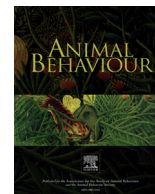




Contents lists available at ScienceDirect

Animal Behaviour

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

Special Issue: Cognition & Language

Rules, rhythm and grouping: auditory pattern perception by birds

Carel ten Cate^{a, *}, Michelle Spierings^{a, b}^a Institute of Biology Leiden, Leiden University, Leiden, The Netherlands^b Department of Cognitive Biology, Vienna University, Vienna, Austria

ARTICLE INFO

Article history:

Received 17 August 2018
 Initial acceptance 17 September 2018
 Final acceptance 7 November 2018
 Available online xxx
 MS. number: SI-18-00589

Keywords:

acoustic perception
 auditory grouping
 bird
 budgerigar
 cognition
 language
 musicality
 rhythm
 rule learning
 zebra finch

Both language and music are universal and characteristic for humans. The evolution of the cognitive abilities underlying language and music are widely debated. A core question is whether these abilities find their origins in a modification or extension of general cognitive abilities for processing auditory input also present in other species. If so, comparative studies of nonhuman animals should reveal similarities in processing abilities. In this paper, we review some examples of such studies. We focus on whether birds (in particular zebra finches, *Taeniopygia guttata*, and budgerigars, *Melopsittacus undulates*) can detect structural patterns based on relational rather than on physical similarities among auditory stimuli – an essential ability for processing and producing language and music. We briefly discuss why birds are suitable model species. Next, we discuss three domains of pattern detection: the ability to (1) detect 'grammatical rules' underlying sound strings; (2) perceive regular rhythms and (3) spontaneously group separate sounds into a larger pattern. In all of these there is evidence that birds show some ability to detect relational patterns. However, there is also variation between species: while budgerigars show relational rule learning, zebra finches attend to local physical similarities between sound strings used for training and testing. For rhythm detection, zebra finches and budgerigars show no clear differences. However, a broader comparison indicates that here too differences are present in the extent to which different bird species attend to relational patterns or to local features. Finally, spontaneous grouping of sounds was shown in zebra finches. The clear variation among bird species in their perceptual and cognitive abilities, in combination with their accessibility for experimental studies, provides opportunities to study the variation in auditory processing mechanisms and how these evolved. This may also provide hypotheses for the evolution of these abilities in humans.

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The use of language and the ability to produce and appreciate music is universal and distinctive for humans. The nature and evolution of the cognitive mechanisms underlying these abilities are topics of extensive debates. For language, the debate centres around the question of the origins of grammatical abilities. One view is that these abilities arose as a consequence of the sudden and relatively recent emergence in modern humans of an ability to process complex, in particular recursive, linguistic structures (e.g. [Berwick & Chomsky, 2016](#)). The other is that they originated from a more gradual evolution in which complex linguistic rule-learning mechanisms arose from domain general learning and sequence-processing mechanisms, supported by cultural evolution (e.g. [Christiansen & Chater, 2015](#); [Tomasello, 2003](#)). For musical abilities,

some favour the hypothesis that they arose as an epiphenomenon of other cognitive traits, for instance those needed for language (e.g. [Pinker, 1997](#)). Others favour adaptive explanations for the evolution of musicality (e.g. [Mithen, 2005](#)), or suggest that musical abilities may be based on perceptual or cognitive traits that evolved to deal with auditory stimuli more generally, such as an ability for auditory stream analysis ([Honing, 2018](#); [Honing, ten Cate, Peretz, & Trehub, 2015](#); [Trainor, 2015](#)). If language and musicality find their origins in a modification or extension of already existing and broadly shared general cognitive abilities for processing auditory input, it might be expected that comparative studies of nonhuman animals can reveal similarities to humans in processing abilities. In this paper, we review some examples of studies that examined such auditory processing mechanisms. In doing so, we particularly focus on the abilities of birds to detect higher-order or abstract patterns, i.e. to detect patterns based on *relational* rather than on *physical* similarities among auditory stimuli. After a brief introduction why we study birds to address the question of shared cognitive abilities, we

* Correspondence: C. ten Cate, Institute of Biology Leiden, Leiden University, P.O. Box 9505, 2300 RA Leiden, The Netherlands.

E-mail address: c.j.ten.cate@biology.leidenuniv.nl (C. ten Cate).

<https://doi.org/10.1016/j.anbehav.2018.11.010>

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Please cite this article in press as: ten Cate, C., & Spierings, M., Rules, rhythm and grouping: auditory pattern perception by birds, *Animal Behaviour* (2018), <https://doi.org/10.1016/j.anbehav.2018.11.010>

discuss three domains of pattern detection: the ability to (1) detect 'grammatical rules' underlying sound strings, (2) perceive rhythm and (3) spontaneously perceive grouping patterns in auditory strings.

