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Bridging the fields of cognition and birdsong with corvids

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Corvids, readily adaptable across social and ecological contexts, successfully inhabit almost the entire world. They are seen as highly intelligent birds, and current research examines their cognitive abilities. Despite being songbirds with a complete 'song system', corvids have historically received less attention in studies of song production, learning, and perception compared to non-corvid songbirds. However, recent neurobiological studies have demonstrated that songbird vocal production and its neuronal representations are regularly influenced by environmental and cognitive factors. This opinion article discusses the literature on 'corvid song' before introducing other flexible vocal behaviors of corvids in both the wild and controlled laboratory studies. We suggest corvids with their flexible vocal control as promising model species to study the links between brain networks for cognition and vocalization. Studying corvid vocal flexibility and associated cognitive processes in both ecological and lab settings offers complementary insights, crucial for bridging the fields of cognition and birdsong.

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Traditional segregation of corvid cognition from birdsong

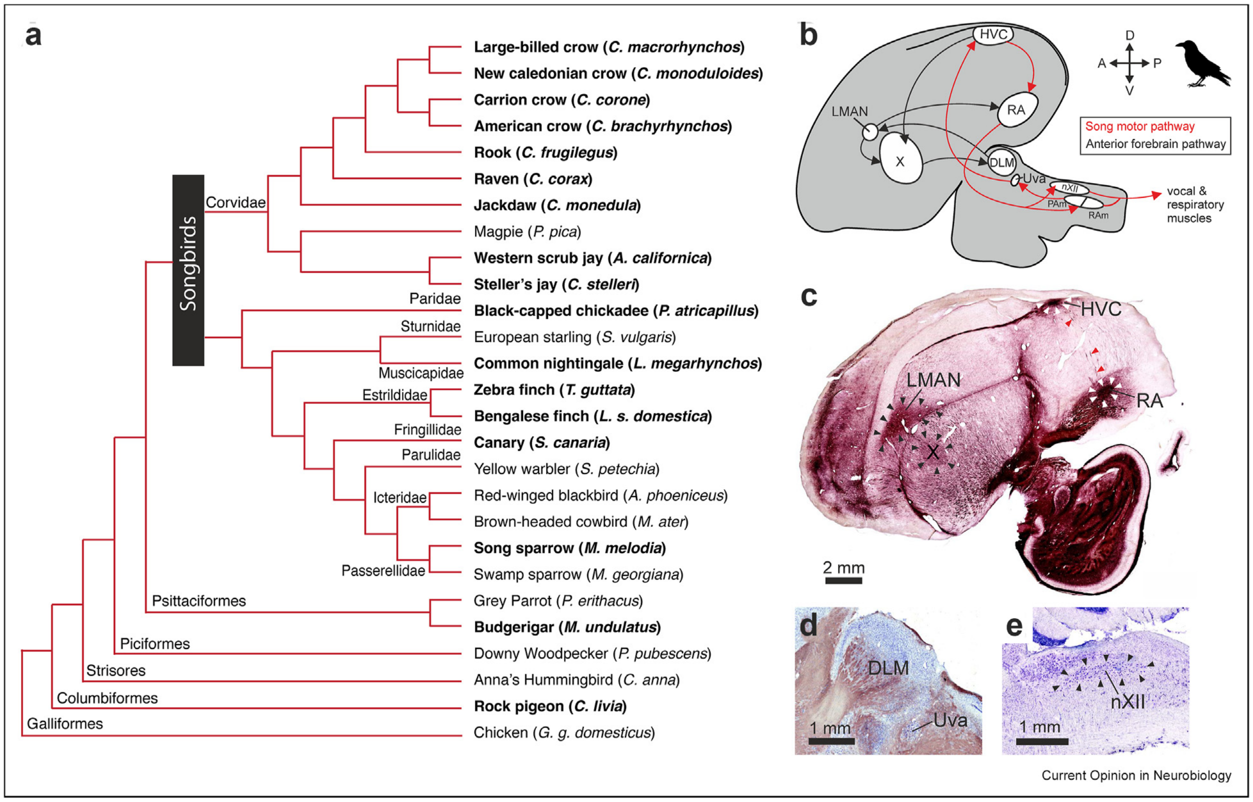
Corvids (crows, ravens, rooks, magpies, jackdaws, and jays) belong to the family Corvidae within the order Passeriformes, which includes all songbirds (oscines, Figure 1a). Despite their kin, corvids are not traditionally subjects in studies focusing on birdsong. Instead, corvids are lauded for their ever-expanding list of cognitive achievements [1]. Different species of corvids show a sense of number [2–4], flexibly categorize [5,6], learn abstract concepts [7,8], and use tools [9].

