



# Temporal pattern processing in songbirds

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Understanding how the brain perceives, organizes and uses patterned information is directly related to the neurobiology of language. Given the present limitations, such knowledge at the scale of neurons, neural circuits and neural populations can only come from non-human models, focusing on shared capacities that are relevant to language processing. Here we review recent advances in the behavioral and neural basis of temporal pattern processing of natural auditory communication signals in songbirds, focusing on European starlings. We suggest a general inhibitory circuit for contextual modulation that can act to control sensory representations based on patterning rules.

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## Introduction

Understanding the neurobiology of language faces a difficult challenge. On one hand, language in the broadest sense is uniquely human, and no animal model can capture its full complexity. On the other hand, animal models are necessary components in any research program with the goal of understanding neural mechanisms in biological detail. While much can be learned about the neurobiology of language using non-invasive neuroscience techniques in humans, such as functional magnetic resonance imaging and electroencephalography, these techniques cannot answer how individual neurons and neural circuits implement language-relevant computations. One path through this challenge is to divide language into sub-processes and focus on those that are both critical to language use, and also shared with other

species [1]. Language is constrained by biology [2–5]. Although this comparative strategy may leave some mechanisms beyond our understanding, it will permit progress in the near term and establish basic neurobiological substrates within which more complex, uniquely human processes, can be proposed and (perhaps eventually) tested. Understanding, in biological detail, even a subset of the brain mechanisms that support language will likely have profound effects on our understanding of language.

This review concentrates on one area with strong potential for understanding how single neurons and neural circuits implement language-relevant, biologically plausible computation: temporal and syntactic information processing. Language and its primary carrier signal, speech, unfold over time, and successful acquisition and comprehension of any language relies critically on the processing of information structured across time [6–8]. Likewise, many animal communication signals, although lacking some features of human language [see Ten Cate, in this issue] [9,10], are also structured in time. This review discusses recent findings on the behavioral basis of syntactic processing in songbirds, highlighting two central ideas: (i) songbirds are able to learn temporally patterned communication signals and (ii) pattern generalization involves abstraction away from the direct sensory representation of the signal. These findings reveal important constraints in real-world auditory signals between knowledge of pattern structure and the sensory representation of pattern elements. We then consider how the combination of pattern and sensory event might be encoded in high-level secondary auditory cortical regions, where recent electrophysiology experiments demonstrate that task-relevant information can be encoded in the population dynamics among single neurons. We propose a basic circuit in which population level representations of sensory signals could be differentially modulated by patterning rules, thus forming a well-defined neural substrate for language-relevant processing.

## Songbirds are sensitive to temporal pattern

Learning temporally patterned acoustic sequences is an important aspect of songbird biology. Many songbird species, such as the European starling (*Sturnus vulgaris*), produce elaborate vocalizations (songs) whose structure is well described by a hierarchical organization, where complex auditory objects composed of simpler spectrotemporal features are patterned across time [11–13]. The most basic unit of starling song is referred to as a note, and separate notes are identified based on the contiguous presence of power in their spectrotemporal representations [11–15]. The arrangement of notes in starling song is

structured into repeatable patterns called motifs, that usually last between 200 and 1000 ms [11,12,16]. In addition, while motif repertoires between starlings are largely unique [12,13,15], motifs can nonetheless be broadly classified into four classes based on spectrotemporal features (whistles, warbles, rattles and high frequency events) shared across all starlings [15]. The songs of adult starlings unfold in time as non-random sequences of changing motifs [13,17], where each motif represents a dynamic, stereotyped, auditory event (see Figure 1). While there is no evidence that variation in the hierarchical structure of birdsong conveys semantic information in the way that human syntax does, this hierarchical organization nonetheless manifests neurophysiologically in the songbird ascending auditory system. Mid-brain and thalamic regions respond best to spectrotemporally simple features [18] and more complex objects (e.g., motifs) are preferentially encoded at higher-level regions [19,20,21]. Several researchers have hypothesized that the temporal patterning of motifs within starling song [14,15,17,22,23] plays an important role in natural social behaviors, including individual recognition [24] and mate selection [25].

