

# Inside the corvid brain—probing the physiology of cognition in crows

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A wealth of behavioral data show that songbirds of the corvid family are endowed with exquisite cognitive capabilities. The neurophysiological basis of this behavioral flexibility has been addressed recently by recording single-neuron activity from the associative endbrain area nidopallium caudolaterale (NCL) in behaving crows. NCL neurons encode sensory and cognitive variables during working memory, but also participate in the translation of cognitive signals to motor behaviors. These findings highlight the NCL as the corvid brain's central executive. Intelligence in birds can be realized with an endbrain design that is radically different from the mammalian neocortex and developed independently via convergent evolution.

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## Introduction

The corvid family of songbirds (jays, jackdaws, crows and ravens) contains some of the most intelligent bird species. Corvids are renowned for their sophisticated behavioral repertoire and cognitive flexibility, traits originally believed to be found only in primates [1,2]. For instance, corvids manufacture and use tools [3,4], take into account the presence of conspecifics during social interactions [5,6\*], exhibit exquisite spatial memory [7], and show signs of episodic-like long-term memory [8]. Moreover, they flexibly provide for future needs [9], master tests of elaborate object permanence [10,11], and swiftly extract general principles to guide behavior [12–14,15\*].

Such behavioral flexibility might seem unexpected because a layered cerebral cortex, the highest integration center in the mammalian brain, is not existent in birds.

Instead of layers, the avian endbrain consists of nuclear organized circuits that originate from a different part of the telencephalic pallium which does not give rise to the neocortex in mammals [16–19]. With this independently evolved endbrain design, the corvid brain affords twice as many neurons as a primate brain of equal mass [20\*\*], adding up to enormous processing powers in a small and densely packed ‘birdbrain’ [21].

In order to enable behavior beyond simple stimulus-response association, brain areas that process information between sensory input and motor output are required. Association areas of the endbrain receive pre-processed information about the outside world from sensory areas. When combined with motivations represented in limbic networks and past experiences stored in memory systems, motor plans for meaningful responses are eventually formed and passed on to primary motor areas. The anatomical connection patterns of the pallial region ‘nidopallium caudolaterale’ (NCL) meet the requirements for high-level association areas. The avian NCL is a multimodal forebrain area that constitutes an integration center which receives input from all sensory modalities and projects to premotor structures, is modulated by dopamine, and interacts with limbic, visceral and memory-related structures. The NCL is therefore considered to be a functional equivalent of the prefrontal cortex (PFC) [22,23] that enables cognitive control in primates. This constitutes a fascinating example of convergent evolution of intelligence and cognitive control centers in the these vertebrates’ brains: However, the implications underlying structural differences between the nuclear avian pallium and the layered mammalian neocortex remain unclear.

The cognitively-advanced corvids provide a ‘window of opportunity’ to decipher the neurophysiological mechanisms of control functions based on different endbrain structures. Here I review recently established electrophysiological experiments in behaving carrion crows (*Corvus corone*) aimed at elucidating the workings of the NCL. The derived data provide novel insight into the role of an important corvid association area in complex cognition.

## Recording single-neuron activity in behaving crows

Measuring the electrical activity of neurons as physical carriers of cognition is key to understanding the workings of the corvid brain. As Barlow [24] wrote, “the neuron

remains the important unit of function for developing a rational account of how behavior is generated". Recording neuronal activity simultaneously with behavioral performance presents a rich and direct opportunity for experimental analysis of the neuronal foundations of cognitive functions that would not be possible in untrained animals.

