 and 65% of root-mean-square sound pressure). If the birds generalized these probes to their corresponding training sounds, we concluded that sound level cues had not been important in the classification of stimuli.

Statistical Analysis

For each bird we pooled the data from all sessions within an experiment, to obtain the Go and No-go responses/stimulus. To assess which responses were significantly different from each other ($P<0.05$), we applied a simultaneous test procedure (STP) based on G tests of independence (Sokal & Rohlf 1995). This procedure identifies homogeneous subsets in a heterogeneous set of frequency data. On the basis of the outcome of the STP tests we assessed the relative importance of the acoustic parameters in discrimination of the training stimuli for each bird qualitatively.

RESULTS

Baseline Discrimination Training Procedure

Six of the eight subjects passed the criterion of 75% correct discrimination of the training stimuli Train A and Train B. The number of trials needed to acquire the criterion varied: 10250, 7215, 4748 and 6862 trials for *S. decaocto* 15, 31, 45, and 47, respectively, and 18308 and 7505 trials for *S. chinensis* 138 and 139, respectively. We failed to train the remaining two birds to perform their operant task: *S. chinensis* 152 did not get past the shaping stage (despite 20 weeks of training), whereas *S. chinensis* 154 did but failed to attain the criterion of 75% correct

baseline discrimination (we stopped the procedure after 50 000 trials).

The post hoc test for potential influences of loudness in discrimination training showed that loudness was not an important cue in classifying stimuli for any of the birds. Go-response ratios of probes were never significantly different from those of their corresponding training sounds.

Experiment 1: Use of Temporal and Amplitude Modulation Parameters

For each bird, Fig. 3 shows the ratios of Go-response to each stimulus, and homogeneous subsets of stimuli as identified by the STP tests, that is, which stimuli do not have significantly different Go-responses.

From these data, we assessed which parameters each bird used to classify the probe stimuli, as follows. (1) If the data consisted of two homogeneous sets, each consisting of a probe and a training sound, as in dove 31 (Fig. 3, experiment 1), then this shows that the parameter type that differed between the two stimuli of a set had not been important for the dove in differentiating Train A from Train B. Therefore *S. decaocto* 31 used amplitude modulation structure, but not temporal structure. (2) If either one or both probes were not in a set with a training stimulus, then the bird used both parameters for classification. Therefore dove 45 (Fig. 3, experiment 1) used both amplitude modulation structure and temporal structure. This must necessarily be true because if only one of two parameters had been used, the probes would be perceptually equivalent to the training stimuli and they would consequently not be in different sets from the training stimuli. The relative importance of the parameters in this case was found as follows. (1) If the probes were together in a set without a training sound, as in doves 45, 47 and 139 (Fig. 3, experiment 1), then both parameters were considered equally important. (2) If the probes were not in a set with each other, but at least one of them was not in a set with a training sound either, as in dove 138 (Fig. 3, experiment 1), or if they were both in a set but one of them was also in a set with a training sound, as in dove 15 (Fig. 3, experiment 1), then the relative importance of the two was found by looking at the relative position of the probes with respect to the training sounds.

The data show that five out of six birds used both parameters to classify the probe sounds. However, the birds varied in the relative weight of each parameter. None of the birds used temporal structure exclusively. One *S. chinensis* (138) gave more weight to temporal structure, but also used amplitude modulation structure. Three birds (*S. decaocto* 45 and 47 and *S. chinensis* 139) used both features, and did not give one feature significantly more weight than the other. One of these (*S. decaocto* 47), however, was close to giving amplitude modulation significantly more weight ($P=0.08$). For *S. decaocto* 15 this difference is significant, so it used amplitude modulation, and to a lesser extent also temporal structure. One *S. decaocto* (31) exclusively used amplitude modulation.