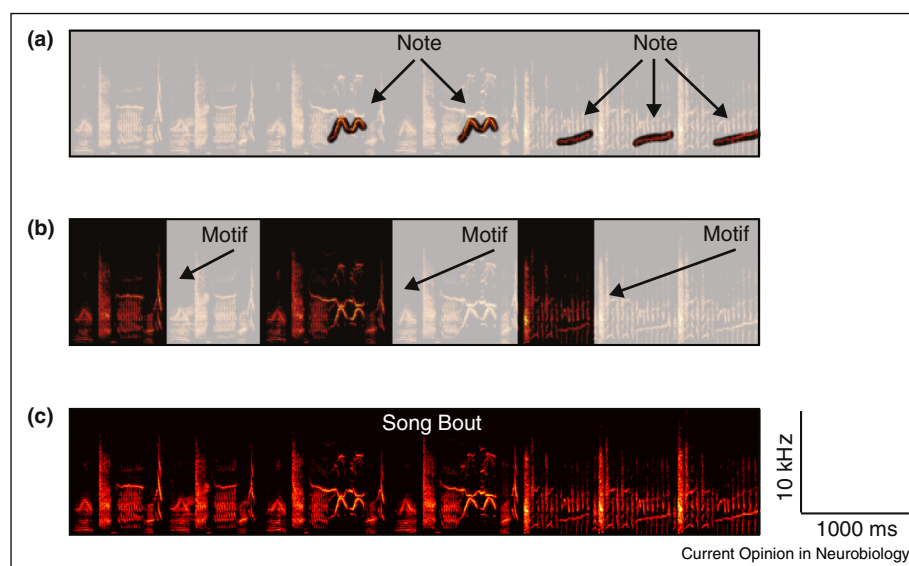
Starlings can use the temporal structure of natural songs to aid recognition of conspecifics. For example, in one study we trained starlings to differentiate sets of songs from different conspecific males [13]. After learning to accurately classify several songs according to singer, subjects could correctly recognize novel (i.e., previously unheard) songs from these same singers [16]. Scrambling the natural order of motifs in these novel songs from familiar singers, however, significantly impaired recognition performance.

Thus, starlings are sensitive to the temporal sequence of motifs in songs [24]. Importantly, the motif repertoires of different singers are largely unique [17], and thus the songs produced by each bird differ in both the ordering of motifs and the spectrotemporal features comprising each motif [14,24]. Starlings are sensitive to the sequence of notes in familiar motifs [14], and use this information to aid recognition. Acoustic differences between motifs are not required to differentiate longer sequences, however, as starlings can readily learn to dissociate motif sequences composed of exactly the same motifs based solely on their patterning [26].

The abilities demonstrated in the foregoing behaviors provide an interesting context within which to investigate neurobiological mechanisms of temporal pattern processing. Before discussing this further, however, it is useful to be clear about our terminology. We use the phrase ‘*temporal processing*’ to broadly reference any behavior in which the animal is sensitive to, attending to, or otherwise using information gained from a series of events arrayed across time. This sensitivity is powerful, as it enables learning of the statistical relationships (i.e., *transition statistics*) between sounds that co-occur or occur in a specific order. In the infant development literature, this ability is referred to as statistical learning [27,28], and classically in the animal communication literature as phonological syntax (see Box 1).

Transition statistics, in their simplest form, are defined for specific pairs (or triplets, etc.) of events, such as speech sounds for infants, or notes [14] or motifs [13] for starlings.

Figure 1



Segment of male starling song used to demonstrate the hierarchical temporal scales of acoustic organization. **(a)** The most fundamental component of songs are notes—bursts of continuous energy throughout their spectrotemporal representations. **(b)** These notes are clustered into stereotyped packages to form motifs. **(c)** These motifs occur in a specific temporal pattern across multiple renditions of a given starling’s song.

**Box 1 Combinatorial semantics**

Classic approaches to animal communication distinguish between 'lexical syntax' and 'phonological syntax' on the basis of combinatorial semantics — how simpler units may combine to create meaning [31]. Lexical syntax refers to temporal sequences in which meaningful sound units combine to convey meaning beyond that carried by the individual units. For example, one might combine the same words into two strings (sentences) with different meanings. Phonological syntax refers to temporal sequences that also convey meaning, but which are built from units that have no intrinsic meaning. Most examples of syntactic patterning in animal communication are consistent with phonological but not lexical syntax. We suggest that the cognitive abilities implied by phonological syntax, that is, working memory, attention, temporal pattern perception, are fertile ground for studying language-relevant neurobiological processes.