In contrast, research on non-corvid songbirds such as finches, canaries, and starlings has traditionally focused on complex, typically species-specific and learned vocal sequences called 'song'. The well-structured courtship song of zebra finches (*Taeniopygia guttata*), the most extensively studied songbird, is learned by juveniles from an adult male tutor and perfected after thousands of iterations [10]. Their stereotyped adult song is leveraged to study the neurobiology of the 'song system' — an easily-mapped circuit of discrete and well-defined brain nuclei dedicated to hearing, learning, and producing songs [10,11].

Corvids, too, are songbirds with a fully developed song system and, as such, provide an opportunity to bridge the fields of cognition and birdsong (Figure 1b [12,13]). Though what immediately comes to mind when prompted with crow vocalizations is not beautiful song but raucous cawing, prior studies have described American crows (*Corvus brachyrhynchos*) producing a 'quiet song'. These descriptions consist of rattles, growls, clicks, cooing, bowing, and nuzzling at their mate and has been hypothesized to promote social cohesion [14]. Rooks (*Corvus frugilegus*) are reported to perch alone to 'sing' softly which may function as 'vocal practice' to maintain their individual repertoires [15,16]. Beyond 'song', corvids are capable of additional vocal flexibility as open-ended learners and vocal mimics. While there are few experimental studies in corvids demonstrating adult plasticity in vocal imitation learning, much anecdotal evidence exists of vocal mimicry of heterospecific vocalizations and even of human speech sounds [14,15,17–21]. It has been hypothesized that one of the main functions of mimicry is to establish and strengthen social bonds either to mates or other members of the flock. Indeed, elements of vocalizations are shared between pairs and group members, suggesting social transmission as adults [19,22–25]. Moreover, vocal flexibility in adult crows, such as instructed changes in the number of vocalizations [3], has clearly been demonstrated in laboratory settings.

Collectively, this brief overview suggests that studying corvid vocalizations provides promising directions for

Figure 1



Crows are corvid songbirds with characteristic 'song system' nuclei. (a) Phylogenetic tree of select songbird and non-oscine species with **bolded** species mentioned in current article. Corvids belong to the family 'Corvidae' as part of the large suborder of songbirds (Oscines or Passeri). Horizontal lines do not indicate phylogenetic distance; tree constructed from data from Refs. [26,96,97] **(b)** Schematic of the crow brain (side view) showing the position of the main nuclei of the song motor pathway (SMP) and the anterior forebrain pathway (AFP). **(c)** Histological slice of a carrion crow brain (side view at about 5.0 mm lateral from the midline, anterior is left). A myelin stain reveals song system structures indicated by white (SMP) and black (AFP) arrowheads. The red arrowheads indicate massive fiber bundles that descend from the song premotor nucleus HVC to the motor nucleus RA. Arrows around LMAN indicate the extent of both LMAN core and shell. Note that individual nuclei do not appear at their largest extent in this example slice. **(d)** The crow's brain also exhibits the song system's thalamic nuclei DLM and Uva (combined myelin and Nissl stain). **(e)** The crow's syringeal nucleus (nXII, Nissl stain). Abbreviations: DLM, nucleus dorsolateralis anterior, pars medialis; HVC, proper name; LMAN, lateral magnocellular nucleus of the anterior nidopallium; nXII, tracheosyringeal nucleus; PAm, nucleus parambiguus; RA, robust nucleus of the arcopallium; RAm, nucleus retroambiguus; Uva, nucleus uvaeformis; X, area X. Histological images are published and unpublished material from Ref. [12].

bridging the fields of cognition and birdsong. For example, a recent cross-species study revealed that vocal learning complexity correlated with problem-solving abilities [26]. Although bird vocalizations are traditionally classified as 'calls' and 'songs', we use 'vocalizations' throughout because no characteristic — be it sexual dimorphism, seasonality, complexity, degree of learning — can consistently delineate 'song' from other forms of vocal communication across species [27,28]. For example, though often called innate, 'calls' can also be learned and flexibly modulated depending on social context. During development, brood parasite chicks can flexibility adjust their begging 'calls' to be host-specific [29]. Zebra finches exchange thousands of short contact 'calls' per day that acoustically converge during pair formation [30]. Many such examples advocate that we extend 'vocal learning' beyond its classical definition of 'song imitation' learning [27,31,32].

