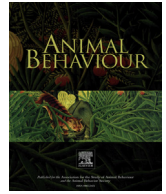




Contents lists available at ScienceDirect

Animal Behaviour

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

Special Issue: Mechanisms & Function

The auditory template hypothesis: a review and comparative perspective

Jill Soha*

Department of Biology, Duke University, Durham, NC, U.S.A.

ARTICLE INFO

Article history:

Received 24 March 2016
 Initial acceptance 20 June 2016
 Final acceptance 4 August 2016
 Available online xxx
 MS. number: SI-16-00260

Keywords:

auditory template
 birdsong
 innate template
 latent template
 preactive template
 song learning

Studies of vocal development in the white-crowned sparrow, *Zonotrichia leucophrys*, and other songbirds led to Peter Marler's formulation of the auditory template hypothesis. According to this hypothesis, young songbirds possess an auditory template system that serves three functions in song learning: to focus attention on appropriate song models during the sensitive period, to facilitate memorization of these models, and later, to guide motor development of song during the sensorimotor phase. Marler postulated two types of innate templates: latent templates that require activation by external input, and preactive templates that do not. Here, I review experiments that examined the specifications of these templates in the white-crowned sparrow and suggest that this system also serves a fourth function, acting to shape the final repertoire at the end of song development. I then discuss the template system in a comparative context, first reviewing the influence of results from several species on the derivation of the auditory template hypothesis and then describing variation in several aspects of auditory templates across species. Finally, I address ways in which the template model can continue to be informative in the comparative study of song learning.

© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

In the context of birdsong learning, an auditory template is a representation of song, encoded in a bird's brain, that guides song development. These representations and how they act in song learning are studied from both behavioural and neurobiological angles (Adret, 2008). Here I focus on the behavioural perspective (for reviews on song template neurobiology, see: Bolhuis & Moorman, 2015; Mooney, 2009).

Auditory templates in avian vocal development were a recurring theme in the work of Peter Marler, and a good starting point for understanding the concept is his classic monograph on song learning in the white-crowned sparrow, *Zonotrichia leucophrys* (Marler, 1970). In that study, Marler examined the effects on song development of several manipulations of the acoustic environment experienced by young males. First, by raising birds without any exposure to tutor songs, he found that male white-crowned sparrows hearing no songs during development produce abnormal, simplified songs. Second, by tutoring at different time periods in development, Marler found that young white-crowned sparrows must hear songs between about 10 and 50 days of age in order to imitate them. Third, by tutoring with both conspecific and

heterospecific song during that age range, he found that males selectively imitate conspecific song.

Based on these results along with earlier findings by others (described later in this review), Marler included a statement of the auditory template hypothesis in his monograph (Marler, 1970). This statement can be summarized as follows. Prior to song memorization, a young bird possesses a crude auditory specification of species-specific song. This crude template guides song development if a bird is raised in isolation; otherwise, it acts as a filter to focus attention on the songs of conspecific adults. As the young bird hears conspecific adult song during the sensitive phase, the template is modified and becomes more precise (i.e. it comes to represent the memorized song models). Finally, when the young bird himself later begins to sing, his vocalizations will be matched to this template. In other words, during motor rehearsal, the template is the internal representation of song to which the bird compares his own vocalizations.

According to the model just described, one template operates throughout a bird's development. It begins as a crude specification, is refined as songs are heard, and finally serves as the representation to which the bird matches his own song. Thus, over the course of development, the template serves three functions: to focus attention on conspecific songs, to facilitate the memorization of those songs and to guide motor development of the bird's own song.

* Correspondence: J. Soha, Department of Biology, Duke University, Box 90338, Durham, NC 27708, U.S.A.

E-mail address: jill.soha@duke.edu.

Subsequently, Marler refined the hypothesis to include two types of templates that, together, serve these same three functions. He initially called these *active* and *latent* templates (Marler, 1984), and later replaced *active* with *preactive* (Marler, 1997; Marler & Nelson, 1992), which I will use here. A preactive template does not require external input before it can influence song development. In other words, it is active even before the young bird hears any song models. If a bird hears no song during the critical period, then the preactive template alone guides motor development. A latent template, in contrast, must be activated by exposure to particular sounds before it can affect song development. In normal song development, preactive and latent templates together influence the final template that guides song motor development (Marler, 1984).

In earlier work, Konishi (1965a)—who was the first to use the term ‘template’ in the context of song learning and whose findings were crucial to Marler’s hypothesis—distinguished between innate templates, which are genetically inherited, and acquired templates, which are learned. Readers might be tempted to equate preactive templates with innate ones and latent templates with acquired ones. This is incorrect, however: both preactive and latent templates are innate. A latent template includes innate specifications for what types of sounds will activate it, and as I will illustrate below, these innate specifications can be different from those of the preactive template. Both of these innate templates normally facilitate song memorization and thus underlie the acquired (learned) template. However, as I will also illustrate below, the acquired template is not strictly limited by the specifications of the preactive and latent templates.