BIRDS AS MODELS

Birds and humans find themselves in very different branches of the evolutionary bush, with a shared reptile-like common ancestor as far back as over 300 Ma ago. At first sight, this evolutionary distance makes birds unlikely models for comparative studies searching for the presence of human-like auditory processing mechanisms. However, despite their divergence, birds and mammals show many similarities in their cognitive abilities (e.g. ten Cate & Healy, 2017), with several bird species being on par with primates (e.g. Emery & Clayton, 2004). And, as already noted by Darwin (1871), bird sounds, in particular the songs of songbirds, show complexities in structure reminiscent of spoken language and have musical qualities that are uncommon among mammals. Also, unlike nonhuman primate species, several groups of birds, most prominently songbirds and parrots, show vocal production learning, i.e. the ability to modify auditory output based upon specific types of auditory input. The above features suggest a convergent evolution of at least some properties of acoustic processing between humans and some bird groups. But however skilled birds may be in learning, structuring and processing their species specific vocalizations, the skills involved might be specialized domain-specific ones. They need not reflect, or be based upon, general cognitive abilities to detect arbitrary and abstract auditory patterns, such as those that can be found in language and music. In this paper we review several experiments that aim to assess the presence of these more general cognitive abilities for pattern detection in birds. Such studies may not only shed light on the cognitive abilities of birds themselves, but can also provide hypotheses on what might have been the cognitive propensities that ultimately provided the human lineage with language and musical abilities.

RULE LEARNING

Every human language is characterized by, among others, a set of rules that determine which and how sounds can be combined to form words and how words can be combined to produce correct and meaningful sentences. Such rules allow us, for instance, to understand that an English sentence like 'John loves Mary' means something else than 'Mary loves John'. We interpret the first sentence as John being the one in love, with Mary being the object of his affection, while this is reversed in the second sentence. This is because English, like several other languages, is a so-called SVO (subject-verb-object) language. We acquire such grammatical rules in general not by explicit instruction, but implicitly, by being exposed to sentences that follow such rules. We next apply these rules to understand sentences never heard before. The question of whether animals are capable of detecting grammatical rules has been addressed for a range of species using the 'artificial grammar learning' paradigm (Petkov & ten Cate, 2018; ten Cate & Okanoya, 2012). In artificial grammar-learning experiments, human adults, infants or animals are exposed to strings of meaningless auditory or visual items arranged according to a particular underlying algorithm, the 'rule'. This exposure can be passive, by just playing or showing example strings, or include some sort of discrimination training in which subjects have to discriminate example strings based on different rules. After such exposure or training, a test consists of presenting novel test strings based on the known or a novel rule. The response to the test strings reveals whether and

what the humans or animals learnt from the strings about the underlying rule.

Studies on birds (ten Cate, 2018) as well as on other animals (reviewed by Petkov & ten Cate, 2018) show that many species are capable of remembering and discriminating auditory or visual strings encountered during training. Several species are capable of generalizing a sequencing pattern beyond training strings to novel strings if these strings consist of items belonging to the same type as the items present in the training strings (e.g. cottontop tamarins, *Saguinus oedipus*: Fitch & Hauser, 2004; rhesus macaques, *Macaca mulatta*: Hauser & Glynn, 2009; European starlings, *Sturnus vulgaris*: Gentner, Fenn, Margoliash, & Nusbaum, 2006; zebra finches, *Taeniopygia guttata*: van Heijningen, de Visser, Zuidema, & ten Cate, 2009; Bengalese finches, *Lonchura striata domestica*: Seki, Suzuki, Osawa, & Okanoya, 2013; pigeons, *Columba livia domestica*, and keas, *Nestor notabilis*: Ravignani, Westphal-Fitch, Aust, Schlumpp, & Fitch, 2015; Stobbe, Westphal-Fitch, Aust, & Fitch, 2012). For instance, both starlings (Gentner et al., 2006) and zebra finches (van Heijningen et al., 2009) can generalize AABB and ABAB sequences, in which A and B stand for two different song motif (starlings) or song element types (zebra finches), to sequences consisting of novel items belonging to A and B types. Starlings can also learn to discriminate AABB and BBAA sequences from ABAB and BABA sequences, in which the As and Bs are thus not linked to specific positions, and generalize this to sequences using novel A and B items (Comins & Gentner, 2014). However impressive such abilities for discriminating and generalizing the trained patterns are, they might be based on the acoustical similarities between familiar and novel strings as the A and B in these experiments refer to specific acoustic types. But grammar rules are not based on auditory similarities but on the relationships between items in a sentence. To demonstrate relational, or second-order, rule-learning abilities, it is necessary to show that the generalization extends to strings consisting of different acoustic categories, e.g. CCDD or DCDC. Whether birds are capable of a generalization based strictly on the relational similarity among items has been addressed in an experiment using both zebra finches and budgerigars, *Melopsittacus undulatus* (Spierings & ten Cate, 2016). Both species are widely used model species for auditory processing in birds. Most of these studies addressed the spectral sensitivities, which have been examined for natural vocalizations (e.g. Dooling, 1986; Dooling, Brown, Klump, & Okanoya, 1992; Sturdy, Phillmore, Price, & Weisman, 1999; Vignal, Mathevon, & Mottin, 2008), artificial sounds (e.g. Burgering, Vroomen, & ten Cate, 2018; Dooling, Leek, Gleich, & Dent, 2002; Lohr & Dooling, 1998; Weisman et al., 1998) and speech sounds (e.g. Burgering, ten Cate, & Vroomen, 2018; Dooling & Brown, 1990; Ohms, Gill, van Heijningen, Beckers, & ten Cate, 2010; Phillmore, Fisk, Falk, & Tsang, 2017). Fewer studies addressed the sensitivity to note sequences in natural (e.g. Braaten, Petzoldt, & Colbath, 2006; James & Sakata, 2017; Lawson, Fishbein, Prior, Ball, & Dooling, 2018) or artificial sequences (e.g. Chen & ten Cate, 2017; Chen, van Rossum, & ten Cate, 2015; van Heijningen et al., 2009; van Heijningen, Chen, van Laatum, van der Hulst, & ten Cate, 2013; Lipkind, et al., 2013).

