Inside the Parrot Beak-and-Tongue Apparatus: Unlocking a Model System for Dexterity Research

Özge Nasa[1] and Alice A. M. I. Auersperg[2]

[1] Messerli Research Institute, University of Veterinary Medicine Vienna, Austria

[2] Messerli Research Institute, University of Veterinary Medicine Vienna, Austria

Author Note

We have no conflicts of interest to disclose. We gratefully thank Dominique Homberger, Adam Hartstone-Rose, Mark O'Hara and Berenika Mioduszewska for kindly granting permission to reproduce or adapt figures from their publications. Their contributions have significantly enriched this review. This research was funded by the Austrian Science Fund (FWF) Project Y-1309.

Correspondence concerning this article should be addressed to Özge Nasa, Messerli Research Institute, University of Veterinary Medicine Vienna, Veterinärplatz 1, 1210 Vienna, Austria. Email: oezge.nasa@vetmeduni.ac.at

Abstract

Dexterity, the flexible and precise control of objects, requires the integration of cognitive abilities, motor coordination, and anatomical specializations. Due to the evolutionary significance of the opposable thumb, dexterity research has traditionally focused on primate species. However, based on a review of current knowledge in parrot morphology, cognition, and neurobiology, we propose that parrots represent a highly promising model system for dexterity research. We highlight lineage-specific morphological novelties that turn the parrot beak-and-tongue apparatus into a multifunctional tool, draw comparisons between the parrot tongue and the primate thumb, and showcase existing studies on Goffin's cockatoos that reveal advanced tool-related problem-solving abilities. Characterized by fine motor control, pronounced inter-individual variability, goal-directed behavior, flexibility, and the optimization of speed through learning, the Goffin's cockatoo model embodies the core components of dexterity.

Keywords: dexterity, motor control, animal cognition, parrot, tool use, object manipulation

Inside the Parrot Beak-and-Tongue Apparatus: Unlocking a Model System for Dexterity Research

"The still virtually absent motor cortex makes even the most gifted and highly developed birds ill-suited for the accumulation of personal experiences, for mastering new, complex motor skills, and particularly for displaying dexterity during unexpected, unpredictable motor problems." (Bernstein, 1996, p. 91)

The origins of dexterity research can be traced back to the pioneering work of the eminent scientist, Nicolai A. Bernstein, who wrote his seminal work, *Dexterity and Its Development*, in the 1950s. The fact that it was published posthumously, almost 40 years later, yet still received acclaim within its field, underscores how far ahead of its time it was. Its delayed publication was largely the result of political suppression, as Bernstein challenged the dominant Pavlovian view, endorsed by the Soviet regime, that movement and motor control consist solely of chains of conditioned reflexes. In his work, he sought to define dexterity by emphasizing the complex interplay between anatomy, physiology, motor control, problem-solving, and cognition. Although his framework was largely anthropocentric, the core principles he articulated remain highly relevant to contemporary studies of its kind (Bongaardt & Meijer, 2000).

General Background

Dexterity is a complex, multidisciplinary concept that resists simple definition due to its inherently cross-disciplinary nature (Metcalf et al., 2014; Yong et al., 2020). As the term *dexterity* in literature is often used interchangeably with related concepts such as motor skill, technical skill, skillful manipulation, and coordination (Diedrichsen & Kornysheva, 2015; Jeannerod, 1988; Latash, 2009; Wolpert et al., 2011), defining its boundaries is excessively difficult.

Most definitions of dexterity derive from occupational therapy research on the human hand (Yong et al., 2020). Poirier (1988, pp. 71-72) described dexterity as "manual ability that requires

rapid coordination of gross or fine voluntary movements, based on a certain number of capacities, which are developed through learning, training, and experience." Backman et al. (1992, p. 209) defined dexterity as "the fine, voluntary movements used to manipulate small objects during a specific task, as measured by the time required to complete the task." Yong et al. (2020, p. 1) described dexterity as "the coordination of voluntary movement to accomplish an actual or simulated functional goal/task accurately, quickly, resourcefully, and adapting to environment or change." Finally, Bernstein (1996, p. 228) defined dexterity as "the ability to find a motor solution for any external situation, that is, to adequately solve any emerging motor problem correctly (i.e., adequately and accurately), quickly (with respect to both decision making and achieving a correct result), rationally (i.e., expediently and economically), and resourcefully (i.e., quick-wittedly and initiatively)."

Most of these definitions share similar core ideas that can roughly be broken down to four components: 1. Motor control as the physical display for dexterous movements. 2. A goal or task specific agency that can be extrinsically or intrinsically motivated. While motor control provides the physical basis for the movement(s), the purpose and goal behind the action, the "why", is emphasized to be just as critical as the "how" (Jeannerod, 1988; Osiurak & Danel, 2018). 3. The development and refinement of dexterity driven by learning, training and adaptive flexibility. 4. Finally, the key characteristics of dexterous movements are identified as adequacy, resourcefulness, and accuracy, which can be collectively summarized under the broader concept of efficiency.