Experiment 1   Experiment 2
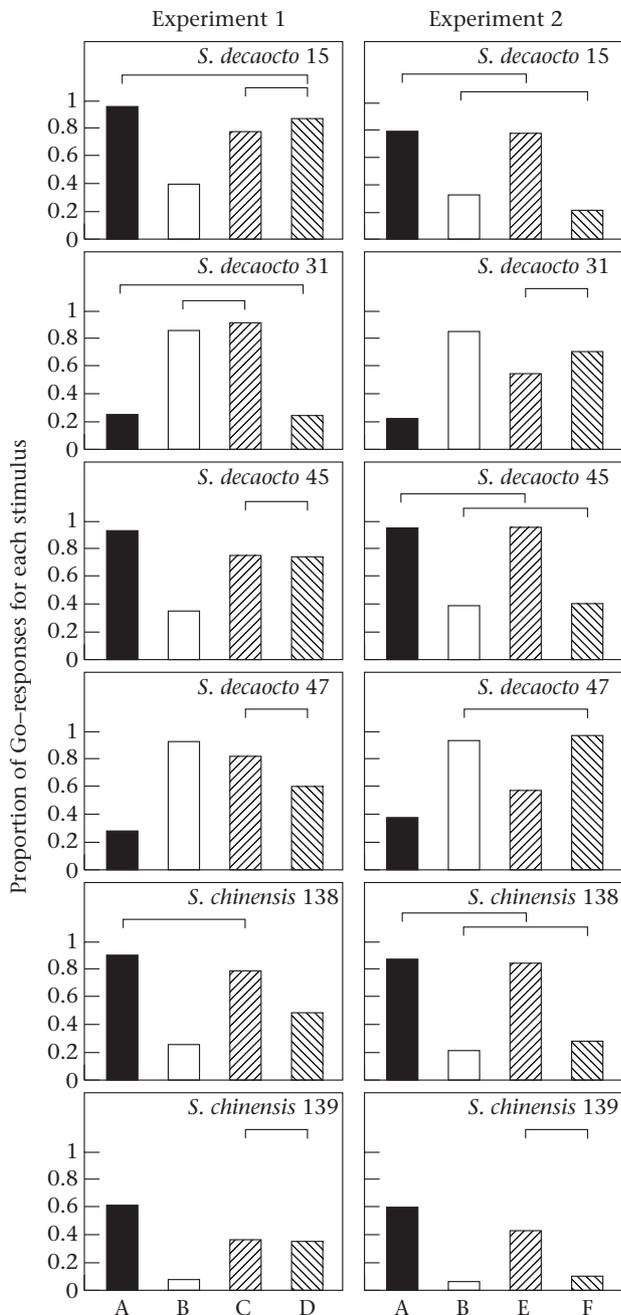
Figure 3. Classification patterns obtained in experiments 1 and 2. Letters beneath the bars correspond to the different stimuli (see Fig. 2). Horizontal brackets indicate which sound stimuli do not have significantly different Go-responses (P<0.05).

Experiment 2: Importance of First Element

Figure 3 shows the ratios of Go-response to the stimuli of experiment 2, and the homogeneous subsets of stimuli as identified by the STP tests. Overall, most birds tended to classify Probes E and F with those training sounds with which they shared most features, that is Probe E with Train A and Probe F with Train B. Only in two birds (*S. decaocto* 31 and 47) was there a noticeable effect of difference between the first element of the probes and training stimuli. This is a first indication that

classification is not based on features of the first element. Conclusive evidence, however, is provided by comparing the classification patterns with those found in experiment 1. If the subject had used the first element alone to classify the probe stimuli of experiment 1, then the Go-responses to Probes E and F would have to be the same as those to Probes C and D, respectively, since they would be perceptually equivalent. In fact, however, none of the subjects retained the classification pattern from experiment 1 to experiment 2. There was only one instance in which the change of probes between the experiments did not lead to a different classification: the responses of *S. chinensis* 138 to Probes C and E are both not significantly different from that to Train A. The same bird, however, did classify Probes D and F in a different way, indicating that it attended to the second and third elements.

DISCUSSION

In experiment 1 we tested which acoustic features *S. decaocto* and *S. chinensis* use when they have to classify coo model stimuli that differ in two parameters only: temporal structure and amplitude modulation structure. One dove used amplitude modulation structure only. The other five used both features, but varied in the relative weights they attributed to temporal structure and amplitude modulation structure. The results show first that the *Streptopelia* species tested not only detected differences in the two parameters that constitute the most important species differences in their natural perch-coo vocalizations, but also used them in combination as a basis for sound classification. Second, the perceptual relevance of these parameters varied considerably between individuals, even within a species. This indicates that the relative contribution of temporal and amplitude modulation features to the classification process is not a fixed characteristic of individuals. Although the number of birds tested is too low to draw firm conclusions about interspecific differences, our data do show that potential species differences in perceptual relevance of the parameters tested are not discrete, that is there is overlap between the species in this characteristic.

In experiment 2 we tested whether the first element of a stimulus played a decisive role in the perceptual classification of coo model stimuli. Earlier studies suggested that for *S. decaocto* the first element of their perch-coo is the most important one in eliciting territorial responses in nature (Slabbekoorn & ten Cate 1999). Our results show that attributing more weight to this part of the acoustic signal is not inherent to the working of perceptual classification mechanisms, as none of the birds predominantly used the first element to classify probe stimuli.