The experiment on the ability for relational pattern learning in zebra finches and budgerigars (Spierings & ten Cate, 2016) was inspired by a seminal study by Marcus, Vijayan, Rao, and Vishton (1999), which showed that 9-month-old infants exposed to either XYX or XYY strings (X and Y being arbitrary speech syllables, not referring to any specific acoustical categories) could differentiate between strings consisting of novel arbitrary syllables arranged in either the familiar pattern or the other pattern. So, differentiation between the two string types must have been due to detection of the underlying rule, hence based on the relational, and not the acoustical, similarity. In our experiment, both zebra finches and

budgerigars were first trained to discriminate a number of XYX strings from XXY strings consisting of zebra finch song elements, using a Go-NoGo discrimination training. Next they were tested with novel strings, which were either rearrangements of familiar items or consisted of novel element types. These test strings were nonreinforced and mixed among rewarded training trials. Zebra finches responded to the novel strings consisting of rearranged familiar items by the degree to which they matched with specific training strings, i.e. they seem to have remembered the position of the specific elements for each training string and responded to similarities in element identity and position between training and test strings. They showed limited responses to test strings consisting of novel element types and did not differentiate these according to their structure. Budgerigars showed a strikingly different pattern. They discriminated all test strings consisting of rearrangements of familiar items by their structure (XYX or XXY). Nevertheless they hardly responded to test strings consisting of novel element types. However, when the budgerigars were switched, from one day to the next, to a set of XYX and XXY training strings fully consisting of element types never heard before, they responded correctly to the two different patterns from the beginning of the training onwards (ten Cate, 2018; Spierings & ten Cate, 2016). Hence, the budgerigars, but not the zebra finches, can differentiate two sets of stimuli based on their underlying structure.

The budgerigar findings suggest that at least some bird species are capable of classifying auditory strings based on relational rather than physical similarities between the constituent items. Apart from some primate species (e.g. Fagot & Maugard, 2013; Thompson, Oden, & Boysen, 1997), this type of relational learning is also known from a few bird species that were trained in a relational match-to-sample task using visual items. Both hooded crows, *Corvus cornix* (Smirnova, Zorina, Obozova, & Wasserman, 2015), and orange-winged amazon parrots, *Amazona amazonica* (Obozova, Smirnova, Zorina, & Waasserman, 2015) could classify novel pairs of pictures according to whether the two pictures of the pair showed the same relation as the shown sample. For instance, if the sample pair showed pictures of a cross and a circle, the birds classified a pair consisting of a triangle and a square, but not two squares, as being similar to the sample. It remains to be seen which other bird species have such relational learning abilities in either the auditory or the visual domain, but in any case, the ability is clearly present. While the experiments discussed above concern very simple rules compared to most linguistic grammar rules, they do concern the learning of relational rules from experience with example strings. They thus indicate that this ability is not uniquely human nor related to having language, although further experiments are required to examine whether (and which) birds can learn more complicated grammar rules than the finite state XYX-XXY rule mastered by the budgerigars.

RHYTHM DETECTION

Not only language, but also music is characterized by patterns that go beyond a sequence of individual notes. There is increasing evidence that all humans share a predisposition to perceive particular musical features, a propensity that is part of 'musicality', which can be defined as a natural, spontaneously developing set of traits based on and constrained by human cognitive abilities (Honing et al., 2015). Similar to language, here also comparative studies aim to address which of these traits can be found in other species (see Hoeschele, Merchant, Kikuchi, Hattori, & ten Cate, 2015; updated in Hoeschele, Merchant, Kikuchi, Hattori, & ten Cate, 2018, for a review) as one of the ways to get insight in the origins of human musicality (Honing, 2018). As several bird species

show evidence of some kind of musical patterning in their natural vocalizations, e.g. in pitch ratios (e.g. Doolittle & Brumm, 2012; Doolittle, Gingras, Endress, & Fitch, 2014) or rhythmic structures (e.g. Janney et al., 2016; Norton & Scharff, 2016; Roeske, Kelty-Stephen, & Wallot, 2018; Rothenberg, Roeske, Voss, Naguib, & Tchernichovski, 2014; Slabbekoorn & ten Cate, 1999), they are obvious candidates in the search for animal musicality. But the presence of such 'musical' features in natural vocalizations does not imply that nonhuman species are perceiving melodic and rhythmic vocal structures in the same way as we do, or that they are capable of detecting arbitrary melodic or rhythmic patterns in artificial stimuli. One feature of musicality that requires such an ability to detect relational patterns among arbitrary acoustic items concerns the perception of rhythms, such as the beat in music.