Corvids show sophisticated vocal behaviors

Corvids use their vocalizations to navigate social relationships

Corvids have complex social lives [33—36] with social structures that can vary widely between or even within species. American crows are cooperative breeders where chicks receive care from not only paretnts, but also from other group members whereas the closely-related European carrion crows (*Corvus corone*) form pairs and are largely territorial. However, in harsh environments, a population of carrion crows has been found to engage in cooperative breeding [35]. This diversity in corvid social structures can help disentangle influences of breeding strategies, developmental trajectories, and prosociality on cognition and vocal flexibility [26,36–38].

Corvids use their vocalizations to manage social relationships by signaling and negotiating identity, relationships, and dominance status [16,34,39]. For example, crows can differentiate between the calls of known and unknown conspecifics [40] and link vocalizations to visual features of the vocalizer [41]. Beyond identifying the individual, vocalizations can signal group belonging [42] and these socially ('culturally') transmitted group signatures are a likely by-product of vocal learning [19]. Vocal discrimination of individuals and their group belonging is critical to many adaptive behaviors — such as the decision to mob a predator (Figure 2a [4,34,43], and to distinguish between the trusted warning vocalizations of group members or the sometimes deceptive vocalizations of neighbors [43]. Ravens (*Corvus corax*) can even infer dominance relationships and violations of dominance predictions from hearing vocal interactions alone (third—party relationships [44]). Therefore, cognitive capabilities such as 'transitive inference', the capability to deduce relations between objects that have not been explicitly compared before, or recognizing embedded structures in sequences are proposed to be involved in processing complex corvid hierarchical structures [37,45,46].

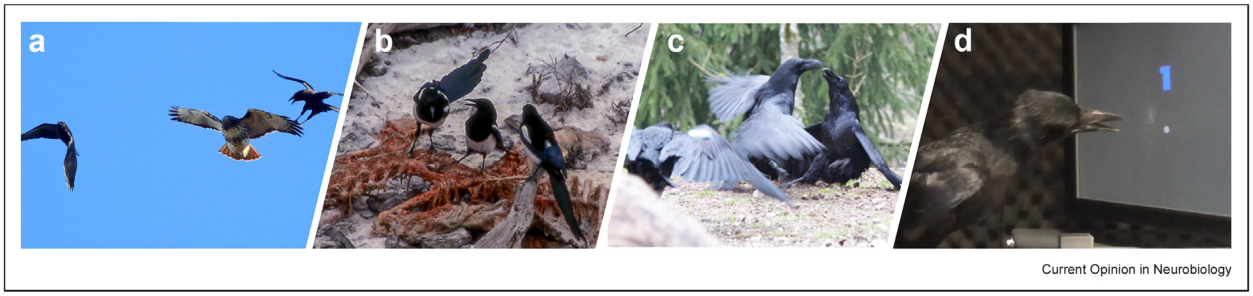
Outside of long-term monogamous partnerships, some species of corvids navigate complex fission-fusion dynamics with ontogenetic and seasonal changes in the size and composition of social networks [33,36]. In winter, corvids compete for access to unpredictable food sources like carcasses with other scavengers and conspecifics (Figure 2b). Ravens produce individually-distinct vocalizations, 'haa calls', when discovering food [33,34,47], particularly when that food is monopolized by others. Playbacks of these vocalizations attract other ravens, suggesting a recruitment function [47]. Typically less dominant ravens often seek social support due to the competitive nature of foraging which sometimes results in conflicts. During these conflicts (Figure 2c), appeasement vocalizations are strategically used, with the victim adjusting their signals based on present individuals - showing an audience effect [33,48]. Victims increase vocalization rates when bystanders are related kin but decrease rates when bystanders are bonded partners of the aggressor, who potentially intervene on behalf of the aggressor [48]. Flexibly adapting responses to conspecifics during vocal interactions involves integrating diverse sensory stimuli and internal states [34,49], often requiring a balance between field and laboratory studies to disentangle their respective contributions.

Carrion crows can flexibly control their vocalizations

Historically, animal vocalizations were thought to be inextricably linked to internal states like arousal, where an animal's vocalizations would be driven by immediate stimuli with inherent value or valence, such as a mating partner, predator, or food item. From this historical perspective, audience effects extend arousal-based explanations. For example, Zebra finches sing more variably when alone (undirected) compared to when they sing to females (directed) [50,51], with corresponding context-dependent neurophysiological changes in song nuclei. Acoustic changes in pitch, tempo, and entropy, along with changes in brain temperature and presong heart rate suggests that increased arousal upon seeing a female drives differences in directed versus undirected 'song' [50,51].