To that aim, crows were trained to perform tasks that contain distinct task periods in which specific sensory, cognitive and motor representations can be investigated in a controlled way. Inspired by the success of nonhuman primate studies [25–28], variations of delayed response tasks have been used in combined behavioral–neurophysiological studies in crows. In such tasks, stimuli need to be encoded, maintained and processed according to task contingencies. Cognitive processes such as learning, memorization, categorization, association memory and rule switching can be disentangled and investigated

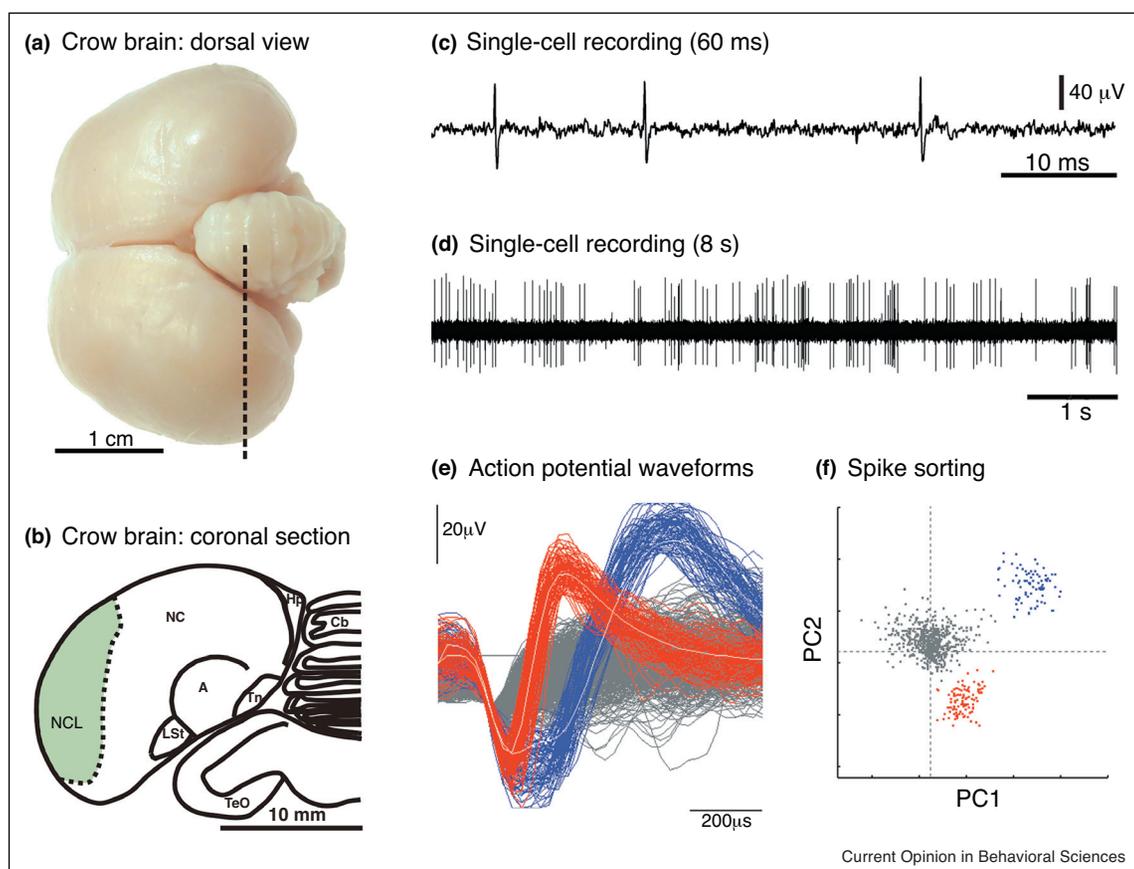
according to the specific task design. While the crows performed under stimulus control, the electrical activity of individual nerve cells (*i.e.*, their action potentials) was monitored by means of chronically-implanted and movable microelectrodes positioned within the NCL (Figure 1). Contributions of NCL neurons along the temporal trajectory of a single trial are described in the following: from encoding, maintenance and processing in working memory, until finally action selection.