The topic of rhythm perception in arbitrary stimuli by animals got sudden attention with the discovery that both Snowball, a sulphur-crested cockatoo, *Cacatua galerita* (Patel, Iversen, & Bergman, 2009a; Patel, Iversen, Bergman, & Schulz, 2009b), and Alex, a grey parrot, *Psittacus erithacus* (Schachner, Brady, Pepperberg, & Hauser, 2009), could synchronize head and body movements with the beat of several popular songs. This synchronization was maintained over tempo changes of these songs (Patel et al., 2009a, 2009b). Initially it was suggested that the rhythmic entrainment shown by the parrots was due to them being vocal learners, with only vocal learners possessing the required neural substrate to use auditory input to produce contingent motor output (Patel et al., 2009a, 2009b). A survey of YouTube movies searching for evidence of animal species that showed behavioural entrainment to music initially seemed to support this hypothesis, as entrainment was only found among species known to be vocal learners (Schachner et al., 2009). However, with the finding of entrainment in a California sea lion, *Zalophus californianus* (Cook, Rouse, Wilson, & Reichmuth, 2013), a species not known to show vocal production learning, this linkage has become less clear (Wilson & Cook, 2016). Also, a closer scrutiny of the species showing entrainment in the study by Schachner et al. (2009) showed that, apart from an Asian elephant, *Elephas maximus*, all other species were parrot species (ten Cate, Spierings, Hubert, & Honing, 2016). Although the list also contained several songbird species, none of these showed entrainment. This raised the question whether parrots are special. For instance, one reason why parrots, but not other birds, might show entrainment is that several parrot species have displays in which more or less rhythmic movements like headbobs occur. So, it could be that other species might also perceive a regular or beat pattern, but lack the ability to express this in their behaviour. This shifts the question why some, but not all, vocal learning species show rhythmic entrainment from the production to the perception of rhythmic patterns.

The entrainment to the beat by Snowball and other parrots suggest a perceptual sensitivity to 'regularity' versus 'irregularity' or 'isochrony' versus 'heterochrony', as the perception of such a pattern is required for showing entrainment. At first sight, the question whether birds or any other animal species can perceive regularity in an auditory pattern of pulses might seem trivial. Habituation experiments have shown that various species habituate more quickly to isochronous pulse series (i.e. pulses separated by a fixed interpulse interval) than to heterochronous pulse series (e.g. laboratory mice, *Mus domesticus*: Herry et al., 2007; zebrafish, *Danio rerio*: Shafei Sabet, Neo, & Slabbekoorn, 2015). However, this may be based on a sensitivity to *absolute* timing, i.e. attending to the precise duration of an interpulse interval and use of the duration of the preceding interval as prediction for the next one, rather than noticing that all interpulse intervals over a series of pulses are of equal duration (see also Benichov, Globerson, & Tchernichovski, 2016). In contrast, perception of isochrony is based on a

sensitivity to *relative* timing; detecting that pulses are regularly spaced over a longer series, independent of any specific duration of the intervals (Geiser, Walker, & Bendor, 2014; Honing & Merchant, 2014). This makes the perception of isochrony also an example of pattern detection based on detecting global, relational similarities among stimuli. One critical test for such a perceptual ability is whether discrimination between an isochronous and a heterochronous string of pulses is maintained over tempo changes. The study of Snowball, showing that he kept synchronizing his behaviour with the musical beat over tempo transformations suggests that he perceived the isochrony. However, the evidence for other bird species, tested in a more systematic way on their abilities to discriminate different pulse patterns and to maintain discrimination over tempo changes, is mixed (reviewed by ten Cate et al., 2016). Pigeons, for instance, could not be trained to discriminate an isochronous series of pulses from a heterochronous series of pulses, and showed only a limited ability to maintain the discrimination between two different pulse patterns over tempo changes (Hagmann & Cook, 2010). They were most likely attending to the absolute intervals between pulses rather than the overall metric or regular structure of the sound strings (Hagmann & Cook, 2010). Starlings (Hulse, Humpal, & Cynx, 1984a, 1984b; Humpal & Cynx, 1984) and jackdaws, *Corvus monedula* (Reinert, 1965) showed more evidence of attending to the overall relative temporal structure of sound strings. These species are both songbirds, which may suggest that songbirds might be better at rhythm detection than nonsongbirds such as the pigeon. However, an experiment in which zebra finches (songbirds) were trained to discriminate an isochronous pulse series from several heterochronous ones showed that they did not maintain this discrimination over tempo changes (van der Aa, Honing, & ten Cate, 2015). Unfortunately, the various experiments are very diverse in their stimuli and methodology and allow no direct comparison between the abilities of a parrot like Snowball and nonparrot species.