For many animal vocalizations, arousal-based explanations suffice, as they do for some non-linguistic human vocalizations. However, even 'innate' vocalizations like infant cries are influenced by native language, demonstrating some vocal flexibility [52]. Adult human speech

Figure 2



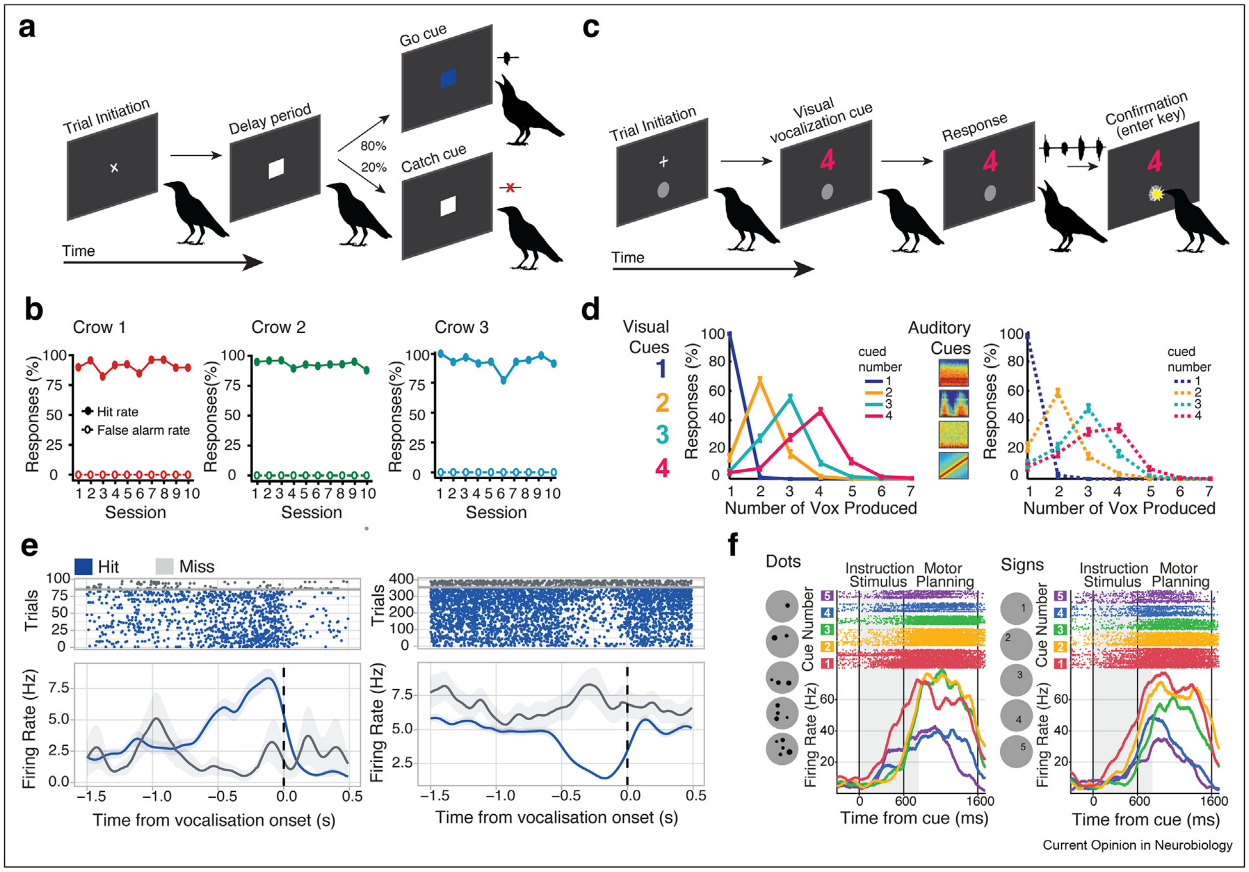
Corvid and non-corvid songbirds display vocal flexibility. **(a)** Crows mobbing a hawk. Mobbing behavior is elicited by recruitment. Photo from Tom Murray on Flickr (Creative commons license). **(b)** Foraging group of magpies scavenging from a carcass in winter. Photo from Jim Peaco of the National Park Service, public domain. **(c)** Ongoing fight between two ravens where a bystander is about to intervene on behalf of the victim or aggressor. Photo from Ref. [33]. **(d)** Crow vocalizing to a visual cue in front of a touchscreen monitor. Photo from Andreas Nieder.

also has affective components [53]; Prosody reflects internal states and can be more informative than emotional lexical content. However, in addition to affective influences, humans can deliberately produce speech sounds. So, the question remains whether non-human animals, like corvids, can also bring their vocalizations under cognitive control.

