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Neuroscience of cognitive control in crows

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Crows, a group of corvid songbird species, show superb behavioral flexibility largely stemming from their advanced cognitive control functions. These functions mainly originate from the associative avian pallium that evolved independently from the mammalian cerebral cortex. This article presents a brief overview of cognitive control functions and their neuronal foundation in crows.

Crows as cognitive high performers

Crows and ravens comprise a group of roughly 50 species of the genus *Corvus* in the family Corvidae, or corvids, a family of songbird species (order Passeriformes) (Figure 1A). As versatile opportunists, crows are distributed worldwide and have coexisted with humans for thousands of years. This and their unusual intelligence have made them the frequent subjects of mythology and folklore. In Norse mythology, for instance, the god Odin possesses the two ravens named Huginn ('thought') and Muninn ('memory') that fly all over the world to gather information as a foundation of Odin's powers.

Crows possess superb cognitive control functions (also called 'executive functions'). These brain processes are internally generated (top-down) and are recruited when automatic stimulus–response associations and habits are inadequate for mastering unexpected challenges. Cognitive control comprises three core functions that can all be found in crows: working memory, inhibitory control, and cognitive flexibility [1].

Crows exhibit all the characteristics of genuine working memory when briefly memorizing and processing relevant information while safeguarding it against distraction. With a working memory capability of up to four features, they rival monkeys. In addition to keeping past memories retrospectively 'online', working memory also allows crows to prospectively plan ahead into the near future, for instance when planning the number of self-generated actions (Figure 1C) [2].

Crows exert inhibitory control (subdivided into 'interference control' and 'self-control') by controlling their attention, behavior, or affect to override prepotent representations or external lures. As a sign of interference control, crows manage to sustain their voluntary attention to maintain focused while resisting distractions. In addition, crows demonstrate advanced self-control in delay of gratification tasks by ignoring less preferred but immediate rewards while waiting for up to 5 minutes for better but temporally delayed rewards [3]. Pigeons, by contrast, find it difficult to wait even for a few seconds and prefer to opt for the smaller immediate reward [3].

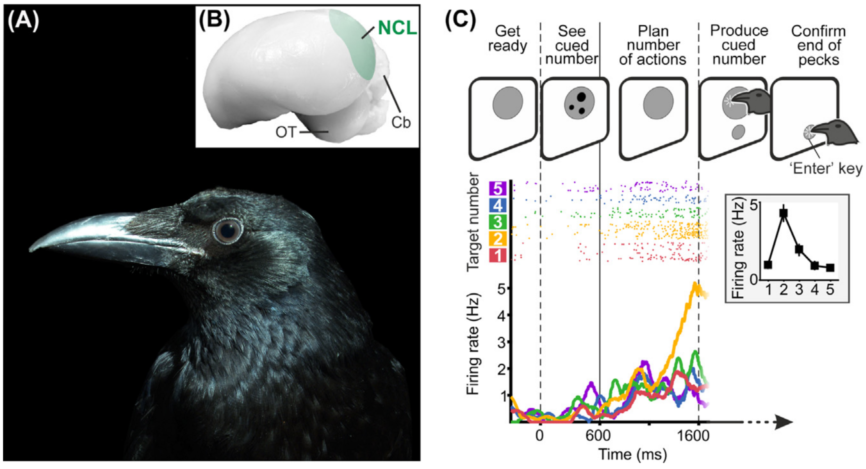
Behavioral flexibility is witnessed when corvids understand the principles of goal-directed tasks and choose between strategies when the 'rules of the game' change. For instance, crows can switch in an instant between two abstract principles applied to image pairs (e.g., 'choose same picture' vs. 'choose different picture'), even for pictures they have never seen before [4], whereas other birds such as pigeons struggle with such tasks. Clearly, cognitive flexibility allows crows to go beyond fixed stimulus–response action patterns.

Outside the laboratory, crows use and combine several of these executive functions to end up with rich behaviors in ecological contexts. For instance, crows have been reported to manufacture tools and even use tools designed to manipulate other tools ('meta-tool use') [5]. Crows also harness their cognitive skills to meet the additional demands of social life when collaborating with partners or outwitting their rivals [6]. All these cognitive behaviors are characterized by a high degree of reflectiveness and goal-directedness, hallmarks of cognitive control.

Intelligence originating from the crow telencephalic pallium

Many of the cognitive feats of crows have been traditionally thought to be restricted to primates where they are attributed to the cerebral cortex or 'neocortex', a uniquely mammalian layered structure in the pallial telencephalon. However, birds do not have a layered cerebral cortex. Instead, they have evolved the pallium into radically different and more nuclear integration centers since diverging from their common ancestor with the mammalian lineage ~320 million years ago. The crow pallium is tightly packed with neurons, so much so that its neuronal densities substantially exceed those found in mammals [7,8]. Remarkably, corvids have the same or greater telencephalic neuron counts as monkeys with much larger brains. As an example, ravens have the same number of pallial neurons (~1.2 million) as a capuchin monkey, even though the capuchin monkey brain is fourfold heavier [7]. Because neurons are the processing units of the brain, this unusually high neuron count likely contributes to corvid intelligence [9].