However, these components are difficult to consider in isolation, as they often are prerequisites of each other, interact and overlap (Steinberg & Bock, 2013). As Bernstein (1996, p. 146) observed: "Actions are not simply movements. Most of them are whole sequences of movements that together solve a motor problem. Each such chain consists of different movements

that replace one another systematically, leading one to a solution. All the movements, parts of such a chain, are related to each other by meaning of the problem. If you miss one of the links of the chain or mix up their order, you will fail to solve the problem."

The core challenge of motor coordination lies in managing the redundant degrees of freedom (DoFs) inherent in the effector system (for example, the body, the hand, or both), also called Bernstein's "degrees of freedom problem" (Bernstein, 1996; Morasso, 2022). The complexity of motor control increases even further when moving an object in that hypothetical space, as the effector must additionally account for and integrate the object's physical properties, such as its mass and inertia, which can only be accurately determined through exploratory movements (Mangalam et al., 2021). In essence, the "degrees of freedom problem" arises because the brain must select a specific combination of these independent variables to achieve a desired outcome by navigating a vast space of possible movements. Task requirements, innate ecological predispositions for specific actions, as well as training and learning can all enable establishing a movement pattern neurophysiologically, e.g., fixing the use of specific degrees of freedom best suited for the given task (Araújo & Davids, 2011). On the other hand, if an animal is facing unpredictable tasks with variable affordances, trying to rigidly fix pathways can be counterintuitive. Therein, identifying and executing optimal motor solutions, movement sequences that are quick, effective and energy-efficient in a given situation within the available degrees of freedom, is the key feature of dexterity, setting it apart from general motor skill, which does not inherently demand continuous, flexible and context-specific adaptations (Bernstein, 1996).

Dexterity can be deconstructed into multiple components, with motor control representing the most observable aspect and, therefore, often receiving the most attention. However, its foundation lies in the interaction between two principal domains: morphological structure and

cognitive capacity. It is this interplay that gives rise to dexterous behaviors, such as tool use (Figure 3).

In order to address the question of how dexterous manipulation arises in parrots, this article is organized into several interconnected sections. First, we review behavioral evidence for object manipulation and tool use to establish the functional expression of dexterity. Next, we examine the underlying morphological and anatomical specializations of the beak-and-tongue apparatus. Finally, we consider the neural systems that support these movements. Together, these perspectives provide a comprehensive framework for understanding how behavioral, anatomical and neural factors converge to enable dexterous control in parrots.

Dexterity, its Assessments and Tool Use

In most clinical studies, primate hand dexterity is assessed using board-based tasks, where subjects retrieve food items from narrow wells (Chatagny et al., 2013; Kaeser et al., 2014; Pizzimenti et al., 2007; Won et al., 2020), or maze-like tasks, in which food must be obtained through barriers or detours (Frye et al., 2021; Kim et al., 2020; McEntire et al., 2016; Tsuchida et al., 2003). However, these tasks typically focus on quantitative measures such as performance time or task success within a set time frame, features commonly associated with dexterity, but few consider the quality of movement, adaptability, resourcefulness and the ability to respond to changing environments (Elangovan, 2022; Steinberg & Bock, 2013; Yong et al., 2020). These limitations likely stem from the lack of distinction between "dexterity" and "hand function" and are reflected in these assessment tools. Mangalam and Fragaszy (2018) suggested that measuring velocity, trajectory and accuracy of movement, motor synergies and the changes in these variables over time are a few ways that could follow how dexterity is learned and applied.

Dexterity, like any biological trait, should be understood within an evolutionary framework, as it represents an adaptation shaped primarily by the demands of foraging (Gibson, 1986; Stephens & Krebs, 1986). The dexterity demands placed on extractive foraging animals can be substantial, particularly for tasks such as cracking open nuts or probing for food (King, 1986; Parker, 2015; Sanz et al., 2013; Shumaker et al., 2011). These demands increase in complexity when tool use is involved, as animals must then manage, in addition to the redundant degrees of freedom of their own bodies, those of an extended body-plus-tool system with altered dynamics (Mangalam & Fragaszy, 2016). For this reason, we aim to place object- and tool-related dexterity at the center of our analysis.

In their embodied theory of tool use, Mangalam and Fragaszy (2016) proposed that a tool modifies the boundary between the body and the environment by transforming a body-only system into a body-plus-tool system. This transformation introduces at least one external degree of freedom (DoF) while simultaneously reducing and redistributing the existing internal DoFs. Consequently, tool use presents the challenge of perceiving and adapting to these altered DoFs by identifying the relationships among the DoFs in the body-plus-tool system and actively monitoring and responding to them. From a biomechanical perspective, the use of an object qualifies as tool use only if the user regulates the DoFs of the body-plus-object system in a manner that differs from the control of the body-only system. This framework forms the basis of the more recent concept of "tooling" proposed by Fragaszy and Mangalam (2018) which we adopt in this work, as it aligns with the requirements for dexterity outlined above and illustrates how a tool can be used in a dexterous manner.