PREACTIVE AND LATENT TEMPLATES IN WHITE-CROWNED SPARROWS

According to Marler’s (1984) refined model, in a songbird raised without exposure to tutor songs, the preactive template alone guides song development. In the white-crowned sparrow, the resulting ‘isolate’ songs differ from normal wild-type songs in a clear way. Whereas normal white-crowned sparrow songs begin with one or two pure-tone whistles and end with two to four other phrase types (Fig. 1a), isolate songs in this species typically contain only whistles (Fig. 1b). Given that isolate songs reflect the specifications of the preactive template, this means that in white-crowned

sparrows the preactive template specifies whistles. In addition, most isolate songs in this species are segmented into more than one whistle. In the rare instance when a nonwhistle phrase is included, it occurs at the end of the song (Fig. 1b). This indicates that the preactive template also specifies basic aspects of normal song syntax, or song segmentation and phrase sequencing.

What about the latent template in this species? Marler based the idea of preactive and latent templates on the observation that some species-universal song features are present in isolate song and some are not (i.e. some features remain latent if a bird hears no tutor songs). In the white-crowned sparrow, universal features of normal song that are absent from isolate song include the multiple nonwhistle phrase types. These can be categorized as buzzes, note complexes and trills (Fig. 1a). The sequence and structural details of these phrases vary across subspecies, dialects and individuals, but as a group they represent a universal feature of normal white-crowned sparrow song that a young male fails to develop without exposure to song models. Therefore, according to Marler’s hypothesis, the learning of these phrases requires activation of the latent template.

Studies of early song recognition in the white-crowned sparrow provide evidence for a latent template that is activated by nonwhistle phrases. In playback tests, Nelson and Marler (1993) found that upon their first exposure to song during the sensitive period, fledgling white-crowned sparrows give more chirp calls in response to conspecific song than to heterospecific song. Whaling, Solis, Doupe, Soha, and Marler (1997) then examined how the different phrase types of white-crowned sparrow song contribute to this early response bias. Fledglings presented with normal white-crowned sparrow song as well as synthetic songs containing one white-crowned sparrow phrase type each (a whistle, a buzz or a trill, repeated to form a song of normal length) and song sparrow, *Melospiza melodia*, song responded equally strongly to normal white-crowned sparrow song and to each of the phrase types presented individually. Only song sparrow song elicited a significantly weaker response than did normal (whole) white-crowned sparrow song (see Figs. 1 and 2 in Whaling et al., 1997). Thus, upon their first exposure to song after the beginning of the sensitive period, young white-crowned sparrows preferentially respond to each of the conspecific phrase types, not just whistles.

In another experiment, Soha and Marler (2001a) presented fledgling white-crowned sparrows with conspecific and

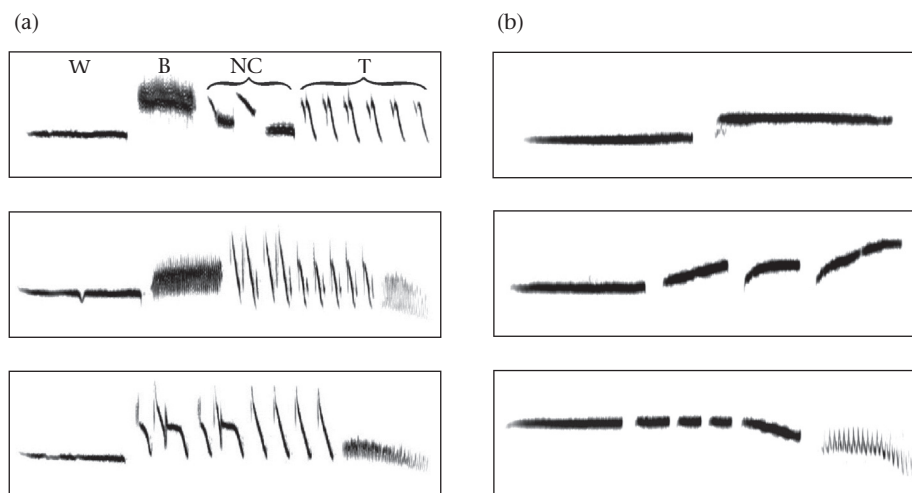


Figure 1. Examples of white-crowned sparrow songs. (a) Three normal songs, recorded from wild birds, with phrase types labelled in the top panel. W: whistle, B: buzz, NC: note complex, T: trill. (b) Three isolate songs, recorded from birds raised in the laboratory without exposure to tutor songs. Each spectrogram image covers a frequency range of 1–8 kHz and a duration of 2 s.

Download English Version:

<https://daneshyari.com/en/article/5538647>

Download Persian Version:

<https://daneshyari.com/article/5538647>

[Daneshyari.com](https://daneshyari.com)