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Territorial raven pairs are sensitive to structural changes in simulated acoustic displays of conspecifics

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Human language involves combining items into meaningful, syntactically structured wholes. The evolutionary origin of syntactic abilities has been investigated by testing pattern perception capacities in nonhuman animals. New World primates can respond spontaneously to structural changes in acoustic sequences and songbirds can learn to discriminate between various patterns in operant tasks. However, there is no conclusive evidence that songbirds respond spontaneously to structural changes in patterns without reinforcement or training. In this study, we tested pattern perception capacities of common ravens, *Corvus corax*, in a habituation–discrimination playback experiment. To enhance stimulus salience, call recordings of male and female ravens were used as acoustic elements, combined to create artificial territorial displays as target patterns. We habituated captive territorial raven pairs to displays following a particular pattern and subsequently exposed them to several test and control playbacks. Subjects spent more time visually orienting towards the loudspeaker in the discrimination phase when they heard structurally novel call combinations, violating the pattern presented during habituation. This demonstrates that songbirds, much like primates, can be sensitive to structural changes in auditory patterns and respond to them spontaneously, without training.

The vocal communication systems of nonhuman animals possess a number of similar features, representing either homologues or analogues of particular attributes of language (Fitch, 2000, 2005; Hauser, 1996; Hurford, 2007). For example, primates and nonprimate mammals produce vocalizations that, like the elements in human speech, can inform a receiver about the production context (Arnold, Pohlner, & Zuberbühler, 2011; Manser, 2001; Seyfarth, Cheney, & Marler, 1980) and the caller-specific features, e.g. identity (Proops, McComb, & Reby, 2009; Townsend, Allen, & Manser, 2012) and/or its body size (Fitch & Fritz, 2006; Reby & McComb, 2003). However, in human language the smallest elements possess little or no contextual denotation by themselves; it is combinations of elements that create meaning. Humans excel at forming and comprehending such combinatorial structures (Schulz, Schmalbach, Brugger, & Witt, 2012). To better understand the evolution of these capacities, multiple experiments on acoustic pattern perception by nonhuman animals have been conducted in the last decade (ten Cate & Okanoya, 2012). Many mammals naturally produce sequences containing different call types (Collier, Bickel, van Schaik, Manser, & Townsend, 2014) and certain primate species combine different calls depending on the current context (Arnold & Zuberbühler, 2006, 2008; Candiotti, Zuberbühler, & Lemasson, 2012; Ouattara, Lemasson, & Zuberbühler, 2009). Sensitivity to structural changes in patterns of acoustic elements has also been studied with primates under laboratory conditions. In two habituation–discrimination studies, cottontop tamarins, *Saguinus oedipus*, and squirrel monkeys, *Saimiri sciureus*, showed spontaneous differential responses to novel arrangements of familiar acoustic elements (Fitch & Hauser, 2004; Ravignani, Sonnweber, Stobbe, & Fitch, 2013). The stimuli consisted of sequences containing human spoken syllables (tamarins) or pure tones (squirrel monkeys) from two different categories. During the habituation phase, monkeys were exposed to sequences of various lengths, following a particular pattern. In the test phase, subjects looked more often at the sound source when they heard structurally novel arrangements of the same elements. Animals' responses

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in these experiments were not reinforced, and were thus mediated only by the novelty of the test stimuli to untrained animals.

A successful operant conditioning study on European starlings, *Sturnus vulgaris*, further suggested that testing with conspecific vocalizations may increase the salience of stimuli and hence improve the animals' performance in artificial grammar learning experiments (Gentner, Fenn, Margoliash, & Nusbaum, 2006). However, for nonhuman primates testing pattern perception with conspecific calls presents major potential problems. To construct a pattern with call recordings, the chosen calls would have to be acoustically diverse to the extent that they could perceptually be assigned to at least two distinct categories. At the same time, the calls would have to be of similar behavioural relevance and hence best be linked to the same context. Nonhuman primate vocal behaviour is highly context specific with very little acoustic variation within individual calls (Janik & Slater, 1997, 2000; Nowicki & Searcy, 2014). If more than one call type is produced in the same overall context, the call combination might convey qualitatively different information (Arnold & Zuberbühler, 2008), or address two different audiences (Fedurek, Slocombe, & Zuberbühler, 2015). In the case of primates, studies with natural vocalizations thus risk conflating item-based reaction with pattern perception. However, many songbirds, being vocal learners, produce several different discrete acoustic elements used in the same context. For example, a population of wild common ravens, *Corvus corax*, in western Switzerland was shown to produce 79 distinct call types in a simulated territorial interaction, with the individual males exhibiting a repertoire of 4–19 and the females 5–18 long-distance calls (Enggist-Dueblin & Pfister, 2002). Hence, songbirds can readily be tested with artificially created patterns of their own vocalizations (Berwick, Okanoya, Beckers, & Bolhuis, 2011).