Usually, degrees of freedom are measured by the independent joint movements that can occur within a biomechanical system such as the body or a limb. Each joint contributes to the overall DoFs by allowing movement in one or more planes, such as flexion and extension or

abduction and adduction (Li, 2006). When all joints of the human hand and wrist are considered, it typically exhibits around 27 anatomical DoFs (Rahman & Al-Jumaily, 2013). Some animals use non-jointed, hydrostatic structures, such as lips, tongues, trunks, or tentacles, to grasp objects (Costes et al., 2024; Kier, 2012). Unlike jointed limbs with discrete degrees of freedom (DoF), these organs require an approximate framework to describe their motions. For instance, octopus arms lack a rigid skeleton and function as muscular hydrostats, composed of densely packed muscle fibers arranged in various orientations. Despite their flexibility, these arms can reconfigure into stiffened, quasi-jointed structures, enabling movements similar to those of vertebrate limbs (Zullo et al., 2022).

This implies that, from a purely morphological perspective, animals whose bodily characteristics encompass a higher number of DoFs possess a greater potential for dexterous tool use. Becoming a tool user is of course not solely dependent on morphological possibility. For example, from a purely morphological perspective, capuchins and baboons exhibit a higher manipulative potential in their hands than chimpanzees; however, in terms of actual tool use behavior, chimpanzees are significantly more advanced tool-users (Liu et al., 2016) and although gorillas have hand proportions closer to humans than chimpanzees (Almécija et al., 2015), only the latter use tools in the wild. Morphology alone cannot account for advanced dexterity and manipulation without considering the facilitating role and evolutionary development of the brain and the ecology of the respective species (Almécija & Sherwood, 2017; Baker et al., 2024; Napier, 1962). Cognitive ingredients for the development of tool use that have been proposed to include working memory capacity to enable the hoarding of information but also the ability to recombine information and to learn concepts (Call, 2013; Hunt et al., 2013). An important ecological predisposition seems to be a propensity to manipulate objects and particularly to combine objects (Auersperg et al., 2014b; Call et al., 2013; Cenni et al., 2024; Rat-Fischer et al., 2014; Tan, 2017).

This highlights the critical role of neural circuitry, including sensory processing and motor planning areas, in enabling complex tool use.

Gripping and Grasping: Primate Hand versus Avian Beak

To manipulate objects dexterously, animals must first secure them through gripping or grasping. Due to the evolutionary significance of the opposable thumb, research on gripping has mainly focused on human and non-human primate hand models (Karakostis et al., 2021; Kivell, 2021). The most widely recognized distinction in primate grip morphology is between *power grips* and *precision grips* (e.g. Marzke, 1997; as reviewed in Fragaszy & Crast, 2016), though a broader range of grip types exists (Christel, 1993). The power grip can be performed by all primates and is characterized by the simultaneous prehension of all digits pressing an object against the palmar surface (e.g. Napier, 1960). Precision gripping is defined to describe instances in which the object being manipulated is held between the palmar surfaces of the fingers and the opposing thumb (Napier, 1960). Old World monkeys and apes (except for colobus monkeys) can all, in principle, perform true pad-to-pad thumb opposition; however, their contact area and pressure are smaller than in humans (Alba et al., 2003; Christel, 1993). Consequently, when grasping e.g. small food items, they typically employ alternative precision grips, such as tip-to-tip or pad-to-side/thumb-lateral grips (Almécija & Sherwood, 2017).

Particularly noteworthy in terms of primate hand dexterity are in-hand movements involving the repositioning of objects within the hand through both simultaneous and sequential digit actions. For instance, to change the position of an object within the hand, chimpanzees have been observed holding the object between the index and middle fingers, then flexing these digits to draw it into the palm. Subsequently, the object is rolled over the index finger and grasped between the index finger and thumb, demonstrating a coordinated sequence of digit movements (Crast et al.,

2009). Moreover, different types of grips may be employed either simultaneously or in sequence to manipulate multiple objects. Beyond the standard pattern of grasping a single object in one hand, primates have also been documented using compound grips, in which multiple objects are held within the same hand. For example, a monkey may use a *storage grip*, a power grip involving the palm and digits 4 and 5, to hold one or more objects, while concurrently using digits 1–3 to acquire an additional object (Macfarlane & Graziano, 2009).

Fishing for various food resources with stick-like tools is one of the most frequently observed and well-documented examples of flexible tool use in the animal kingdom (Shumaker et al., 2011). In the wild, chimpanzees flexibly adjust both their choice of tools and grip types depending on the demands of the termite nest they forage from (Lesnik et al., 2015). They typically begin by using robust twigs in combination with power grips, and at times even employ their whole body, to perforate the nest's hardened exit holes. Once access is achieved, they switch to finer twigs and employ precision grips to fish for termites, flexibly alternating between grip and tool types if e.g. the initial perforations are not sufficient (Lesnik et al., 2015). This flexibility in tool use and grip types was also observed under experimental conditions (Bardo, 2016, 2017).

Alongside primates, birds are considered the most proficient non-human tool users (Emery & Clayton, 2009; Shumaker et al., 2011). While primates primarily use their hands for food acquisition and processing, birds rely on their beaks for similar functions. The term *"facial hand"* has gained some traction in recent literature (Bhullar et al., 2016; Wild, 2015; Wild & Zeigler, 1999), reflecting growing interest in comparisons between the primate hand and the bird beak. Unlike primate hands, bird beaks exhibit a far greater range of structural diversity, often highly specialized for specific dietary and ecological niches (Grant, 1999; Navalón et al., 2018; Olsen, 2017; Sheard et al., 2023; Zusi, 1993). However, although structurally different, hands and beaks can exhibit similar biomechanics. *Pinching*, for instance, defined as gripping an object between two body parts while

applying opposing forces, can occur either between digits or between mandibles (Deich et al., 1985; Sugasawa et al., 2021; Zeigler et al., 1980), and may be considered a form of precision grip.