Against the above background, we embarked on a study in which zebra finches and budgerigars were trained and tested on the same stimulus set (ten Cate et al., 2016). Using these species also provided the opportunity to see whether the species difference shown in the grammatical rule-learning task described above (Spierings & ten Cate, 2016) would also be present in the domain of rhythm perception. The training set consisted of two strings (Fig. 1a), both consisting of two pulse types – a low-pitched soft one ('unaccented pulse') and a higher-pitched louder one ('beat'). Overall, the interpulse intervals were regular and identical for both strings, but the difference was in the position of the 'beats', which were regularly spaced in one string and irregular in the other. Both zebra finches and budgerigars were capable of discriminating the strings. Next nonrewarded test trials were presented among reinforced training trials. One set of test sounds consisted of a tempo change in which elements as well as the interpulse intervals between them were shortened or lengthened by 25% compared to the training stimuli (Fig. 1b). Overall, the zebra finches failed to discriminate the strings when lengthened, but maintained discrimination when shortened (Fig. 1d).

The budgerigars reduced their responses to the test strings and failed to discriminate the two string types. When the test strings were shortened by 25%, but now by reducing the durations of interpulse intervals only or elements only, both species failed to discriminate, although zebra finches still showed a trend to do so (see ten Cate et al., 2016, for further details on these results and those described below). However, when a 25% tempo change over the full stimulus length was created by either inserting or leaving out one of the unaccented pulses (Fig. 1c), both species maintained the discrimination between the two strings (Fig. 1e). This suggested that both species can cope with tempo changes of the beat pattern,

but only when the 'background' of unaccented pulses and interpulse intervals remain identical to the training strings. This interpretation is also supported by the finding that adding or removing unaccented pulses in between the beats, thus changing the intervals between the neighbouring pulses but leaving the interbeat intervals intact, also resulted in a loss of discrimination (ten Cate et al., 2016). Again, both species behaved similarly in these tests. So, it seems that both species use a combination of local features (unaccented pulses, interpulse interval duration) and more global ones (beat pattern) to respond to rhythmic stimuli. The similarities between zebra finches and budgerigars in this experiment are a clear contrast to the species difference observed in the rule-learning study. So, the ability for relational learning shown in one context is not linked to its presence in another context, suggesting that cognitive abilities in one domain need not be representative of those in others.

What can we conclude from this experiment and earlier ones on rhythm perception in birds in general? On the one hand the different studies suggest at least some degree of regularity perception in various species. On the other hand, the results vary quite a bit among species, with great parrots like Snowball and Alex on one end and pigeons on the other end. However, although the abilities of great parrots to entrain with a musical beat indicate an ability to detect 'rhythm' or 'regularity' as such, experiments on these species comparing the learning about various rhythmic patterns by using stimuli that allow a precise analysis and systematic experimental manipulation of different features that may be of importance to the parrots are still lacking. Also, the methodological differences among the studies of different species limit the comparability of their findings. There is a clear need for testing more species on various patterns to reveal how birds perceive such patterns and what they attend to. Nevertheless, the currently available evidence tentatively suggests a graded scale for the sensitivity to regularity, with no strong divide between vocal learners and nonlearners or between parrots and other bird species.

PERCEPTUAL GROUPING

All the above-mentioned studies concern the detection of relational auditory patterns after having been trained with stimuli that represented such a pattern. However, humans and nonhuman animals can also perceive patterns that require no specific training. A well-known example is perceptual grouping. Humans have a strong tendency to spontaneously group visual or auditory items, based on Gestalt principles such as 'proximity' or 'similarity' of items. Nonhuman animals also show visual grouping biases (e.g. Vallortigara, 2012), but auditory grouping has not received much attention. An example of an auditory-grouping bias in humans is the so-called 'iambic-trochaic law' (ITL). When two sounds alternate, humans generally perceive them as a concatenation of duplets. When the alternation concerns duration, the grouping is generally short-long, i.e. with emphasis on the second sound, a pattern known as an iamb. When the alternation concerns pitch or intensity, they are grouped with the highest or loudest first (i.e. high-low and loud-soft), a pattern known as a trochee. The ITL applies to the perception of different types of sounds, ranging from musical tones to speech (e.g. Hay & Diehl, 2007). In different languages, the speech stream is often characterized by more or less systematic fluctuations in pitch, intensity and duration, which may demarcate meaningful linguistic categories (see Langus, Marchetto, Bion, & Nespor, 2012, for a review). The ITL grouping bias can guide the perception of a speech stream and therefore provides infants with cues about the underlying structure of their language. In line with this, infants tested at 4 months of age