To test this, we trained crows to call on command in a controlled laboratory environment (Figure 2d). When carrion crows were trained to initiate or withhold vocalizations in response to visual cues (colored squares on a computer monitor), they could volitionally do so (Figure 3a [54]). The start of each trial was followed by a variable delay before either a Go cue prompted vocalization or a No-Go cue prompted inhibiting a response. They performed well above chance (Figure 3b).

Inspired by studies in black-capped chickadees (*Poecile atricapilla*) who scale the number of 'dee' notes in their alarm calls with the size of the predator, thereby conveying the magnitude of perceived threat [55], we extended this work to evaluate if crows could control not only the initiation but also the number of vocalizations [3]. We trained three carrion crows to flexibly produce 1 to 4 vocalizations in response to arbitrary stimuli (Figure 3c). They successfully controlled the number of vocalizations, reflecting signatures of the approximate

Figure 3



Uncovering behavioral and neural mechanisms for flexible vocal production in crows. (a) Visual Go-No Go detection task requiring the crow's vocal response. After a variable waiting period indicated by a white square, a blue square (i.e. the GO cue) appeared on 80 % of trials prompting the crow to produce a vocalization to receive a food reward. On the other 20 % of trials, the white square remained (catch trials) and the crow refrained from vocalizing. **(b)** Hit and false alarm rates across ten sessions for all 3 crows. Subplots A&B are adapted from Ref. [54]. **(c)** Vocal production task in which crows had to produce a defined number of 1–4 vocalizations. A visual or auditory cue instructed the crow to produce an associated number of vocalizations. After producing the vocal sequence, the crow had to peck the screen ('enter key') to report it was done. **(d)** Behavioral performance curves of the three crows combined for visual (left) and auditory cues (right). Colored functions show how often the crows produced a specific number of vocalizations when a specific target number (peak of the respective functions) was cued. Subplots C&D are adapted from Ref. [3]. **(e)** Two example neurons recorded from crow NCL while a crow performed the task shown in A (Top, each dot represents an action potential; Bottom, spike-density function). This neuron increases (left) and decreases (right) neuronal activity during trials with volitional vocalizations (Hit) compared to trials without vocalization (Miss). Subplot adapted from Ref. [80]. **(f)** Example number-selective neuron recorded from crow NCL during a non-vocal task. The crow saw either a dot array or a numeral the crow had learned to associate with a given numerical value as instruction stimuli. After a delay, the crow translated the cue into the corresponding number of pecks. This example neuron showed highest activity for instructed number 1 for both dot and sign protocols. Subplot adapted from Ref. [2].

number system, such as numerical distance and size effects (Figure 3d). Longer reaction times were noted for higher numbers, and the acoustic features of the first vocalization predicted the sequence's total number, suggesting vocal planning. This study demonstrates that crows can control an abstract, cognitive feature of a vocalization—its number. These results indicate that evolution has enabled corvids to bring vocalizations under cognitive control, a skill previously only demonstrated in nonhuman primates with their vastly distinct brain anatomy [11]. In summary, while animal vocalizations are presumably often driven by arousal states, the ability to volitionally control vocalizations suggests a more complex interplay between affect and cognition [56].

Vocal flexibility in non-corvid songbirds relies on their brain's song system

Corvids are not the only songbirds exhibiting vocal flexibility. Different non-corvid species can adjust the timing, pitch, sequence, or length of repetitions of their vocalizations, vocal flexibility that has been shown to rely on a special set of song-related brain nuclei, the 'song system'. The two pathways of the song system [10] both extend from the vocal premotor nucleus HVC (proper name): (1) The song motor pathway (SMP), driving vocal production in a moment-to-moment fashion via the robust nucleus of the arcopallium (RA) [10,57], which drives vocal brainstem motoneurons directly and via a vocal midbrain structure: the dorsomedial nucleus of the intercollicular complex (DM [10,58]. (2) The anterior forebrain pathway (AFP), enabling vocal motor exploration and, therefore, vocal learning [59,60] (Figure 1b). HVC receives sensory information from multiple modalities, including auditory, visual, and somatosensory inputs [61,62]. This suggests that song system dynamics can be influenced by environmental cues resulting in cases of vocal flexibility that we briefly discuss below.