Like great apes, some birds, mainly island-living species, also use stick tools to access food in hard-to-reach places such as crevices and holes. Among birds, woodpecker finches (*Cactospiza pallida*) were the first species reported to use stick tools as probes to extract insect larvae from tree crevices (Eibl-Eibesfeldt, 1961; Eibl-Eibesfeldt & Sielmann, 1962). These finches have demonstrated the ability to select tools of appropriate length, modify tools to meet specific task requirements (Tebbich & Bshary, 2004), and even manufacture tools from non-native plant species (Tebbich et al., 2012).

Stick tool use in the New Caledonian Crow (NC) has been extensively researched over the past three decades (Hunt, 1996). These crows display remarkable sophistication in manufacturing and using tools. They can produce both hooked and non-hooked tools from various plant materials to extract wood boring larvae from trees (Hunt & Gray, 2002) and can flexibly craft hooked tools from artificial materials, such as wire, in laboratory settings (Weir et al., 2002). They can also flexibly make, use and choose tools for purposes different to the wild in captive settings (e.g. Gruber et al., 2019; Hunt & Gray, 2004; von Bayern et al., 2009, 2018).

Notably the NC is not only dependent on tool obtained food (Rutz et al., 2010), it is also morphologically adapted to tool use. Its beak is relatively straight compared to other *Corvus* species (Matsui et al., 2016). Moreover, the bill is deep, short, and stout, with a particularly straight cutting edge on the upper mandible and an upturned, reinforced lower mandible. Its shortness allows for higher in-lever/out-lever ratios when gripping stick tools between the mandibles, resulting in a stronger, more secure grasp, with the authors suggesting parallels to a precision grip (Matsui et al., 2016). The straight profile of the bill also minimizes obstruction of the crow's frontal visual field, providing a clear line of sight to the tool's working end (Troscianko et al., 2012).

Additionally, the tomium of the lower mandible curves upward toward the tip, creating a scooped profile that positions tools closer to the visual axis and reduces parallax errors during manipulation. Together, bill morphology and visual field guidance have likely coevolved to support the species' remarkable tool-using abilities (Matsui et al., 2016; Troscianko et al., 2012). Mangalam and Fragaszy (2016, p. 116) argued that "holding a probe in the beak adds one or more DoFs between the beak and the probe and redistributes the DoFs of the beak-only system by coupling the lower and upper jaws into a rigid structure that moves as a unit."

Considering this, New Caledonian crows possess fewer degrees of freedom in their beak-plus-tool system, which operates as a relatively rigid mechanism compared to the diverse grip types and in-hand movements seen in apes. Yet, in terms of the sophistication of their manufactured tools and their use, NC crows can match great apes in some respects (Klump et al., 2015, 2019). There is also evidence of cumulative technological evolution in NC crows (Hunt & Gray, 2003), underscoring how cognitive processes drive the dexterous output of the system, despite the mechanical constraints imposed by the DoFs.

Another bird species known for exhibiting tool use in the wild is the Kea (*Nestor notabilis*). This species was observed to purposefully and persistently use stick tools to probe into trap-boxes (originally meant for stoat population control), attempting to access bait (usually eggs) over the span of 2.5 years (Goodman et al., 2018). In captivity, Kea readily learn to use tools for extractive foraging in experimental settings (Auersperg et al., 2010, 2011). In a comparative study of tool-use innovation involving a multi-access box, keas were more haptically explorative and discovered more solutions in the first session than NCs, although NCs were more efficient in using stick tools (Auersperg et al., 2011). Due to the overlength of their strongly curved upper beak, which is an adaptation to digging in the ground, most kea struggled with innovating stick tool use, but a single subject named Kermit succeeded through a flexible multi-step technique including his feet: 1.

Kermit would pick up the tool at the proximal end by holding it between both mandibles 2. He would combine the proximal tool end with the tool opening (a small hole) 3. He would switch between his beak and his foot, still pressing the tool end against the opening. 4 Having freed this beak, he would then grab the distal end of the tool between his mandibles and start pushing the stick into the hole. Another notable example of innovative tooling is Bruce, a disabled kea. This 8-year-old bird, missing his upper mandible, devised a self-care tooling strategy by employing small pebbles to assist with preening (Bastos et al., 2021). Bruce systematically selected pebbles of appropriate size, secured them between his tongue and lower mandible, and ran them along his feathers; he retrieved or replaced dropped pebbles, used them in over 90% of object-preening interactions, and was the only individual in his group to exhibit this behavior (Bastos et al., 2021). Notably, Bruce can also refunction his tongue into what is usually achieved with the upper mandible when picking up objects from the ground: He uses his tongue to press the object down, against the lower mandible.