## Neuronal representations in the NCL

### Sensory information

In order to fulfill its role as central executive, the NCL needs access to incoming sensory information. The relevance of sensory input needs to be evaluated and, if important, selected and integrated with other information common to the goal at hand. Many NCL neurons

Figure 1



Electrophysiological recordings in the endbrain of carrion crows. **(a)** Dorso view of a crow brain showing the large telencephalic hemispheres (left is anterior). Vertical dashed line indicates section level shown in B. **(b)** Coronal section through a crow's brain indicating the borders of the nidopallium caudolaterale (NCL) in the caudal telencephalon. A, arcopallium; Cb, cerebellum; Hp, hippocampal formation; LSt, striatum laterale; NC, nidopallium caudale; NCL, nidopallium caudolaterale; Tn, nucleus taeniae amygdalae; TeO, tectum opticum. **(c)** Example of a 60 ms recording trace with three action potentials from the NCL of a behaving carrion crow. **(d)** An 8 s recording trace from the NCL of a behaving carrion crow. **(e)** Action potential waveforms (red and blue, respectively) of two isolated NCL neurons. **(f)** The same waveforms as in (e) shown in the two-dimensional principal component space (PC1 versus PC2) used to sort single units. Two single-unit waveforms cluster together (red and blue) and are separated from each other and the noise distribution (gray). Adapted from Refs. [13,30].

represent basic visual features, such as global visual motion information [29]. An even larger fraction of NCL neurons (ca.  $\frac{3}{4}$  of the population) encode stimuli rich in sensory parameters (*e.g.*, complex images) [30]. NCL neurons are not only activated by visual stimuli, but often respond selectively to specific parameter modifications with increased discharge rates. Neurons are tuned to particular motion direction [29], or specific images [30]. Such selective sensory responses constitute the first processing step for discriminating sample items. As expected for telencephalic association areas that receive highly processed information from secondary sensory areas, average visual response latencies range between 110 ms and 150 ms [29,30].

### Abstract categories

Rather than representing each detail of a sensory stimulus, the classification of stimuli into behaviorally meaningful categories endows animals with superior behavioral flexibility. Classifying items according to their number is a particular abstract category. It allows animals to abstract from the sensory attributes of elements to arrive at the quantitative category ‘numerosity’. Ever since Koehler and his co-workers explored the numerical capabilities of birds [31], corvids have been known to excel relative to other birds. Recently, relative numerosity discriminations (*i.e.*, always choosing the larger of two sets) have been shown to exist in trained jungle crows [32], but also in untrained crows and jackdaws that spontaneously selected the larger of two small food quantities [33,34]. In tasks requiring absolute numerosity discriminations, carrion crows have been shown to discriminate the specific number of items in small [35<sup>\*</sup>] and large visual item sets [36]. They managed numerosity discriminations irrespective of the physical appearance of the array. For instance, when four dots are displayed in a square-like arrangement or as a straight line, both are judged as instances of numerosity four.

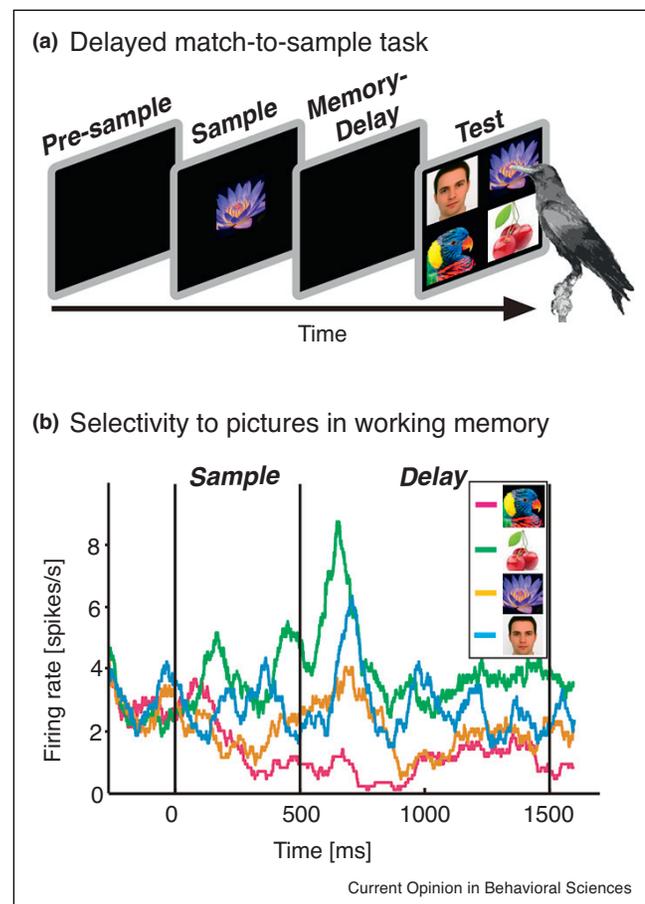
Subsequent recordings in discriminating crows found many neurons in the NCL that were tuned to individual numerosities ranging from 1 to 30 items. They show the largest discharge rates for their ‘preferred numerosity’ [35<sup>\*</sup>,37]. The characteristics of both the neuronal and the behavioral tuning functions showed close correspondence. Moreover, numerosity selectivity was impaired during error trials. Both findings argue that the neuronal discharge of NCL neurons is the neuronal basis for the crows’ performance.

