



## More than one way to see it: Individual heuristics in avian visual computation



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### ABSTRACT

Comparative pattern learning experiments investigate how different species find regularities in sensory input, providing insights into cognitive processing in humans and other animals. Past research has focused either on one species' ability to process pattern classes or different species' performance in recognizing the same pattern, with little attention to individual and species-specific heuristics and decision strategies. We trained and tested two bird species, pigeons (*Columba livia*) and kea (*Nestor notabilis*, a parrot species), on visual patterns using touch-screen technology. Patterns were composed of several abstract elements and had varying degrees of structural complexity. We developed a model selection paradigm, based on regular expressions, that allowed us to reconstruct the specific decision strategies and cognitive heuristics adopted by a given individual in our task. Individual birds showed considerable differences in the number, type and heterogeneity of heuristic strategies adopted. Birds' choices also exhibited consistent species-level differences. Kea adopted effective heuristic strategies, based on matching learned bigrams to stimulus edges. Individual pigeons, in contrast, adopted an idiosyncratic mix of strategies that included local transition probabilities and global string similarity. Although performance was above chance and quite high for kea, no individual of either species provided clear evidence of learning exactly the rule used to generate the training stimuli. Our results show that similar behavioral outcomes can be achieved using dramatically different strategies and highlight the dangers of combining multiple individuals in a group analysis. These findings, and our general approach, have implications for the design of future pattern learning experiments, and the interpretation of comparative cognition research more generally.

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## 1. Introduction

### 1.1. Processing of sensory regularities by humans and other animals

Humans are strongly inclined to discover and process structure in sensory stimuli (Gombrich, 1984). Appreciating the overall symmetry of a building or painting, delighting in themes and variations in music, or parsing a sentence in our native language are all examples of tasks that require sophisticated structural processing. Whether natural or man-made, complex visual, auditory or tactile

inputs are usually categorized by humans using relations established between their constituent components (Conway & Christiansen, 2005). Such structure-based learning is an important part of humans' everyday sensory experience, regardless of whether these learning processes are statistical or explicitly rule-based (Peña, Bonatti, Nespor, & Mehler, 2002).

Some cognitive resources required to process structure are shared across domains (e.g., music and language) and possibly with other animal species. Aspects of human working memory capacities, for example, appear to be both domain-general (Chiappe & MacDonald, 2005; Janata, Tillmann, & Bharucha, 2002; Kirkham, Slemmer, & Johnson, 2002) and shared with a broad range of animal species (Chiappe & MacDonald, 2005; Kawai & Matsuzawa, 2001; Murphy, Mondragón, & Murphy, 2008). Similarly, several species can learn that some pairs of events co-occur more often than others (see ten Cate & Okanoya, 2012 for

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an overview of how other animals process transitional probabilities). However, some structural computations at the core of human cognition may be difficult or even impossible for other animals to process. Empirical investigations of human specificity require use of the comparative method (Fitch, 2014; Fitch, Huber, & Bugnyar, 2010), where different species are tested on matched tasks to draw biological inferences concerning a particular cognitive trait. This method can, for example, be applied to estimate which cognitive prerequisites for language or music emerged during recent human evolution and which arose earlier in primate, mammal or vertebrate evolutionary history (Fitch, 2005).

### 1.2. Processing “context-free” structures across species and domains

Pattern perception experiments can be formalized using quantitative frameworks. For example, formal language theory is a branch of mathematics and computer science that offers analytical tools to measure complexity of structural patterns (strings composed of minimal holistic elements (Jäger & Rogers, 2012)). Formal language theory has recently been adopted in perceptual experiments in humans and non-human animals (Fitch & Friederici, 2012; ten Cate & Okanoya, 2012). Formal language theory provides a rigorous mathematical framework and non-ambiguous notation to clearly state hypotheses and to sharpen research questions (Fitch, 2014). Researchers choose some abstract rule system or “grammar” of interest, and use it to produce visual or auditory test stimuli that either follow or violate the rule(s) (Jäger & Rogers, 2012; Reber, 1969).