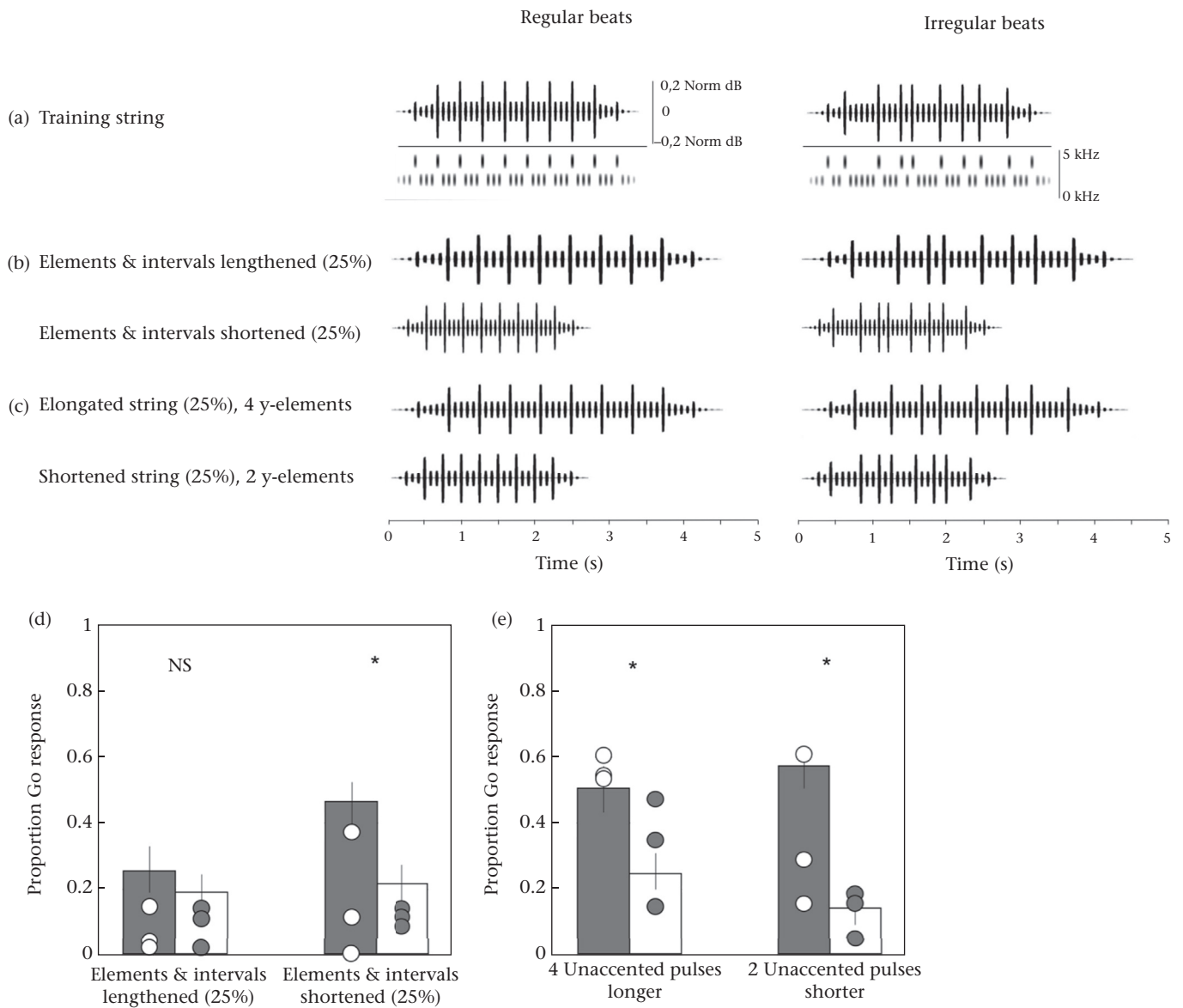


Figure 1. Beat detection by zebra finches and budgerigars (based on ten Cate et al., 2016; see there for a full overview of all tests and results). (a) Amplitude (top) and spectrogram (bottom) of training strings. The regular string was always the Go stimulus and the irregular one was the NoGo stimulus in a discrimination training. (b, c) Nonreinforced test stimuli manipulating the interbeat interval in the indicated way. (d, e) Mean \pm SE proportion of Go responses for six zebra finches to regular (grey bars) and irregular (white bars) test strings in (b) and (c), respectively, and individual data for three budgerigars (grey circles: irregular test strings; white circles: regular test strings). *Indicates significant differences ($P < 0.05$) in the proportion of Go responses by zebra finches to regular and irregular test strings. Budgerigar data were tested at the individual level (results not shown).

already show a sensitivity to the difference between iambic and trochaic stress patterns and develop a preference for the stress pattern of their native language (Friederici, Friedrich, & Christophe, 2007; Weber, Hahne, Friedrich, & Friederici, 2004), and even newborns already show grouping biases (Abboub, Nazzi, & Gervain, 2016). Although infant and adult grouping biases for tones are influenced by the dominant pattern of their native language (e.g. Iversen, Patel, & Ohgushi, 2008), this seems to predominantly affect the perception of variation in duration of tone stimuli as iambs, while the perception of tone stimuli varying in pitch or intensity as trochees seems more universal and independent of the native language (e.g. Molnar, Lallier, & Carreiras, 2014).