### Retrospective working memory

To solve a delayed response task, features of sensory information need to be maintained ‘on line’ in working memory. Persistent (or sustained) neuronal activity throughout the memory phase of a delay period is widely believed to reflect active maintenance and goal-directed transformation of stimulus information in working

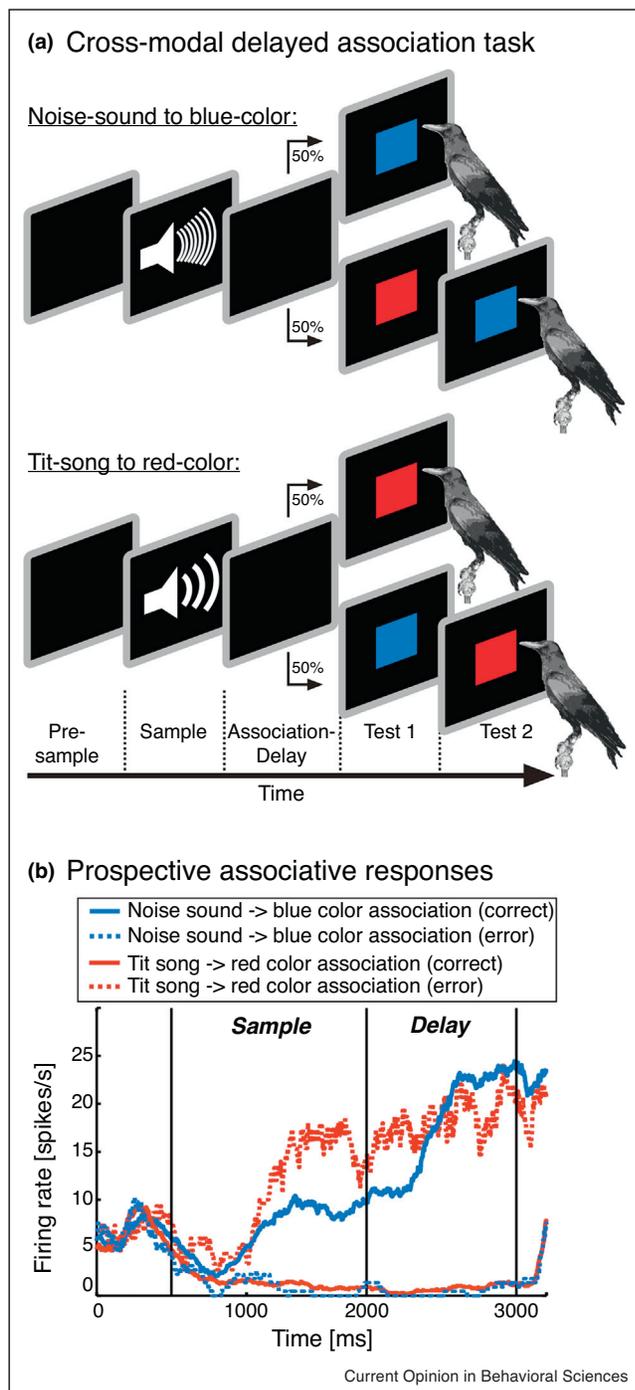
memory [25–28]. Since earlier attempts to attribute sustained delay activity in pigeons to working memory remained inconclusive because of the behavioral task [38,39], crows were trained on a visual delayed-match-to-sample (DMS) task using four different sample stimuli per session (Figure 2). Recordings showed that many NCL neurons temporarily maintain visual information after the stimulus disappeared [30]. Such neurons exhibited persistent and sample-selective activity during a brief delay period. Selective delay activity for the four sample images allowed the birds to hold relevant information in memory and correlated with discrimination behavior. This suggests that sustained activity of NCL neurons