Flexibility in 'song': pitch, sequence, repetition, and timing of vocalizations

Even though the adult zebra finch's single courtship 'song' remains stable throughout the bird's life, individual vocal elements (i.e. syllables') can be altered experimentally by targeting them with distorted auditory feedback (DAF), such as short bursts of white noise [63,64]. Here, birds learn to adjust the pitch of specific syllables to evade disruptive feedback and this ability builds on a mechanism for active song maintenance that relies on an intact AFP [64]. In Bengalese finches (*Lonchura striata* domestica), not only the acoustic features but also the sequencing of syllables can be modified experimentally with aversive DAF or a social reward (i.e. a video of a conspecific) [63,65]. These experiments leverage the spontaneously occurring variable syllable transitions in the Bengalese finch's song, which are also a feature observed in canaries [66,67]. In both species, HVC neurons reflect sequence variations by encoding not only syllable identity but also their sequential position relative to previous or following syllables [66,67]. Additionally, manipulations of different song nuclei can increase or decrease sequence variability such as the number of syllable repetitions, highlighting the causal involvement of the song system in the flexible modulation of 'song' content [51,65,68,69].

This vocal flexibility is present in other social contexts. Tracking the development of affiliative 'stack' and 'tet' interactions between newly formed zebra finch pairs reveals that over days, acoustic features of these vocalizations converge as they become tightly-coupled exchanges [30]. Playback regimes demonstrate that both male and female birds can dynamically adjust their vocalization timing to prevent overlap [30]. This flexibility in timing declined with RA lesions and is controlled by inhibition in HVC [70]. Interestingly, the female zebra finches' ability to flexibly adjust the timing of their vocalizations was on par or exceeded those of males, suggesting that their anatomically smaller 'song system' is sufficient for the temporal coordination of vocalizations [30]. While the song system in carrion crows is essentially the same as in other songbirds, in carrion crows, unlike in female zebra finches, the sexual dimorphism is absent, making the song system nuclei in female crows indistinguishable in size from those in males [12]. Females 'sing' in over 70 % of songbird species suggesting that female vocal learning is ancestral [71] and should be studied more [27,28]. For example, pairs of white-browed sparrow-weavers (*Plocepasser mahali*) synchronize their duets using the auditory feedback generated by the vocalizations of the duet partner to alter ongoing HVC activity locked to each individual's own vocalizations [72]. Taken together, these studies provide important insights into how the 'song system' contributes to vocal flexibility at the level of the neural circuit. However, it remains unclear how neuronal dynamics enable ultra-flexible vocal behavior, such as the common nightingale's (*Luscinia megarhynchos*) ability to immediately imitate vocal elements of conspecific rivals or of a whistling human experimenter [73].

Neural circuits bridging cognitive and 'song' functions

Cognition without a neocortex

Many of the cognitive abilities observed in corvids were traditionally believed to be exclusive to primates, which have a layered 'cerebral cortex' in the telencephalon [1]. However, birds don't have a layered cerebral cortex. Instead, since diverging from their common ancestor with mammals approximately 320 million years ago, they have evolved the pallium into distinctly different integration centers, known for their nuclear organization [1]. The corvids' pallium is tightly packed with neurons, so much that its neuronal densities substantially exceed those found in mammals [74]. Remarkably, ravens have the same number of pallial neurons as a capuchin monkey, even though the capuchin's brain is four times as heavy. As neurons are the processing units of the brain, this unusually high neuron count likely contributes to corvid intelligence [75].