One controversial strand of comparative pattern learning research concerns animals’ ability to process supra-regular (e.g., “context-free”) structures, which incorporate relationships between multiple non-adjacent elements. Mastery of such relationships is a necessary (but not sufficient) prerequisite for using human language (Fitch & Friederici, 2012). An early study compared pattern-learning abilities in humans and cotton-top tamarins (Fitch & Hauser, 2004) using syllable streams that either followed an *alternating* pattern (female–male–female–male, etc., notated as  $(AB)^n$ ), or a *matched block* pattern (female–female–...–male–male–..., notated  $A^nB^n$ ). In terms of formal language theory, processing the alternating stimulus requires weaker computational capabilities than the block pattern (see Fig. 1 for a visual equivalent of these two types of pattern). While humans could readily discriminate both syllable patterns, the monkeys only mastered the less computationally demanding alternating pattern (Fitch & Hauser, 2004). A further study, using operant testing, investigated whether starlings could learn the same block pattern ( $A^nB^n$ ) composed of starling vocalizations (Gentner, Fenn, Margoliash, & Nusbaum, 2006). After intensive training, the birds discriminated such patterns from ill-formed variations, featuring different combinations and orderings of the constituent starling calls (Gentner et al., 2006). The apparently superior performance of starlings over monkeys could represent a species difference reflecting the complexity of starlings’ natural vocalization

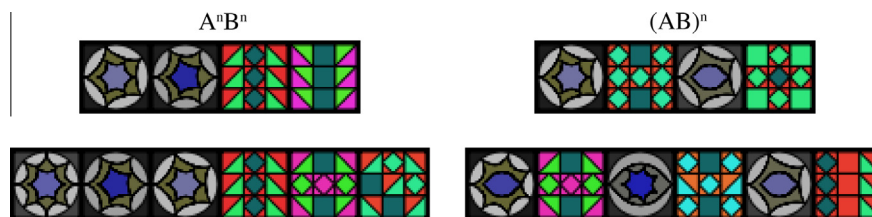
(although for counter-hypotheses see ten Cate & Okanoya, 2012; van Heijningen, de Visser, Zuidema, & ten Cate, 2009). However, starlings underwent an extensive training period, unlike the monkeys, who received no feedback or training.

Similar patterning abilities were subsequently investigated in zebra finches, a bird species that exhibits a relatively simple song structure (van Heijningen et al., 2009). Although a group-level data analysis suggested that, like starlings, zebra finches mastered the intended “complex” pattern, a more detailed analysis of the performance of individual birds revealed that each bird was using a simple rule, often only taking a tiny portion of the chosen stimulus into account. van Heijningen et al. (2009) thus concluded that none of their zebra finches actually learned the grammar, despite apparent success at a group level, and suggested that the same reasoning could be applied to the previous starling results (Gentner et al., 2006). The dispute has not yet been resolved and has given rise to debate (Gentner, Fenn, Margoliash, & Nusbaum, 2010; ten Cate, van Heijningen, & Zuidema, 2010) and additional studies in further species (Abe & Watanabe, 2011; Rey, Perruchet, & Fagot, 2012; Stobbe, Westphal-Fitch, Aust, & Fitch, 2012).

Thus, although a number of species can parse “computationally simple” stimuli, corresponding to regular languages at the lowest level of the formal language hierarchy (Abe & Watanabe, 2011; Fitch & Hauser, 2004; Gentner et al., 2006; Herbranson & Shimp, 2008; Ravnani, Sonnweber, Stobbe, & Fitch, 2013; ten Cate & Okanoya, 2012), perception of patterns at higher complexity levels – supra-regular (Jäger & Rogers, 2012), i.e., beyond simple chaining of contiguous perceptual tokens – has yet to be convincingly demonstrated in non-human animals. Thus, there is still no consensus on (a) which nonhuman species, if any, can master supra-regular rules and (b) precisely how complex patterning rules are learned and processed in cognitive experiments. The latter question is the focus of the research described here.

### 1.3. Artificial grammar learning: Common problems need a novel solution

Previous research has shown that a number of factors can influence the overall outcome of pattern learning experiments. Participants may achieve (partial) success in these experiments by using simple heuristics and perceptual shortcuts, rather than learning the intended abstract rules (van Heijningen et al., 2009). During training, participants may learn some simple “heuristic” or “strategy”, which although simpler than the “correct” rule, nonetheless earns them rewards and results in above-chance performance. When this heuristic is applied to novel test stimuli where it does not fit, misclassification results. Detailed analysis of individual participants’ responses to patterns of similar length, but inconsistent with the generating rule, are necessary to determine which particular decision strategy was used by a participant during the training phase. This type of analysis is particularly suitable for the large quantities of data resulting from operant conditioning experiments like the ones described here.



**Fig. 1.** Example of training patterns. Top: an AABB (equivalent to  $A^2B^2$ , left) and ABAB (equivalent to  $(AB)^2$ , right) pattern; bottom: same patterns for  $n = 3$ . During the training, birds were simultaneously presented with an  $A^n B^n$  and an  $(AB)^n$  stimulus (with  $n = 2$  or  $3$ ) and were rewarded for pecking on one of them, depending on the experimental group to which they were randomly assigned.

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