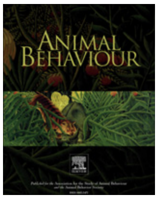
Animal Behaviour 78 (2009) 1301–1307

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



A behavioural mechanism explaining noise-dependent frequency use in urban birdsong

Wouter Halfwerk*, Hans Slabbekoorn

Institute of Biology, Leiden University

ARTICLE INFO

Article history:
Received 18 May 2009
Initial acceptance 2 July 2009
Final acceptance 10 September 2009
Available online 14 October 2009
MS. number: 09-00329

Keywords:
acoustic adaptation
ambient noise
behavioural flexibility
frequency-dependent masking
great tit
Parus major

Acoustic signals are usually very effective in long-distance communication. However, in many habitats animals suffer more and more from signal interference caused by traffic-generated low-frequency noise. Recent observations suggest that birds are able to change the pitch of their song to reduce masking interference, but we still lack experimental evidence. Theoretically, some bird species, when confronted with increased noise levels, may be able to switch to song types in their repertoire with higher frequencies. We tested this hypothesis in the great tit, *Parus major*, by exposing singing males to low-frequency 'city' noise in their natural territories and comparing frequency characteristics of songs before and after song type switching. We also exposed birds to high-frequency, 'inverse' city noise, as well as to white noise as a control. Great tits adjusted temporal switching behaviour in response to noise exposure. Song types that were less masked by the noise treatment were sung for longer durations. As a result, all five birds that switched during the low-frequency noise treatment switched to song types with a higher minimum frequency. Similarly, seven of nine birds that switched while exposed to high-frequency noise switched to song types with lower maximum frequencies. These results provide experimental evidence for a short-term behavioural mechanism explaining noise-dependent frequency use in birdsong.

Many animals use acoustic signals to transmit biologically relevant information. However, their habitats can be noisy because of biotic and abiotic sounds, which can interfere with signal detection and limit the range over which mates can be attracted or territories defended (Klump 1996; Warren et al. 2006). As a consequence, noise-dependent selection on effective signal transfer may have had an evolutionary impact on the acoustic design of animal vocalizations (Morton 1975; Wiley & Richards 1978; Ryan & Brenowitz 1985). Urban areas, but also many natural habitats, are increasingly dominated by the evolutionarily novel selection pressure of anthropogenic noise (Slabbekoorn & Ripmeester 2008). Traffic-generated low-frequency sounds in particular have become a likely selection pressure that many animals have to cope with to avoid signal interference (Slabbekoorn & Peet 2003; Pohl et al., in press).

In general, animals can use different strategies to deal with unfavourable noise conditions (reviewed in Brumm & Slabbekoorn 2005). Information transfer from sender to receiver depends ultimately on the signal-to-noise ratio at the receiver's end (Klump 1996; Warren et al. 2006). A common strategy by which senders may cope with unfavourable noise conditions concerns an upregulation of signal amplitude in response to elevated noise levels as reported for birds and mammals (Potash 1972; Manabe et al. 1998). Senders may also respond to noisier conditions by increasing signal duration or signalling rate, as reported for birds, frogs and mammals (Brumm et al. 2004; Penna et al. 2005; Leonard & Horn 2008), or by timing their signals to avoid temporal overlap (Brumm & Slabbekoorn 2005). Another more recently discovered strategy is a change of frequency structure of an animal's vocalizations to reduce spectral overlap between signal and noise, which has been repeatedly shown in singing birds (Slabbekoorn & Peet 2003; Brumm & Slabbekoorn 2005; Wood & Yezerinac 2006) and possibly in marine mammals (Rendell et al. 1999).

Noise-dependent frequency use in birdsong can be a short-term or long-term adjustment. It may concern genetic or ontogenetic change, immediate signalling flexibility, or a combination of these (Patricelli & Blickley 2006). An exclusively genetic explanation seems unlikely for noise-associated acoustic variation within populations (Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). An ontogenetic explanation may account for some of the variation in bird species that develop adult song through experience and learning. For instance, a young bird arriving in a noisy territory may copy those songs from its neighbour(s) that are least affected by masking, and retain those songs in its repertoire that are effective under the local noise conditions (Slabbekoorn & den Boer-Visser

---

* Correspondence: W. Halfwerk, Behavioural Biology, Institute of Biology, Leiden University, Sylviusweg 72, 2333 BE Leiden, The Netherlands.

E-mail address: w.halfwerk@biology.leidenuniv.nl (W. Halfwerk).

0003-3472/$38.00 © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2009.09.015

2006). However, another explanation for noise-dependent acoustic variation could be a short-term flexibility through an immediate feedback mechanism. This explanation does not necessarily exclude the previous two, but could potentially be responsible for noise-associated patterns found both within (Slabbekoorn & Peet 2003; Wood & Yezerinac 2006) and between populations (Slabbekoorn & den Boer-Visser 2006).