This explicit tie between sequence information and the sensory representations of specific events can limit generalization. For example, knowing that event 1 is normally followed by event 2, may tell you very little about what to expect if you just heard event 3. Yet, the generalization of sequence information across different events is central to human development and language acquisition [29<sup>\*\*</sup>,30], and important to clearly define in a program investigating comparative neurobiological mechanisms. We refer to sequence information that generalizes beyond the training stimuli as a '*temporal patterning rule*', or '*rule*' for short [25,31–34]. Such rules can be used to determine whether a given sequence of events follows a familiar pattern or not, and as a metric of similarity between two patterns. Importantly, rules may operate at different levels of abstraction away from the veridical sensory representation of the constituent events (see Box 2), but always require some judgment of similarity between events. Understanding the neurobiological implementation of temporal patterning rules, therefore, requires careful articulation of both the rule and the representation of the elements over which the rule is operating. Likewise, understanding how sensory information can constrain rule use is a prerequisite to future neurophysiological investigation.

Several lines of evidence support the notion that starlings can use temporal patterning rules, that is, generalize learned sequence information beyond sets of training stimuli. We trained starlings to classify sequences of motifs that subscribe to forms  $(AB)^n$  and  $A^nB^n$  (see [35]), where  $2 \leq n \leq 4$ ; [36<sup>\*</sup>]. Here, A and B each represent a set of 8 motifs from perceptually distinct classes of starling song motif known as warbles and rattles, respectively. This experiment demonstrated that starlings were able to classify patterns without relying on numerous alternative solutions (e.g.,  $A^1B^3$ ,  $A^1B^3$ ,  $A^2B^3$ ,  $A^3B^2$ , AAAA, BBBB, ABBA, BAAB). In addition, once starlings have acquired knowledge of these patterns based on training with 16 sequences, classification can

**Box 2 Similarity and rules**

To aid the readers' intuition for how we are defining *rules*, consider the two following three-event sequences: A–B–C and E–F–G, where different letters denote discriminable sensory events. For the pattern of events in each sequence to be considered similar, that is, described by the same rule, the events themselves must bear some similarity to one another. This similarity may be a function of underlying classes or categories from which the corresponding events in each sequence (A and E, B and F, and C and G) are drawn respectively, such that the rule could be stated as '*a class 1 event followed by a class 2 event followed by a class 3 event*'. These categories may be defined perceptually, where all members share a given physical attribute (or set of attributes), or more abstractly, where all members share an associated function. Alternatively, the events may be classified according to their relative relationship to other events in the sequence, such as a series of tones where the sequence of pitches is 'high-low-high', and the determination of whether a tone is 'high' or 'low' is made relative to the tones that precede and follow. In any of these cases, the power of the rule lies in its application to sequences that have not previously been experienced (i.e., novel sequences). The rule can only be applied however, if the elements in those sequences bear some similarity to patterned elements that have been experienced.

As the reader can appreciate, patterning rules are closely entwined with judgments about the similarities and differences between underlying elements, and to associative learning. The interplay between similarity, rules, and associative learning has a long history of careful study in cognitive science and psychology. While these relationships are perhaps best understood in the context of categorization, they have also been discussed in terms of human artificial grammar learning, that is, the study of pattern learning. Full discussion of these relationships is beyond the scope of the present review, but some readers may find recent work investigating these relationships useful (see [33,86]).

be transferred to other small sets of novel sequences of the same warbles and rattles that follow the learned patterns [36<sup>\*</sup>]. Thus, starlings can generalize learned patterns over sets of familiar elements.

This study of pattern learning in starlings [36<sup>\*</sup>], as well as similar results in Bengalese finches [37<sup>\*\*</sup>], have drawn criticism, based on the concern that subjects might have employed some *simple* strategy (e.g., primacy, recency, 'phonetic generalization') to solve the task [38–41]. A recent study addresses these concerns [42]. Using more difficult task, we trained starlings to recognize the patterning forms XXYY and XYXY, where on any given trial an X could represent a motif from *either* set A or set B (and vice versa for Y) and therefore subjects needed to distinguish AABB and BBAA patterns from ABAB and BABA. This stimulus design removes the possibility that subjects solve the task by anticipating the presence of certain acoustic cues in specific locations of the pattern, because all motifs are equally likely to occur in every position of the sequence. In addition, instead of training subjects on just a subset of all possible patterned sequences (as in [36<sup>\*</sup>], where only 16 out of 8092 possible sequences were used in training), nearly all possible sequences (at least 16 300 out of 16 384) were used during

training, and no single sequence was presented more than twice. This procedure provided two distinct advantages for assessing songbird pattern learning abilities: (1) it renders potentially trivial solution strategies useless (e.g., no specific motif or category of motif occurs more frequently in any position), and (2) it precludes identification of serendipitous acoustic cues that might be present in the smaller sets of training and testing sequences [38] used in early work [36<sup>\*</sup>]. Learning to classify XXYY and XYXY patterns correctly is only possible by recognizing differences in the temporal structures governing the organization of motifs [42].