Within the avian pallium resides a high-level association area termed the 'nidopallium caudolaterale' (NCL) (Figure 1B). The NCL has all the anatomical substrates that the brain's central executive requires: input from all (secondary) sensory areas,



Trends in Neurosciences

Figure 1. The telencephalic brain area 'nidopallium caudolaterale' (NCL) of crows contains neurons representing cognitive control functions. (A) Photograph of a carrion crow (*Corvus corone*). Photo courtesy of Tobias Machts. (B) Lateral view of a crow brain (left = anterior). The nidopallium caudolaterale (NCL, green color) is located at the posterior pole of the telencephalic pallium. Abbreviations: Cb, cerebellum; OT, optic tectum. (C) NCL neurons signal the planned number of self-generated pecks. (Top) Task layout. Crows were trained to judge the numerical values from 1 to 5 in cue displays (numerosity 3 shown as an example) and to flexibly plan and perform a matching number of pecks. After the presentation of the cue numerosity, a motor planning period enabled the crows to prepare the number of pecks. Next, the crows needed to generate the number of pecks matching the numerical values of the cue stimulus by pecking on a touch-sensitive screen. To indicate the final peck amounting to the instructed number, the crows had to peck at an 'enter key'. (Bottom) Neuronal activity of a NCL neuron (temporally correlated with the task layout) recorded while a crow performed the task. During the planning period, number-selective sensorimotor neurons increased their activity in response to a specific impending target number. This example neuron increased firing when the crow planned two pecks (orange curve). Neuronal activity is shown as dot raster histogram (top panel, each dot representing one action potential) and as corresponding spike-density functions. Responses to specific numerical values are color-coded. Inset (right) shows the tuning curve of the neuron during motor planning (after [2]).

connections with hippocampal structures to support long-term memory and spatial cognition, links with limbic structures representing internal states and needs, and output to (pre-)motor structures permitting goal-directed actions. The NCL is often called a functional equivalent of the prefrontal cortex (PFC) – the part of the cerebral cortex that fulfills these functions and contributes crucially to many high-level cognitive functions in primates including humans.

Supported by a recently published anatomical atlas to navigate the crow brain [10], the neurophysiological mechanisms underlying crow executive functioning can be studied under controlled conditions in behaviorally trained crows. While the crows perform tasks employing varying subcomponents of executive functions, simultaneous recordings of neuronal activity reveal the neuronal mechanisms of corvid control functions. This line of research showed that neurons in the crow NCL – similarly to their counterparts in the primate PFC – orchestrate processes along common themes in the service of cognitive control. Neurons in the NCL group incoming percepts into meaningful categories that can be seemingly effortlessly generalized to new circumstances. For instance, NCL neurons are tuned to cardinal number ('numerosity') of set sizes and can represent the learned magnitude categories [11]. NCL neurons can hold information 'online' in working memory to bridge temporal gaps between events, actions, and consequences, as well as for processing information in an instant according to abstract principles such as 'same' versus 'different' [4]. As a signature of complex planning behavior, specialized NCL neurons signal how perceived numerical information in working memory is translated into the number of self-generated actions (Figure 1B) [2]. Given the active and voluntary nature of cognitive control functions, it is conceivable that even the subjective experiences of crows are actively represented by NCL neurons as a marker of their sensory consciousness [12].

Concluding remarks

Crows show advanced cognitive control functions that endow them with great behavioral flexibility, allowing them to efficiently adapt to changing environments. These cognitive control capabilities emerge in the avian brain which exhibits a building plan radically different from that in mammals and lacks the organization of the mammalian cerebral cortex. Within the pallial telencephalon, executive functions emerge from the workings of the associative brain area NCL that operates at the apex of the telencephalic hierarchy. Neurons in the crow NCL encode categories, signal the application of abstract concepts, represent the maintenance and manipulation of memory contents, and predict the planning of impending actions, all processes that seem to be subjectively experienced by the crow. During the convergent evolution of complex cognitive skills in birds and mammals, the crow telencephalon was shaped via comparable selection pressures and computational demands. The crow pallial endbrain therefore constitutes a fascinating evolutionary variant to the primate cerebral cortex. Leveraging this line of research in crows will provide unique insights into the evolutionary trajectories of cognitive control functions.

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Declaration of interests

The author declares no conflicts of interest.

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