While keas seem to exhibit the cognitive prerequisites for tool use, their beak morphology presents significant challenges for precise stick tool manipulation. However, the example of the kea (and to some extent NCs) highlights the phenomenon that morphological limitations can be overcome by behavioral flexibility, supporting the principle of goal-directed behavior as the underlying driver of dexterity.

The Goffin's Cockatoos and Dexterous Tool Use

An interesting case of tool innovation was reported in a captive male Goffin's cockatoo (*Cacatua goffiniana*) named Figaro (Auersperg et al., 2012). Figaro consistently and reliably crafted and used stick-type tools to rake in food through a mesh-wired wall, skillfully manufacturing them from two different materials and employing a variety of steps and techniques. He also demonstrated remarkable flexibility in tool use, dynamically adjusting the position and movement

of his self-made tools to track a moving cashew target. His efficiency improved significantly across trials, indicating a learning curve in tool manufacture and manipulation. Later, in controlled experiments, this tool use was socially transmitted to other members of the group (Auersperg et al., 2014a). These and other studies paved the way for subsequent studies that eventually documented tool use in wild Goffin's populations on Indonesia's Tanimbar Islands (O'Hara et al., 2021) and in a feral population in Singapore (Mioduszweska et al., 2023, unpublished data; Osuna-Mascaro et al., 2018).

Several characteristics make tool use in Goffin's cockatoos particularly unique. They neither exhibit stereotyped tool use nor construct complex nests; instead, they breed in burrows, a trait considered ancestral to the species (Forshaw & Knight, 2010). As such, forming complex relationships between objects is not part of their innate behavioral repertoire (Kenward et al., 2006; Mioduszewska et al., 2019). The acquisition of tool use in this species is an individually acquired and innovative behavior that can be socially transmitted (Auersperg et al., 2012, 2014a; Laumer et al., 2017; Rössler et al., 2020). Captive Goffin's that acquire tool use via social transmission seem to engage in goal/result emulation, rather than strict imitation of observed behaviors (Auersperg et al., 2012, 2014a). Naïve individuals exposed to tool-using conspecifics develop their own techniques to solve tool-related tasks, rather than replicating the demonstrator's exact motor patterns. In contrast, NCs acquire functional tool use at an early age even in the absence of social exposure, while social cues seem to play a role in tool use refinement and culture (Holzhaider et al., 2010; Kenward et al., 2005, 2006).

Goffin's cockatoos demonstrate great flexibility in tool manufacture, crafting tools from a range of natural and artificial materials (Auersperg et al., 2016). For example, when presented with a large piece of cardboard, they use their mandibles to cut out a suitably sized strip by making a

series of small, precise bites along a straight edge, effectively perforating the cardboard parallel to its margin (Auersperg et al., 2016).

The Goffin's cockatoos appear to exhibit a degree of functional understanding of the tools intended function, even prior to active use. For example, they manufacture cardboard tools of varying lengths based on the depth of the test boxes, suggesting anticipatory adjustment to the task's demands (Auersperg et al., 2016, 2018). Further, they demonstrate the ability to assess tool functionality in decision-making tasks: when presented with a non-functional tool, they opt for an immediately available but lower-quality food item; however, when given a functional tool, they choose it over the immediate reward to obtain a higher-quality food item (Laumer et al., 2016).

Composite tool use refers to the concurrent use of two distinct objects, each serving a complementary role, to accomplish a single goal (Shumaker et al., 2011). This means not only managing the degrees of freedom (DOFs) of a single tool, but also simultaneously coordinating the independent DOFs of a second tool and their dynamic interaction. In captivity, Goffin's cockatoos have demonstrated composite tool use by first inserting a ball into a setup, followed by using a stick to push the ball toward a target, ultimately solving the task and retrieving a nut (Osuna-Mascaró et al., 2022). In line with this, they can flexibly recognize when a task requires a tool set (more than one tool) and are capable of transporting two tools simultaneously in their beaks when needed. This behavior resembles the *storage grip* observed in apes (Fragaszy & Crast, 2016) and demonstrates both advanced planning and the capacity to adapt their actions to the specific demands of a task (Osuna-Mascaró et al., 2023).

Finally, they consistently exhibit pronounced inter-individual variation in the styles and techniques employed to solve tool-related problems that present multiple degrees of freedom, highlighting both their behavioral flexibility and innovative capacity (Laumer et al., 2017; Nasa et al., in prep; Osuna-Mascaró et al., 2022). The three birds that succeeded in the composite tool