In addition to demonstrating that starlings are able to learn motif-patterning rules from trial-unique exemplars, our recent work [42] adds further insight into the nature of the patterning rules themselves. More detailed analyses of the starlings' behavior in response to select subsets of the training stimuli indicate that performance did not rely on simply comparing which motif or pairs of motifs occurred in given locations of the pattern. Rather, the starlings appear to be accumulating evidence from at least 3 (if not all 4) of the motifs in the sequence before making a decision about which pattern a sequence follows. In the future, more work will need to be done in order to identify the patterning rules acquired in this study; regardless, the evidence firmly shows that songbirds can generalize learned temporal relationships between multiple items in a sequence.

### Constraints on pattern generalization

Although considerable debate exists (and will likely continue) regarding the complexity of various rules that birds and other non-human animals can learn [43], it is nonetheless clear that at least some rules are learnable. But all rules are defined over some context, and because the rules we are interested in understanding are defined over sensory events, it is crucial to understand both the nature of the relevant sensory events and their interactions (if any) with the rules in question (see Box 2). To explore these issues we again trained starlings to recognize differently patterned strings of motifs, but instead of focusing on the overtly reinforced patterns, we asked how the perceptual organization of the pattern elements contributes to or constrains learning and generalization [44].

We trained two groups of starlings to distinguish patterns of the form XXYY from XYXY, where on each trial X and Y represented a motif from either set A or B. Thus, the subject needed to distinguish AABB and BBAA patterns from ABAB and BABA patterns; A and B were defined sets of motifs. Following training on a small subset of all possible XXYY and XYXY sequences, we transferred subjects to 500 novel sequences built from the same sets of A and B motifs. Crucially, for one group of starlings, the motif sets (A and B) preserved natural, perceptual category boundaries of warble and rattle motifs [17,22]. For the other group, however, the same motifs were

pseudo-randomly assigned membership into sets A and B [44] (see Box 2).

This seemingly subtle alteration of the way that pattern elements were organized had profound effects. Both groups of starlings were able to learn the XXYY and XYXY patterns regardless of whether they were implemented over sets of perceptually organized motifs or pseudo-randomly organized motifs. Surprisingly, however, only the birds trained with motif sets that followed the natural boundaries were able to generalize pattern knowledge to novel motif sequences. These results suggest that pattern learning may be agnostic to the perceptual structure of underlying elements, but these same perceptual differences tightly constrain the generalization of pattern knowledge.