NCL as a cognitive integration center involved in volitional vocal production

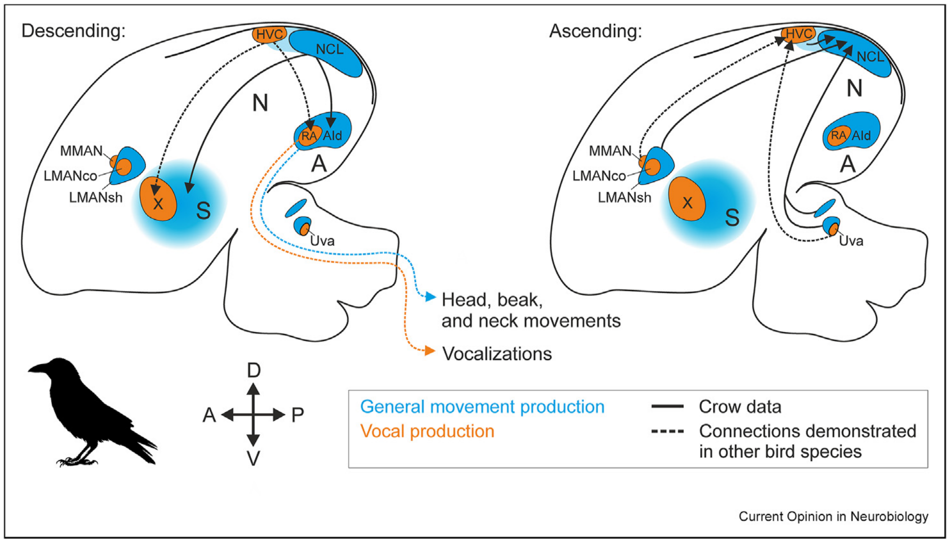
Within the avian pallium resides a high—level association area termed 'nidopallium caudolaterale (NCL)'. The NCL has all the anatomical features the brain's central executive requires: input from (secondary) sensory areas, connections with hippocampal structures to support long-term memory and spatial cognition, links with limbic structures representing internal states, and direct outputs to motor areas permitting goal-directed actions [76,77]. Reflecting its complex connectivity, a recent multitude of studies has demonstrated the involvement of NCL neurons in various higher cognitive functions [78,79]. Among these functions, the representation of quantity is a particularly interesting example (Figure 3f) [2,6,8] given the crows' ability to flexibly control the number of their calls (Figure 3c,d [3]). Together, these findings prompt the question of whether NCL activity can affect vocal production through direct or indirect connections to any of the song system's nuclei.

As a first step to investigate whether the NCL is involved in vocal production, we recorded single—neuron activity from the NCL in crows while they vocalized upon command in a controlled experimental setup. Activity of NCL neurons could predict whether crows would produce an instructed vocalization or not (Figure 3e [80]). Importantly, the neuronal activity observed during the preparation of volitional vocalizations differed from the activity preceding spontaneous vocalizations; these neurons signaled the voluntary initiation of vocalizations, rather than just any vocal output. However, it remains unclear how this signal may reach the 'song' system, which drives all vocalizations through brainstem vocal and respiratory nuclei (Figure 1b [10]).

NCL in the context of the song system

In crows and other songbirds, NCL is located directly lateral and posterior to the song premotor nucleus HVC in the caudal nidopallium [81] (Figure 4). Like NCL, HVC sits at the interface of ascending multisensory inputs and descending premotor outputs [61,77]. Although NCL is likely not monosynaptically connected to its neighbor HVC, its local connectivity extends medially invading the secondary auditory structure 'HVC-shelf', which, in turn, sends very sparse projections into HVC [82]. Although sparse, these fibers

Figure 4



Parallel descending and ascending connections of the vocal premotor nucleus HVC and the general premotor nucleus NCL. Dark blue: Selected structures of the crow's general motor system [83]. Light blue: continuity of NCL's local connectivity extending to the direct vicinity of HVC (i.e., HVC-shelf) [77,82]. Orange: Select nuclei of the crow's song system [12]. Connections between those nuclei (dashed lines) are inferred from and have been demonstrated in other songbird species [10]. Abbreviations: A, arcopallium; AId, dorsal intermediate arcopallium; N, nidopallium; NCL, nidopallium caudolaterale; DLM, nucleus dorsolateralis anterior, pars medialis; HVC, proper name; LMANco and LMANsh, core and shell of the lateral magnocellular nucleus of the anterior nidopallium; MMAN, medial magnocellular nucleus of the anterior nidopallium; RA, robust nucleus of the arcopallium; S, striatum; Uva, nucleus uvaeformis; X, area X. Figure adapted from Ref. [82].

could potentially route NCL signals to HVC and future studies will determine whether this input is relevant for flexible vocal production.