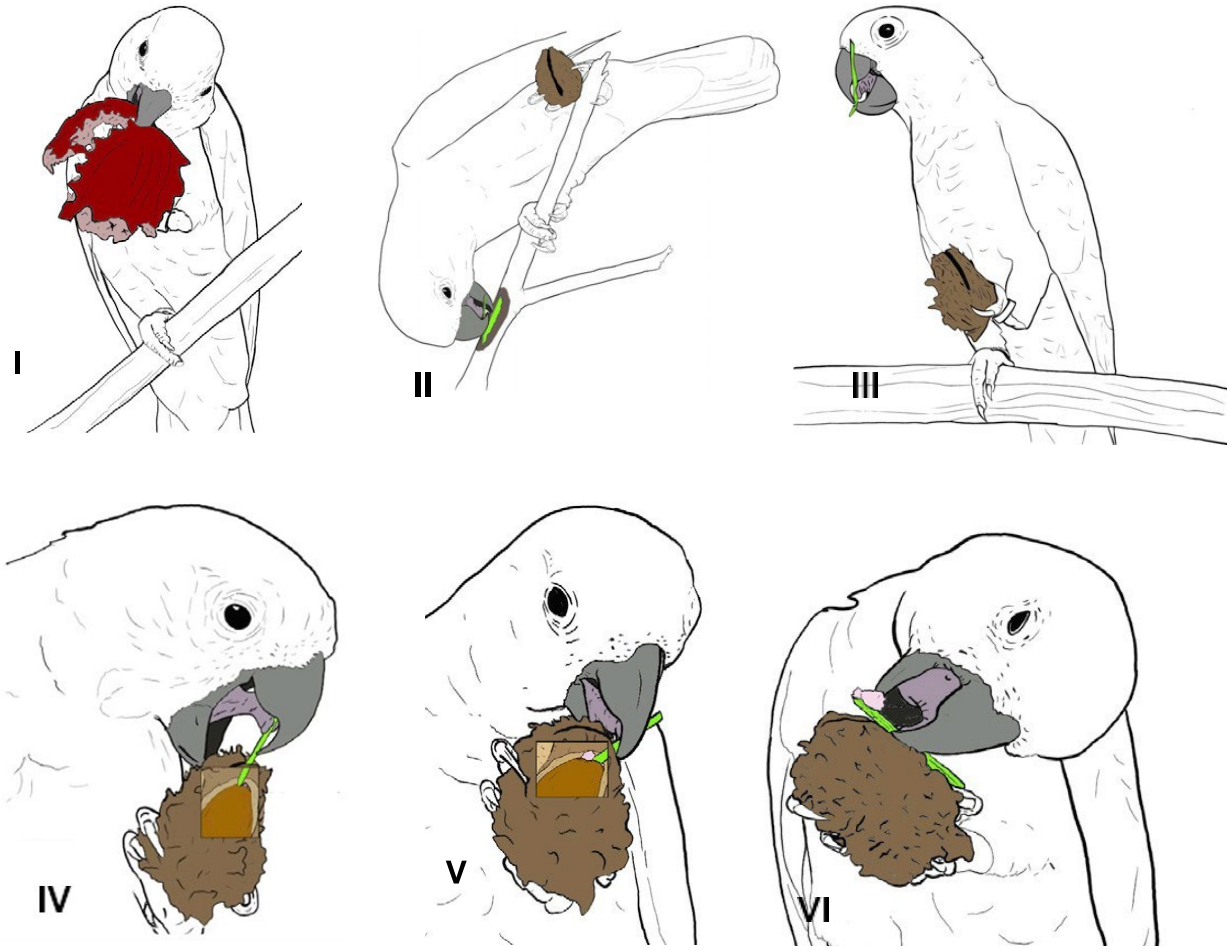
task, showed three distinct styles of solving the task: Figaro gripped the stick at one end with his beak and used a frontal insertion technique, swinging his head or walking forward to push the stick directly at the ball; he showed rapid improvement and high precision, even repositioning the stick if needed. Pipin uniquely used his foot to grasp and insert the stick, then guided it with his tongue and beak, demonstrating flexible coordination and positioning himself close to the ball for direct pushing. Fini gripped the stick near the front, often used her tongue to push it in repeated thrusts, positioned herself near the platform, and preferred a raking (pulling) motion through the lateral slits; she sometimes used her claw to move or even directly push the ball to solve the task.

In a following experiment, a seemingly simple stick-tool task involving a baited box with many degrees of freedom, ten Goffin's cockatoos demonstrated four distinct tool-use techniques: *Needling, Foot Insertion, Securing*, and *Figaro's Technique* (Nasa et al., in prep). These methods differed in various aspects, such as whether the bird primarily used its tongue, foot, or the box itself to stabilize the stick, and whether the stick was held at its proximal or distal end. These variations partly reflect earlier findings by Osuna-Mascaró et al. (2022) and show notable similarities to termite-fishing techniques observed in apes (Osuna-Mascaró et al., 2021). Remarkably, with the exception of one style adopted by a single individual, the birds distributed evenly across the techniques. Importantly, no technique proved more efficient than the others in terms of trial completion time, highlighting individual variation without performance trade-offs. It seems that when a task allows for multiple equally effective motor solutions, i.e., offers several degrees of freedom to achieve the same goal, this flexibility often results in a broader diversity of individual strategies. However, as noted, measuring only trial duration may not adequately capture true dexterity. Future experiments could provide deeper insight by analyzing detailed movement patterns to determine which techniques are more resourceful or efficient in terms of motor control and energy expenditure.