Several studies have shown that songbirds can learn to discriminate between patterns of different complexities in operant-conditioning paradigms, based not only on structural but also prosodic and phonological cues (Gentner et al., 2006; van Heijningen, Chen, van Laatum, van der Hulst, & ten Cate, 2013; Seki, Suzuki, Osawa, & Okanoya, 2013). While songbirds thus clearly possess the cognitive capacity to learn about patterns, it has so far not been shown whether they show similar sensitivity to patterns without reinforcement. Would songbirds, like monkeys in previous studies, show a spontaneous response to an unfamiliar arrangement of known elements based solely on the novelty of the pattern, without training? Habituation–discrimination experiments can reveal such spontaneous reactions (ten Cate & Okanoya, 2012). A previous study aimed at demonstrating this capacity in Bengalese finches, *Lonchura striata domestica* (Abe & Watanabe, 2011), but this study only used a single conspecific song for the acoustic stimulus; thus it is possible that the birds discriminated between the playbacks based on superficial resemblance rather than the pattern itself, a fatal confound (Beckers, Bolhuis, Okanoya, & Berwick, 2012). A recent study confirmed that songbirds are indeed very sensitive to just how a sequence sounds, not necessarily how its elements are arranged. In a go–no-go task, zebra finches, *Taeniopygia guttata*, were operantly conditioned to discriminate between two patterns of spoken syllables by prosodic cues, and were subsequently also able to identify the target pattern in the absence of these particular cues (Spierings & ten Cate, 2014). In this study, prosody seemed to be the most salient cue rather than the structure of the test sequences. Hence, the question whether songbirds are sensitive to structural changes without reinforcement remains open.

In the present study we tested common ravens in a habituation–discrimination experiment using conspecific stimuli arranged into patterns used in a previous primate study (Fitch & Hauser, 2004). Common ravens are among the largest songbirds, have large brains and possess complex cognitive capacities which are in many respects comparable to those of primates (Heinrich, 2011). They are highly responsive to playbacks of conspecific vocalizations (Boeckle, Szipl, & Bugnyar, 2012), and discriminate between the calls of familiar and unfamiliar individuals (Szipl, Boeckle, Wascher, Spreafico, & Bugnyar, 2015). Ravens can acoustically identify former affiliation partners (Boeckle & Bugnyar, 2012), and are capable of third-party recognition of in- and out-group individuals based on playbacks of vocal interactions (Massen, Pasukonis, Schmidt, & Bugnyar, 2014).

To increase the behavioural relevance and cognitive salience of our stimuli, we used raven long-distance calls as the elements of the tested patterns. Territorial breeding pairs typically combine long-distance calls alternately to produce pair-specific vocal displays, possibly in order to strengthen and advertise the pair bond as well as to advertise their joint claim on the territory (Enggist-Dueblin & Pfister, 2002). Long-distance calls are acquired during ontogeny and facilitate individual discrimination (Boeckle & Bugnyar, 2012). Because male ravens are larger than females, they have longer vocal tracts and produce long-distance calls with lower resonance frequencies. Hence a call sequence of two individual ravens of two different sizes is acoustically recognizable as a joint display of a territorial pair (Boeckle, 2012). Similarly to a previous primate study (Fitch & Hauser, 2004), which used syllables of two categories as the elements to create the patterns, one spoken by a man, the other by a woman, we used the sex of the birds to define our categories, one containing calls of male ravens and the other calls from females. We hypothesized that territorial raven pairs would be highly attentive to sequences of long-distance calls of a male and a female raven, especially because this stimulus could be interpreted as a territorial vocal display of an unfamiliar but coordinated breeding pair intruding upon the subjects' territory.

We tested whether raven subjects would show differential responses to changes in the pattern of long-distance calls. For accurate comparison with the previous primate study (Fitch & Hauser, 2004) we used the same pattern for the habituation phase, and in the first test at the discrimination phase employed the same types of violations. This first test also included control sequences to investigate whether the subjects could generalize across the tested pattern. We further implemented a second test to see whether ravens could internalize the syntactic rule used to generate the stimuli of the habituation phase. Given the behavioural relevance of the set-up and the cognitive capacities of common ravens, we hypothesized that subjects would show discrimination in the first test. As there is currently no conclusive evidence that nonhuman species perceive more complex patterns (ten Cate & Okanoya, 2012), we did not necessarily expect ravens to discriminate in the second test, particularly given our experiment's lack of reinforcement.

METHODS

Subjects

The project was conducted with 24 adult common ravens housed in pairs (thus 12 males, 12 females) in outdoor aviaries at a variety of zoological gardens, research stations and with private keepers in Austria, Germany and Sweden. All pairs had attempted to breed or bred successfully, and were reported to frequently engage in joint displays, suggesting that they considered their home aviary their territory. Birds at all sites were already habituated to unfamiliar humans standing in front of their aviary taking pictures and video recording them (e.g. visitors at zoos; former experimenters, documentary film teams at research stations).