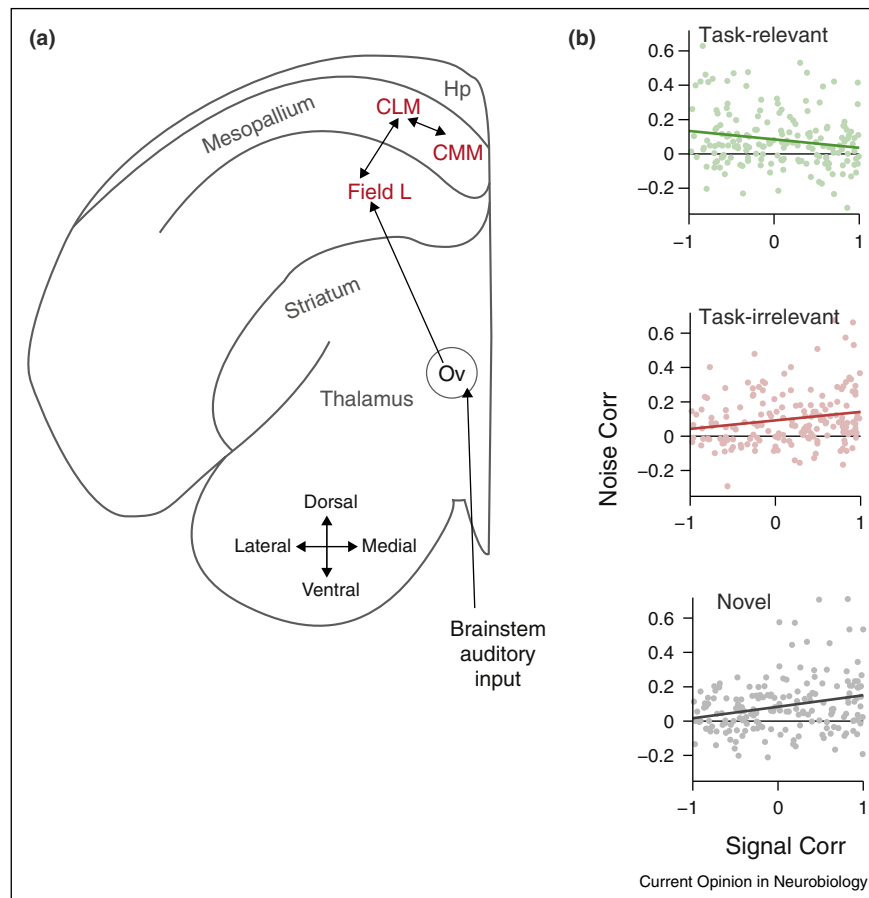
In so far as the sensory events that constitute a given sequence can be categorized in different ways, the rules that operate on the concomitant categorical representations will be differently constrained. In the foregoing examples, it is clear that pattern knowledge is implemented over perceptually well-defined sets of motifs. Definition of these sets likely reflects a combination of our operant training and the animals' prior experiences with different motifs in the context of other song-driven behaviors. One question deserving of future attention is the extent to which acquired patterning rules can generalize to sequences of novel elements. Our results suggest that such generalization is possible, but that it will be tightly constrained by how these elements fall into the same open-ended perceptual or functional categories that are used to carry the patterning information during training (see Box 2). This behavioral interaction between temporal patterning rule and element abstraction (i.e., categorization) has important implications for understanding the neurobiological basis of temporal pattern knowledge and thus language.

### Neurophysiology

We hypothesize that the same close ties to sensory encoding of elements evidenced in the foregoing behavioral results, will also hold for a neurobiological understanding of temporal pattern processing. That is, the neural representation of a temporal patterning rule should be closely connected to the sensory events (and event categories) over which the rule operates. The sensory regions that encode pattern elements, therefore, are useful targets to study the neurobiology of temporal pattern processing with cellular and circuit-level precision.

The temporal pattern elements of starling songs are motifs, and motifs are preferentially encoded in the higher-level regions of the auditory telencephalon. The songbird auditory system (Figure 2a) follows the general vertebrate plan [45]. Field L2a is the primary telencephalic target of the auditory thalamus, nucleus ovoidalis

Figure 2



**(a)** Schematic of the avian auditory system. Reprinted from [61]. **(b)** Plots showing the signal and noise correlations between pairs of neurons in response to task-relevant, task-irrelevant and novel motifs. Regression lines are indicated by color lines. Reprinted from [69].

(Ov) [46], and is the input layer for a circuit, homologous to mammalian primary auditory cortex [47,48], that includes L1, L3, and caudal mesopallium, CM (Figure 2a). Field L sub-regions also project to the caudo-medial nidopallium, NCM. The NCM and lateral CM (CLM), in turn, share reciprocal connections with the medial CM (CMM).

Encoding of songs in the songbird forebrain mirrors the coarse, hierarchical increase in selectivity observed for complex signals in mammalian visual [49,50] and auditory cortices [20,51]. Neurons throughout the songbird auditory forebrain show selectivity to species-specific vocalizations [52–54], that generally increases from Field L2, to L1 and L3 [55,56], and then NCM and CM [19,20,24,52–54,57–59]. Although the detailed circuitry within and between field L, NCM and CM remains poorly understood, the increasing selectivity between regions is consistent with a functional hierarchy [60] that is tuned

throughout to conspecific song [18,21], and further refined by experience [57–59,61–64].