To understand the behavioural mechanism underlying noise-dependent frequency use, we need to know how a spectral change in song comes about. Spectral shift of the whole song in response to noise has not been reported, but a shift in spectral energy distribution towards higher frequencies was, for example, found for song sparrows, *Melospiza melodia* (Wood & Yezerinac 2006) and European blackbirds, *Turdus merula* (Ripmeester et al., in press). The latter species also revealed temporal variation in the proportion of high and low song components, such that the overall spectral distribution was shifted upwards for birds from noisy urban areas compared to those of more quiet forests (Ripmeester et al., in press). Birds could also change the acoustic design of their songs by incorporating more narrow-banded elements which have lower detection thresholds in the presence of a noise masker (Pohl et al., in press). However, the most obvious candidate for a mechanism of short-term flexibility seems to be song type selection (Slabbekoorn & den Boer-Visser 2006). Birds may respond to rising levels of low-frequency noise by singing higher-pitched song types.

Great tits, *Parus major*, provide a suitable model system to investigate whether and how song type selection may be underlying noise-dependent frequency use (Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006). Individual great tit males have a small repertoire of up to nine song types and the frequency characteristics of song types within an individual's repertoire can vary considerably (Franco & Slabbekoorn 2009). Furthermore, great tits sing with eventual variety, repeating the same song type for several minutes before switching to a new song type. Such singing style may provide an individual with ample signal feedback to decide when and to what song type to switch. Great tits adjust switching behaviour during social interactions by selecting song types to match songs of neighbours (McGregor & Krebs 1989), and are known to use song types not recently sung in response to unfamiliar songs (Franco & Slabbekoorn 2009). It is currently unknown whether they are also able to adjust their song type use under varying noise conditions based on frequency-dependent masking.

We tested whether masking by experimental noise affected song type switching behaviour in great tits. We exposed singing males to artificial city-like low-frequency noise in their natural territories and compared frequency characteristics of songs before and after switching. We also exposed birds to high-frequency noise, which had an inverse energy distribution relative to the 'city' noise, and to white noise as a control exposure stimulus. This allowed explicit testing for upward and downward shifts related to masking avoidance. We predicted that birds would switch to songs with a higher minimum frequency in response to 'city' noise, whereas they would switch to songs with a lower maximum frequency in response to the high-frequency 'inverse' noise. In terms of temporal adjustments, we had no a priori expectations about treatment-dependent variation.

METHODS

Study Species and Area

Great tit songs typically consist of one to four different notes (defined as a continuous sound trace on a spectrogram) grouped together in a stereotypical pattern called a phrase. The same phrase is delivered in series called strophes of about 3 s followed by a 2 s break. Strophes are sung in bouts of several minutes after which birds can stop singing or switch to singing strophes of a different phrase. Great tits have a small repertoire of two to nine distinct phrase patterns which are also referred to as song types and these song types can be identified readily on a spectrogram (McGregor & Krebs 1982; Lambrechts & Dhondt 1986). Song frequency use in great tits ranges from around 2.5 to 8.0 kHz and song types can differ by about 1 kHz in frequency characteristics both within and between subjects (see e.g. Fig. 1). In a population-wide survey by Slabbekoorn & Peet (2003) individuals showed differences in average minimum song frequency use of as much as 0.9 kHz, while habitat-dependent differences in song frequency use can be over 0.3 kHz at the population level (Slabbekoorn & den Boer-Visser 2006).

Experiments were carried out before sunrise (0400–0600 hours) from the end of March to early May 2008 in the suburban area of Utrecht Overvecht, The Netherlands (52°07N, 5°06E). Great tits in our study area started singing relatively early, 2 h before sunrise, possibly as a result of artificial light levels (Bergen & Abs 1997). Singing activity remained high until sunrise, providing a convenient time window to perform our experiments. We mapped the distribution of territories in March and we recorded several singing male great tits before sunrise to determine normal switching rate. These birds switched on average every 4 min to a new song type.

Noise Exposure Experiments

We exposed singing great tits to a noise treatment using one of three different stimuli: low-frequency city-like noise ('City' noise), an inverse version of 'City' noise ('Inverse' noise) and white noise ('White' noise). The experiment started when the focal bird

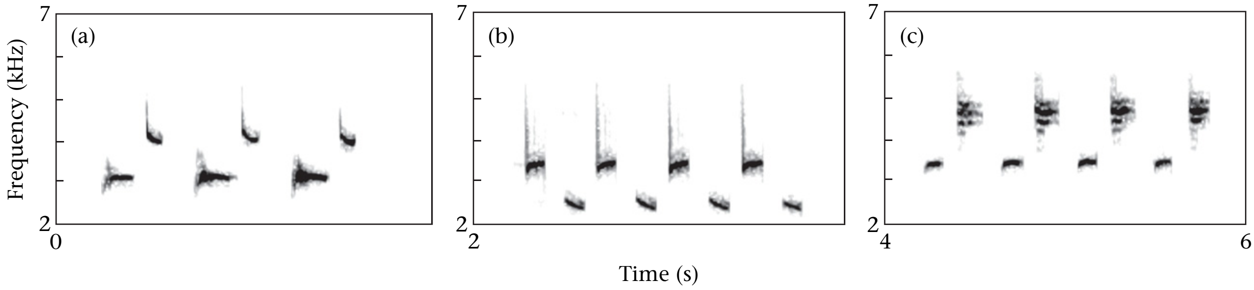


Figure 1. (a, b, c) Three great tit song type examples from our study population showing variation in peak frequency of the low-notes and high-notes. The song types in these examples consist of two notes and are delivered in series called 'strophes'. Song type frequency characteristics can vary discretely both within and between individuals. (b, c) Song types B and C are recorded from the same individual and switching between these song types results in a low-note frequency change of 1.2 kHz.