The universal human tendency for perceptual grouping of sounds raises the question whether this auditory grouping is also present in nonhuman animals. Few studies addressed this question,

limited to rats and budgerigars. Laboratory rats, *Rattus norvegicus*, showed a trochaic bias for grouping tones varying in pitch, but no grouping tendency for tones varying in duration (de la Mora, Nespore, & Toro, 2013). Also, both rats and budgerigars are able to distinguish two-syllabic words with trochaic stress from words with iambic stress (Hoeschele & Fitch, 2016; Toro & Hoeschele, 2017). However, whether birds show spontaneous grouping biases seemed not to have been explored. We examined this question, again using zebra finches (Spierings, Hubert, & ten Cate, 2017). We used three different types of training sets. Each set consisted of two tones differing in either pitch, amplitude or duration. Each combination of two tones was arranged in two strings of four tones, which were alternating in opposite ways, e.g. low-high-low-high versus high-low-high-low (Fig. 2a). The length and speed of the tones was comparable to that in the natural songs of zebra finches. After a peck on a demand key, one of the strings was played.

Depending on which string it was, the birds had to peck a response key to the left or to the right of the demand key. Surprisingly, the experimental groups trained with the two training strings with alternations in amplitude or duration failed to learn the discrimination (apart from two individual birds; see Spierings et al., 2017), despite the fact that the relative differences between the loud and soft, or the long and short tones were well within the range in which they should be discriminable by the birds. However, the birds trained on the strings with pitch alternations did learn to discriminate the training strings. Next, they were presented with test trials. To examine whether zebra finches had a spontaneous grouping bias, we used test strings that were ambiguous in structure: they consisted of a long series of 26 tones alternating in pitch, with a fade-in and fade-out at the beginning and end of the strings. If the pitch of the tones was the same as, or within the range of, the training tones (but not when outside this range, see Spierings et al., 2017), the ambiguous strings were classified significantly more as having a high-low pattern, i.e. perceived as a string of trochees rather than one consisting of iambs (Fig. 2b), even when the tones they heard were unknown to them. In an additional control test with a single tone repeating (no alternation), the zebra finches

responded equally often with pecking the left or the right response key, showing no bias. So, without being explicitly trained to do so, the zebra finches showed a clear trochaic grouping bias to tones alternating in pitch. In this respect they resemble rats and humans, which both spontaneously show a trochaic grouping of pitch variation (Hay & Diehl, 2007; de la Mora et al., 2013). The absence of an ability in most (but not all) zebra finches to discriminate the training strings with alternations in intensity and duration may indicate that a spontaneous grouping tendency along these dimensions, if present, is much weaker, again similar to rats and humans.

Our finding demonstrates the presence of auditory grouping in a bird species. It should be noticed that the training strings did not necessitate any grouping to discriminate the strings. Given that zebra finches are able to discriminate tones by their absolute frequency (e.g. Weisman et al., 1998), it would have sufficed if they attended simply to the frequency of the first and/or last tone of a training string to classify it. Instead, during training, they apparently developed a higher-order percept, in this case trochaic grouping, of the training strings. Our study should be seen as a first exploration of this topic and studies on other species are required