Dexterity in action is perhaps most vividly demonstrated by observations of wild Goffin's cockatoos opening hard-shelled Waiwai fruits in their natural habitat (O'Hara et al., 2021; see Figure 1). When presented with this fruit, the cockatoos begin by grasping it firmly with one foot, typically the left, while balancing on the other. Using a series of repeated, parallel bites, the birds methodically remove the fibrous outer pericarp, exposing the hard inner endocarp that protects the nutritious seed matter. This initial preparation alone can take over two minutes and requires precise, coordinated movements. Once the endocarp is revealed, the birds select a suitable branch and detach a fragment, which they then carefully modify using their beak and tongue. This modification involves stripping bark and making selective cuts to shape the tool for the task at hand. Remarkably, the cockatoos manufacture up to three distinct types of tools, each tailored for a specific function: fine, sharp tools for initial probing; medium, sturdier tools for more forceful extraction; and thick, blunt wedge tools for prying open fissures in the endocarp. With the tool crafted, the cockatoo holds it at the distal end between its upper mandible and muscular tongue, inserting it vertically into a fissure in the endocarp. The bird then shifts the tool horizontally by tilting its head, using it as a lever to pry out pieces of seed matter. Throughout this process, the cockatoo dynamically adjusts both the alignment of the tool and the fruit, often probing with its tongue to check for progress and consuming any exposed seeds before repeating the sequence. On average, a single fruit extraction involves the use of up to eight different tools, each one inserted multiple times and often replaced or refined as the task progresses.

Figure 1

Opening of a hard-shelled Waiwai fruit using tools by a Goffin's cockatoo



Note. Image series depicting the opening of a Waiwai fruit by a Goffin's cockatoo. (I) The fibrous outer pericarp is first removed through a series of repeated bites. (II) A suitable piece for a pre-tool is detached from a branch. (III) The pre-tool is shaped into a functional tool through in-beak manipulation and the removal of small fragments. (IV) The refined tool is then secured between the tongue and the maxilla and inserted into the fruit to probe and cut along fissures. (V) A wedge-like tool is subsequently used to widen the fissure. (VI) Finally, a medium-sized tool is employed to scoop out the seed matter. From "Wild Goffin's cockatoos flexibly manufacture and use tool sets," by M. O'Hara, B. Mioduszewska, R. Mundry, Yohanna, T. Haryoko, R. Rachmatika, D. M. Prawiradilaga, L. Huber, & A. M. I. Auersperg, 2021, *Current Biology, 31*(20), 4512–4520.e6 (https://doi.org/10.1016/j.cub.2021.08.009). CC BY-NC. Reprinted with permission.

Particularly striking in the Goffin's cockatoo is the remarkable coordination and control it exhibits over its feet, tongue, beak, and the various degrees of freedom of the tools themselves throughout this complex, multistep process, a process that flexibly adapts from one fruit and tool to the next. When it comes to gripping a stick tool, the Goffin demonstrates at least two distinct methods (see Figure 2). It can hold the tool between the upper and lower mandibles, a grip that closely resembles the "power grip" seen in primates, providing strength and stability for forceful actions. Alternatively, and perhaps more impressively, the Goffin can grip the tool between the upper mandible and its muscular tongue. This "precision grip" allows for fine, nuanced control over the tool's orientation and movement, with the tongue actively pressing and stabilizing the tool against the upper mandible. The incorporation of the multi-directionally movable tongue enables the bird to make dynamic and subtle in-beak adjustments, comparable to the in-hand movements seen in apes, and apply varying degrees of force as needed, crucial for tasks like probing fissures or levering out seeds.