Figure 2



Working memory coding in NCL during a delayed response tasks. (a) In the classical delayed match-to-sample (DMS) task, a sample stimulus was shown that the crow had to memorize over a brief delay period. In the final test period, the crow chose the image identical to the sample item from an array of four items by pecking at the correct choice image to receive a reward. (b) In crows performing the DMS task shown in (a), neurons selectively encoded the working memory of specific complex pictures. The spike density histogram shows the time course of the average and smoothed action potential rates of a single neuron to the four sample items. This example neuron maintained a significantly higher persistent activity for the cherry picture (green) during the memory delay. Vertical lines indicate onset and offset of the sample stimulus. Adapted from Ref. [30].

Figure 3



Cross-modal association activity. **(a)** In a delayed association task, crows were trained to associate two acoustic sounds with color images. If a noise sound was played as sample, the crow had to choose the blue color test image. If a tit song was played in the sample period, the red test image was the correct choice. In 50% of the trials, the first test color was a match, whereas the first test stimulus was a non-match in the other 50% of the trials. **(b)** When crows performed the delayed association task shown in (a), NCL neurons prospectively represent the associated color. This example neuron selectively encoded the crow's correct pairing of the noise sound with the color blue (solid blue line), but remained inactive for trials in which the crow

is a neuronal correlate of visual working memory in the corvid brain and serves to bridge temporal gaps as a workspace for processing immediately past visual information.

### Prospective associative signals

Simple memorization of fleeting sensory information is often not sufficient for adaptive behavior in ecological situations. Many of the complex behaviors exhibited by corvids depend on learned associations between arbitrary stimuli. Cross-modal associations in which the elements of a pair of associates belong to different sensory modalities are particularly challenging because they require integration of separate sensory channels [40,41].

To address the neuronal correlate of this capacity, crows were trained to associate each of two auditory signals with a visual item displayed after a brief delay time [42,43] (Figure 3a). During recordings, more than half of the population of recorded neurons showed association-selective activity. NCL neurons responded with sustained activity across the temporal gap for one of the paired associates, but not for the other. For example, the neuron displayed in Figure 3b showed elevated discharges during the delay whenever the crow associated a noise sound with the blue target, but remained silent when ever the crow responded to the tit song-red target association. That way, neurons signaled the memorization of the learned audio-visual associations. Associative activity was predictive of the crow's behavior: if a neuron did not represent its preferred association in trials in which this association was in effect, the crow made behavioral errors and associated the wrong stimuli. In this cross-temporal, cross-modal association task, sustained delay activity did not reflect a retrospective memory signal of the auditory sample but rather a prospective associative signal related to the upcoming visual associate [42].

To study the neuronal processes giving rise to association neurons, single neurons in NCL were recorded before and during association learning of crows [44]. The task was designed such that the progressive neuronal linking of novel sample stimuli to their associates could be followed and compared to the representation of already familiar associations that had to be retrieved from long-term memory. NCL neurons exhibited a common, prospective code for both familiar and newly learned paired associates [44]. Such associative neuronal representations were rapidly established for novel stimuli within the first

wrightly associated the tit song with the color red. Interestingly, such association neurons predicted the crow's prospective behavior; Whenever the crow erroneously chose the color blue after a tit song (red dotted lines), the neuron responded as if the noise sound had indicated an association with the color blue. Layout as in Figure 2b. Adapted from Ref. [42].

few trials of associative learning and were in accordance with the crows' behavioral accuracy.