The average number of trials needed to reach baseline discrimination was 9148. Cynx (1995) trained domesticated pigeons, *Columba livia,* in on average 5250 trials for an auditory Go/No-go discrimination task. Slower discrimination training in our experiments could be due to a number of reasons. One is that the species tested are less tractable than those more typically used in

psychoacoustic experiments. Also, our birds originated from the wild and were not hand reared. However, we tried to avoid possible adverse effects related to tractability by leaving the birds undisturbed in their operant cage for 5 days in a row during tests. In addition, all birds had been kept in our laboratory for more than 1.5 years prior to the experiments, and had adapted well to living in a cage. Another possibility explaining slow discrimination learning could be that the training stimuli are very difficult to discern for the subjects. However, this seems unlikely in our case. The differences in duration of elements and pauses of Train A and Train B are much greater than the known thresholds for this parameter in birds (Dooling 1982) and from our results it is clear that the differences in amplitude modulation structure are at least as salient as those in temporal structure. We think that the most likely explanation for slower discrimination training in our experiments is that this is inherent to the species used. Zebra finches, *Taeniopygia guttata*, trained by Cynx (1995) using the same experimental design and stimuli as for the pigeons, needed on average only 2250 trials. This shows that the number of trials needed very much depends on the species being trained.

To what extent can we relate our findings to vocal recognition in a natural context? We used synthetic sound models, which differ from natural perch-coo vocalizations in a number of aspects. A similar operant design with natural signals can address a number of interesting questions but it cannot reveal with certainty to which features of the vocalizations birds are listening (Dooling et al. 1992). For our purpose, we are necessarily restricted to a design with synthetic stimuli of which specific properties are manipulated while others are held constant. The use of sound models is justified as long as the information left out is unimportant for the question of interest. In our case, we reduced the set of varying parameters of natural coos by leaving out frequency modulation and components of amplitude structure that do not contribute to the trill quality. Both features are unlikely be important when *S. decaocto* and *S. chinensis* have to discriminate their own species' perch-coo from those of congeners. Their perch-coos show little frequency modulation (Fig. 1), and the frequency modulation that is present does not differ much between the species. Components of amplitude structure other than the one tested are not likely to be important for recognition in nature either, since they are aperiodic, slowly changing and relatively small, and therefore sensitive to unpredictable change through environmental influences, especially in such low-frequency, pure-tone signals (Michelsen 1983). Temporal structure and amplitude modulation structure are probably also relevant features for the *Streptopelia* species not tested in our study, as these parameters constitute the main species differences in the genus. Other parameters that could be used are pitch and timbre. In general, however, both are likely to be of secondary importance because the majority of species (including the ones tested here) overlap in the carrier frequency they use, and produce relatively pure-tone vocalizations. So the two parameters we selected are

likely to be important for perceptual classification in the wild.

The acoustic feature that has been identified as the most distinctive species difference between perch-coos in the *Streptopelia* genus, that is, temporal structure (Slabbekoorn & ten Cate 1999), appears not to be the perceptually most relevant one, although the majority of our birds used it. Limitations in how sound production mechanisms can change may constrain the evolution of amplitude modulation parameters more than that of temporal parameters in turtle-doves. Nevertheless, amplitude-modulated vocalizations do occur throughout the *Streptopelia* genus: seven of the 17 species have amplitude-modulated perch-coos (Slabbekoorn et al. 1999), while some of the remaining species produce other coo types that are amplitude modulated. Furthermore, potential species differences in the characteristics of amplitude modulation patterns, for example modulation rate and shape, have not yet been studied, but could play a role in species recognition or other signal functions. So perhaps amplitude modulation features in bird vocalizations have not received enough attention in comparative analyses as a feature contributing to interspecific differences. Lack of attention to amplitude modulation in acoustic analysis and its implications have been discussed recently for budgerigar, *Melopsittacus undulatus*, calls (Banta Lavanex 1999).

Overall, we can conclude from our results that temporal structure, as suggested on the basis of acoustic and statistical analyses, is a factor that sympatric turtle-doves are likely to use for species discrimination in nature. The fact that another parameter, amplitude modulation, appears to be even more salient in perceptual classification illustrates that both signal variation and receiver sensitivity need to be studied to understand the importance of acoustic signal variability.

Acknowledgments

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