Neural encoding in NCM and CM in particular is strongly shaped by both the stimulus acoustics and the learned behavioral relevance tied to different motifs [57–59,61]. In NCM, response modulation to learned stimuli appears as a rapid and long-lasting stimulus-specific response weakening to more behaviorally relevant (i.e., familiar) stimuli [59,65], an effect that emerges in part from stimulus specific response modulation through local inhibition [64]. Neurons in both CMM and CLM appear to encode the acoustic features that differentiate motifs. That is, the spiking patterns of neurons in both regions convey significant amounts of information about motif identity, and this stimulus specific information is greater in medial CM than in lateral CM [58], though we note that the absolute magnitude of information measures is difficult to compare. In any case, associative learning

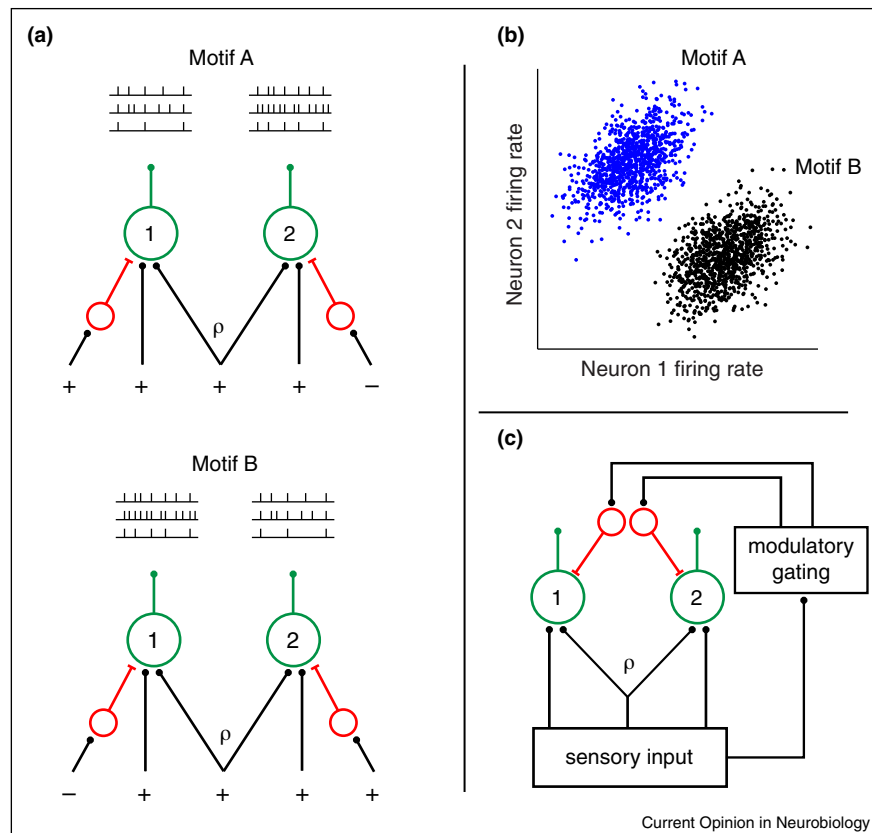
clearly modulates the stimulus-specific responses throughout NCM and CM.

To understand the relationship between neural encoding of stimulus features and familiarity in more detail, we recorded from CM in birds that had been trained to recognize a set of motifs that carried task-relevant information, and another set that carried task-irrelevant information [66\*\*]. Because both sets of motifs were paired equally with reinforcement, the differences between responses evoked by task-relevant and task-irrelevant motifs had to be tied to information about the specific behaviors conveyed (or not) by each motif rather than reinforcement. Consistent with prior studies, we observed a strong effect of stimulus familiarity in CMM [66\*\*]. That is, both the task-relevant and task-irrelevant motifs drove strong responses in CMM, compared to novel

motifs. In contrast, only the task-relevant motifs evoked responses significantly greater than novel motifs in CLM. This is consistent with the idea that CLM plays an important role in structuring the flow of auditory information into sensorimotor regions (e.g., HVC [67] more directly involved in the execution of behaviors.