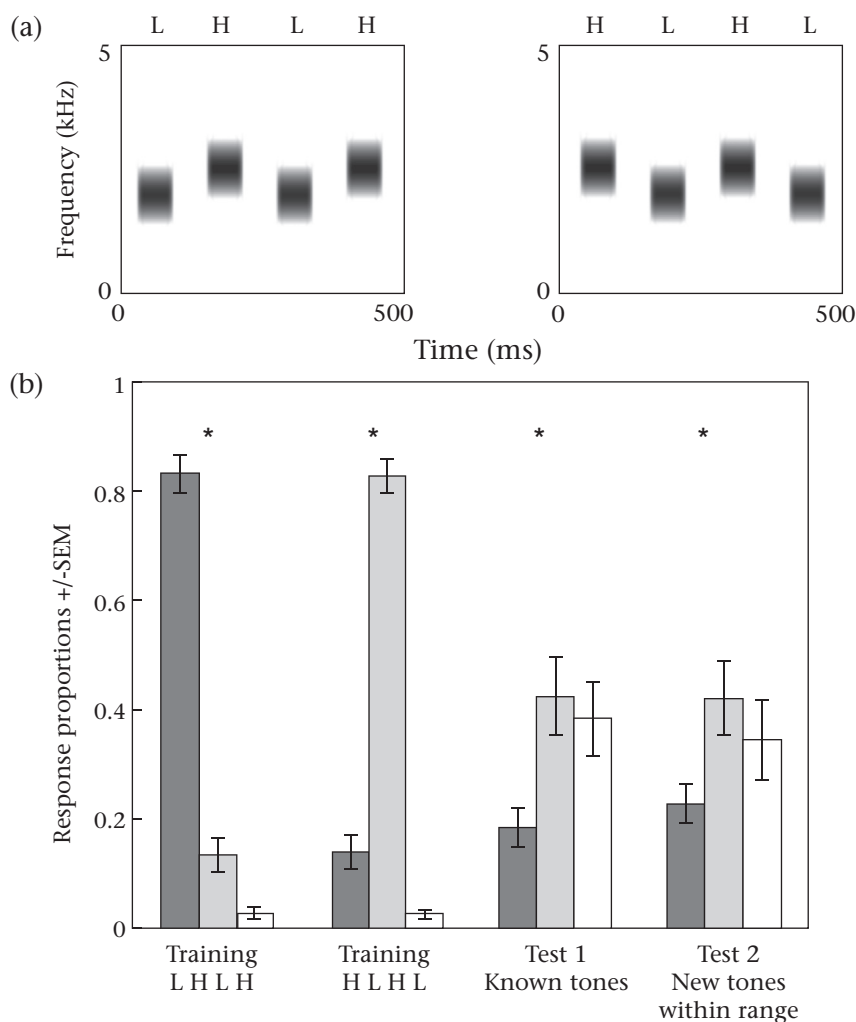


Figure 2. Perceptual grouping by zebra finches (based on Spierings & ten Cate, 2017; see there for a full overview of experiments). (a) Example of training stimuli differing in frequency alternations. L and H indicate low-frequency and high-frequency tones, respectively. During training the birds had to learn to peck one key upon hearing the stimulus on the left and another key upon hearing the stimulus on the right. (b) Mean \pm SE proportion of responses ($N = 8$) to training and test stimuli (test stimuli consisted of ambiguous long strings of L and H tones). Dark grey bars: responses to the key associated with the LHLH training sound; light grey bars: responses to the key associated with HLHL sound; open bars: absence of a response to a test sound. In both test 1 and test 2, zebra finches pecked significantly more on the key associated with the HLHL pattern, indicating a spontaneous trochaic grouping bias for the ambiguous stimuli.

to examine whether the observed patterns – (trochaic) grouping for pitch, no clear grouping for amplitude and duration – are characteristic for birds in general.

GENERAL CONCLUSIONS AND DISCUSSION

We discussed three domains of auditory pattern perception that are linked to linguistic and musical patterns in humans; rule learning, rhythm perception and perceptual grouping. In all of these there is evidence that birds show at least some ability to detect relational or global patterns. However, there is also clear variation between species. While budgerigars showed rule learning based on the relationship between items in a string, the zebra finches attended to auditory similarities between training and test strings, indicating they relied on perceptual learning and generalization rather than on relational learning. For rhythm detection, zebra finches and budgerigars showed no clear differences. However, a broader comparison among bird species indicates that here too species differences are present. Only few species have been examined in detail so far, but whatever evidence is available suggests that the response of birds trained with rhythmic stimuli is the outcome of an interaction between attending to local acoustic similarities between novel and training stimuli, and attending to a more global pattern of regularity. The grouping experiment indicates that despite the fact that zebra finches do not seem to attend much to the relational or global patterns present in the rule-learning and rhythm experiments, they nevertheless do exhibit a spontaneous grouping bias. It may illustrate that, just like the finding that zebra finches and budgerigars differ in the rule-learning task, but not in the beat detection experiments, the ability to detect a more abstract pattern in one domain of auditory complexity need not predict how the species will respond in another domain. Nevertheless, for all domains reviewed in this paper it is clear that there are more questions than answers – they highlight how little we still know about the processing of more complex auditory stimuli in birds and the cognitive mechanisms underlying these. Also, where species differ, we still lack knowledge about whether these differences originate from variations of the same underlying cognitive mechanism or indicate different mechanisms.

The differences in auditory-processing mechanisms between species, might indicate adaptive specializations. But whether these concern specializations related to the perception of species specific vocalizations and their structure or whether they are not linked to any specific communicative function but are a reflection of differences in more basic and general cognitive abilities spanning several domains awaits further investigation. The over 10 000 bird species and the clear variation among species in their perceptual and cognitive abilities, in combination with their accessibility for experimental studies, provide excellent opportunities to examine the variation in auditory-processing mechanisms and the factors that may have driven their evolution. They also allow for the study of whether and to what extent these mechanisms are linked to vocal production learning and vocal variation. For instance, our zebra finch experiments showed that females were better at discriminating various patterns than males (Kriengwatana, Spierings, & ten Cate, 2016), despite the fact that they show no vocal production learning. The variation among bird species also provides an excellent starting point for examining how various traits relate to one another and to socioecological parameters.

Finally, what can our comparative findings tell us about the evolution of linguistic or musical abilities in humans? It is obvious that no bird species matches the human skills for processing linguistic and musical patterns. At the same time, all studies provide evidence that various species show some basic propensities to

process complex auditory strings in ways that go beyond simple generalization. They also indicate graded differences in these propensities. This suggests that advanced processing mechanisms as those shown by humans might be the outcome of a gradual evolution from simpler mechanisms. What exactly these mechanisms might have been, which steps made the auditory-processing mechanisms more complex and what factors constrained or enabled their evolution are questions we cannot answer at present. However, although similarities in the auditory-processing mechanisms present in birds and humans may be based on convergence rather than shared ancestry, our review indicates that the study of birds provides a useful tool to understand what kind of variation there may be among processing mechanisms for detecting patterns in auditory stimuli and how and why these mechanisms evolved and differentiated.

Acknowledgments

This paper is based upon a presentation by C.t.C. at the presidential symposium 'Animal communication, cognition and the evolution of language' of the Animal Behavior Society meeting 2018. We thank William Searcy for the invitation, and we thank him and the referees for their helpful suggestions on our manuscript. The experiments reported here were supported by the Netherlands Organization for Scientific Research (NWO-GW grant 360.70.452).

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