These data emphasize that NCL rapidly establishes a task-relevant representation of sensory cues that belong together in working memory to guide the crows' flexible behavior. The corvid NCL has a role in synthesizing both external multi-sensory information and internal mnemonic data needed for goal-directed behavior.

### Conceptual rule activity

More important than associations between arbitrary stimuli are conditioned associations between sensory cues and the behavioral instruction, or rules, they signal. For instance, 'stop at red' is a very familiar and concrete rule that is based on simple stimulus-response associations. Intelligence, however, requires an understanding of abstract rules based on overarching concepts of how to act upon stimuli.

Abstract conceptual skills were demonstrated in crows performing relational matching-to-sample (RMTS) tasks [15<sup>\*</sup>]. In RMTS tasks, the relationship between objects constituting a sample ('same' versus 'different') is the feature to be discriminated. For instance, when presented with a sample showing two circles, crows chose a test card displaying two triangles (relational matching, or same-ness), but not the alternative card showing a triangle and a square, and vice versa.

To investigate whether crows would be able to understand and switch between abstract rules in an instant, crows were trained to alternate rule application in a delayed response task. In one trial condition, a rule cue indicated that a test image needed to be matched to the same preceding sample image ('same' rule). In the other trial condition, another rule cue informed the crow that a test image needed to be chosen that was different from the sample ('different' rule). Crows indeed apply these rules successfully with novel images, indicating that they had formed an abstract concept 'same versus different' that they could follow on demand based on rule cues [13<sup>\*\*</sup>]. During electrophysiological recordings, the most prevalent activity in NCL represents the behavioral rules, while abstracting over sample images and sensory modalities of the rule cues. A population of neurons discharged whenever the crows prepared for the 'same' rule, whereas a different ensemble of cells showed elevated firing rates whenever the 'different' rule was in effect. Rule coding was weaker in error trials, thus predicting the crows' behavioral decisions [13<sup>\*\*</sup>]. This suggests that the abstraction of general principles may be an important function of the NCL, mirroring the function of primate prefrontal cortex.

### Directed motor signals in visual search

The processing of cognitive information finally needs to result in the appropriate behavioral output. NCL also plays a role in motor behavior during the execution of movement following cognitive processing. In a DMS task, crows were trained to search and select the previously remembered picture in a choice array of four complex visual pictures on a touch screen. The crows exhibited patterns of performance and reaction times consistent with serial visual search of the choice screen [45]. During this period of visual search and visually guided directed motor behavior, single NCL neurons were strongly tuned to different target positions. NCL therefore also participates in the translation of cognitive processes to specific behaviors in the response period of a task.

Interestingly, the neuronal tuning of NCL neurons to different parameters was not rigidly determined, but could rapidly change according to task demands. This tuning flexibility of NCL neurons is reminiscent of the responses of PFC neurons that can encode a variety of cognitive factors during delayed response tasks [26]. PFC neurons are known to dynamically adapt their tuning properties to different task demands, both at the level of single neurons [46–48] and as a population [49,50]. Perhaps cognitive flexibility in corvids and primates depends on the capacity of the NCL and PFC, respectively, to dynamically encode task relevant information. This property could be a key computational feature facilitating the emergence of complex cognitive behavior in vertebrates.

### Conclusion

Over the last few years, crows have been established as a fascinating model organism in systems neuroscience. The presented findings in corvids emphasize that intelligence in vertebrates can be realized with an endbrain design that is radically different from the mammalian neocortex and independently developed via convergent evolution. Understanding the neuronal code for cognitive control in the corvid brain and comparisons with the primate brain will help clarify neurophysiological solutions that evolution may have found for different vertebrate endbrains. Such data will help to decipher the general principles and evolutionary constraints for the design of clever vertebrate brains [51].

### Conflict of interest

The author declares no conflict of interest.

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