We also examined learning-dependent changes in the population activity of simultaneously recorded, physiologically defined, subclasses of CLM neurons, including narrow and broad spiking neurons (putative parvalbumin positive and efferent projection neurons, respectively) [66\*\*]. Typically, when neurons are similarly tuned (i.e., they have a positive signal correlation), their responses also tend to co-vary trial-by-trial (i.e., they have a positive noise correlation) [68–74]. This is thought to result because the common inputs that convey similar

Figure 3



Hypothetical circuit to modulate signal and noise correlations. **(a)** Green circles denote excitatory neurons; red circles denote inhibitory neurons. The excitatory neurons (labeled 1 and 2) have both independent input and correlated input. The '+' and '-' denote a large and small magnitude input currents, respectively;  $\rho$  denotes the fraction of input that is shared. Both excitatory neurons also receive independent feed-forward inhibition, which is stimulus-dependent. Motif A and motif B drive partially overlapping inputs into these two excitatory neurons. Both motifs drive partially (positively) correlated inputs into neurons 1 and 2, which yields positive noise correlations, but motif A provides independent inhibition to neuron 1 (but not neuron 2). This suppresses neuron 1's response to motif A, without affecting the noise correlation (as long as neuron 1's response is still positive). Excitatory and inhibitory input need not be perfectly cleanly segregated. **(b)** Hypothetical spiking output shows higher firing rates for neuron 2 than neuron 1, but both neurons exhibit positive trial-by-trial correlations (i.e., noise correlations). A complementary scenario yields an opposite pattern of mean firing rates for motif B, but maintains the positive noise correlation (bottom left). **(c)** While the circuit could operate using feed-forward inhibition, additional gating of local inhibitory circuits could come from top down signals that carried information about transition statistics or temporal patterning rules (as well as attention, context, etc.).

tunings also share noise. Surprisingly, however, we found that learning can invert this canonical relationship [66\*\*], leading to population activity in which the signal and noise correlations become more orthogonal, but only for task-relevant motifs (Figure 2b) and only for the population of CLM projection neurons. In theory [75], this more orthogonal relationship can improve population coding because common noise among dissimilarly tuned neurons can be subtracted, which strengthens the signal while dissipating the noise. Indeed, the task-relevant motifs are encoded in the CLM projection neurons with higher fidelity [66\*\*].

We have proposed [66\*\*] a simple neural circuit that can produce the observed pattern of CLM correlations, using stimulus selective drive onto inhibitory interneurons to alter the signal and noise correlations in projection neurons (Figure 3a,b). The stimulus specificity of the inputs to CLM inhibitory interneurons has not been well characterized although nearly all response in CM are stimulus specific by their very nature [58]. It is not hard then to imagine how, in principle, the same stimulus-specificity and task-specificity that is tied in these results to associative learning could be produced by a range of modulatory drives, such as attention, context, or pattern rule, to dynamically alter the sensory representation of a given motif on short timescales. According to this hypothesis, CLM acts as a convergence zone (Figure 3c) where high-level acoustic feature encoding driven by feed forward activity is functionally organized by inhibitory modulation into population responses that can efficiently drive behaviors via sensorimotor target regions. The contextual modulation of sensory responses is not a novel concept in itself (e.g., [76,77]). However, the notion that this modulation may act through local inhibition to tune population responses in sensory regions, and that its dynamic implementation on short time scales may encode temporal patterning rules bears closer investigation. Recent observations [78,79] that contextual rule switches are strongly encoded by neurons in NCL (the caudolateral nidopallium) make this region, which bears many similarities to primate prefrontal cortex [80,81], an attractive target for such investigations.

### Closing remarks

Considerable debate on the neurobiological mechanisms of language has focused on identifying the basis of capacities unique to human language, including the formal grammatical models that capture language's unique features. Here, we take a comparative approach to language-relevant mechanisms that focuses on understanding how a brain encodes any temporal patterning rule. While the uniqueness of language may indeed reflect sensitivities to certain classes of temporal patterning rules, we argue that the space of possible patterning rules is likely to be much more rich than currently appreciated. Characterizing the nature of the (probably many) patterning rules that

animals can use is important, and ultimately may be our best hope to eventually understand how more uniquely human language capacities are implemented at a biologically precise level. Indeed, despite the fact that humans are capable of abstract reasoning [82], there is considerable evidence that sound-based (i.e., perceptual) features of words correlate with abstract features of language, such as case-endings and gender-markers [27,83,84\*,85]. This underlying perceptual structure might provide important scaffolding for acquiring more abstract knowledge of language during development. The kind of category/rule interactions we describe above may provide an attractive neurobiological model for understanding how implicit rules are extracted from patterned acoustic sequences. While a complete neurobiology of language cannot rest entirely on non-human models, comparative studies can reveal neural mechanisms for some language-relevant processes.

### Conflict of interest

Nothing declared.

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Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
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