NCL is an integral part of the 'general motor pathway' [83] (Figure 4), which can control movements of the head, neck, and jaw [83,84]. Several related hypotheses on the evolutionary origin of the song system suggest that HVC is a specialized part of the NCL that could have diverged from NCL via pathway duplication [82–85]. In these frameworks, the 'general motor pathway' is seen as the evolutionary precursor of the entire song motor pathway (**cf.** Figures. 1 and 4) [82–85]. This scenario has functional implications for structures like the HVC-shelf (which engulfs HVC and appears to be continuous with NCL) or its downstream target RA-cup, which have been interpreted as accessory structures to the song system [81]. However, as aptly stated by Michael A. Farries (2001) [83]: "*These accessory structures may be nothing more than the oscine equivalents of the non-oscine regions* [i.e., the general motor pathway] *from which the song system emerged, structures that were literally pushed aside by the growth of specialized subdomains within them that became the song system.*" Following this argument, the vocal domain and the 'general motor' domain of the songbird brain may function largely independently.

Indeed, recent evidence strongly supports the idea of two parallel vocal and non-vocal systems. Parallel to HVC's projection to the song motor nucleus RA, dense NCL fiber bundles project to the avian 'motor cortex' analogue: the dorsal intermediate arcopallium (AId) (Figure 4) [77,81,86]. The molecular and cellular properties of AId and RA are astoundingly similar, suggesting a homology between these two motor areas [86]. Nonetheless, there is no good evidence for an anatomical connection between AId and RA, via which the general motor pathway could influence the SMP [83]. Furthermore, NCL's dense projections to the AId do not protrude into RA in crows and other songbirds, except for extremely sparse individual axons [81,82,87]. Thus, the arcopallium is currently an unlikely location for NCL's influence on vocal flexibility.

Downstream, RA projects to a midbrain structure (DM) that drives vocalizations [10,58]. Electrical stimulation of DM in corvid and non-corvid songbirds elicits vocalizations [88,89]. Interestingly, in non-songbird species, the nucleus DM cannot be identified based on hodological characteristics but electrical stimulation of the mid intercollicular nucleus (i.e. where DM is located in songbirds) also elicits vocalizations [90]. Whether the NCL has indirect access to these midbrain structures remains an open question and highlights the need for additional work on interactions between forebrain and vocal midbrain structures.

Further evidence for the idea that the song system has developed *within* the general motor system comes from the characterization of NCL's projections into the striatum [82,91]. Analogous to how individual HVC neurons in the songbird project either to RA or to the striatal area X of the AFP (c.f. Fig. 1B), pigeon (*Columba livia*) NCL neurons send their axons either to the AId or the medial striatum [91]. By characterizing the pattern of NCL's projections into the striatum relative to area X in crows, we recently found that area X itself is largely avoided by NCL axons while its vicinity is densely innervated (Figure 4 [85]). This finding supports the hypothesis of a 'general AFP' mirroring the connections of the song system's AFP [83].

Parallel (i.e., non-overlapping) projections can also be found on the input side of HVC and NCL ascending from the magnocellular nucleus of the anterior nidopallium (MAN) area and the thalamus (Figure 4) [82,92]. Interestingly, the songbird MAN area appears to fully overlap with the medial nidopallium/mesopallium complex (MNM) which is found in both pigeons and parrots (Budgerigar: *Melopsittacus undulatus*) [77,78,93]. Like NCL, the pigeon and parrot MNM, as well as the songbird MAN area, exhibit direct projections to arcopallial motor areas and are implicated in skilled sequential behaviors, including vocal flexibility [69,78,81,94]. Furthermore, the nidopallium and the mesopallium are associative telencephalic areas [76,77] that are enlarged in corvids compared to other birds [9,95]. Therefore, the corvid MAN area along with the overlying mesopallium form an important candidate region that may be involved in coordinating cognitive and vocal function.

Conclusion

In this article, we promote the wider adoption of corvid songbirds to study the behavioral and neural foundations of cognitive influences on vocal behavior. Behavioral evidence in both corvid and non-corvid songbirds shows that they have varying degrees of cognitive control over vocal production. Some important future directions include exploring how open-ended vocal flexibility interacts with establishing a vocal repertoire for different communicative functions. Additionally, uncovering how vocal flexibility and the associated brain networks change over an individual's lifetime will be important. Different corvid species also allow us to characterize differences in vocal behavior that co-vary with different life history strategies. Finally, beyond corvid species, comparing the neural mechanisms underlying degrees of vocal and cognitive flexibility with other intelligent avian species (e.g., parrots and pigeons) will provide valuable insights. From a neurobiological perspective, the key question is how the song system, which appears to be surprisingly isolated from the rest of the oscine brain, is accessed by the avian brain's central executive. Future research on this topic will uncover the general principles and constraints scaffolding the evolution of clever, vocal animals and their brains.

Declaration of competing interest

The authors declare no competing financial interests.

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Data availability

No data was used for the research described in the article.

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