Figure 2

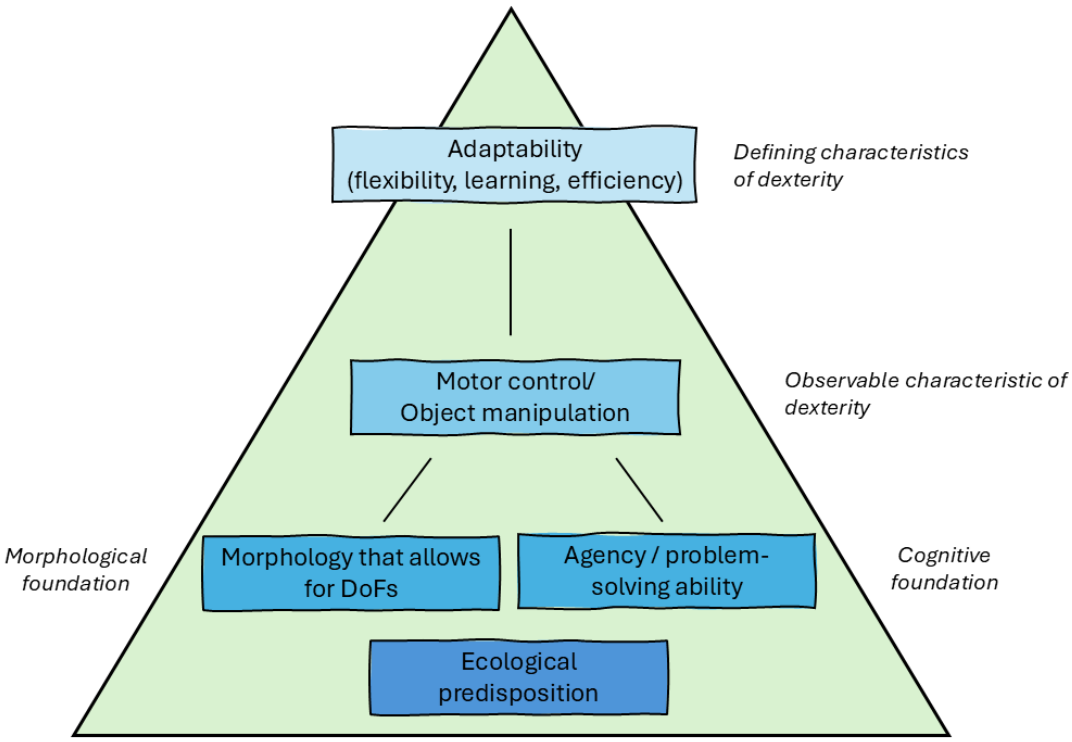
Power vs precision grip

Note. Left: Goffin's cockatoo performing a power grip by holding a stick tool between upper mandible (maxilla) and lower mandible. Right: A Goffin's cockatoo performing a precision grip, pressing its tongue against the stick tool to secure it between the upper mandible and the tongue.

The Goffin's cockatoos case illustrates that dexterous tool use arises from the interaction between ecological predispositions, cognitive capacities and morphological adaptations. What ultimately becomes visible to the observer is the resulting motor control and object manipulation. Experimental studies have shown that their tool use is individually expressed, flexible, adaptable, and learnable, increasing in efficiency with experience and practice, and thus meeting all criteria of dexterity (see Figure 3).

Figure 3

Components of Dexterity



Note. Visualization of the defining concepts of dexterity

From a cognitive perspective, both New Caledonian crows and Goffin's cockatoos exhibit comparable levels of problem-solving ability and behavioral flexibility; thus, it is difficult to rank

one species above the other in terms of cognitive sophistication. However, when examining the morphology of the beak-and–tongue apparatus, Goffin's cockatoos, and parrots more generally, demonstrate specific adaptations that enhance their manipulative capabilities.

Parrot Beak and Tongue Morphology

Parrots (Order: Psittaciformes) represent a comparatively recent lineage within the avian clade (Brusatte et al., 2015; Wright et al., 2008). They have evolved a highly kinetic skull with uncoupled jaw movements (Meekangvan et al., 2006), enabling the beak-and-tongue apparatus to move the mandibles multidirectionally and allowing the tongue to move freely in nearly any direction within the oral cavity (see Table 1 for a summary). Although the exact number of these degrees of freedom remains uncertain, they provide substantial functional versatility that is primarily employed in specialized grasping and food-processing behaviors (Homberger, 1980, 1986, 2003, 2017).

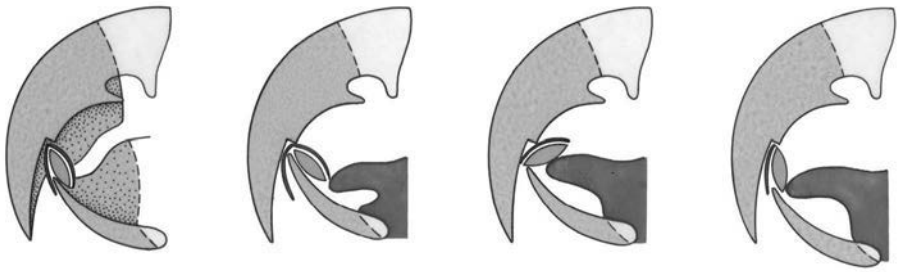
These innovations generate the high bite forces necessary for cracking hard-shelled food sources like nuts and seeds (Carril et al., 2015; Harrison et al., 2024) and support complex manipulative behaviors, such as seed dehusking, a process by which seeds and grains are stripped of their indigestible outer hulls prior to ingestion (Homberger, 1980, 2003). Bright et al. (2019) found that only 2.4% of the phenotypic variation in parrot beak shape could be attributed to dietary preferences. This suggests that morphological adaptations may be driven less by the physical properties of the food items (e.g., hardness) and more by the mechanical demands of food processing, such as dehusking, or finding weak opening points and fissures in woody fruits (Homberger, personal communication, September 12, 2025; O'Hara et al., 2021).

Homberger (1980) first described the seed dehusking behavior of parrots as a highly coordinated and complex motor sequence. In this process, small seeds are fixed between the tip of the upper beak and the tongue, whereas larger seeds are grasped between the tip of the upper

beak and the cutting edge of the lower beak. The seed is then fixed in place between the transverse ridge of the maxilla, also called the tomial tooth, and the lower beak using the tip of the tongue. Through finely tuned tongue and beak movements, the seed is rotated until a structural feature, such as a seam or ridge, on the shell is detected and aligned with the lower mandibles cutting edge. A bite is then applied to split the shell, enabling the lower mandible to wedge between the fractured shell and the kernel. The freed kernel is then brought backward by the tongue; depending on the individual and the seed type, the kernel may be chewed before swallowing (see Figure 4).

Figure 4

Seed dehusking process



Note. mid-sagittal section of the beak showing the seed shelling process. Adapted from "The comparative biomechanics of a prey-predator relationship: The adaptive morphologies of the feeding apparatus of Australian black-cockatoos and their foods as a basis for the reconstruction of the evolutionary history of the Psittaciformes," by D. G. Homberger, 2003, *Vertebrate Biomechanics and Evolution, 13,* 203-228. Copyright 2003 by D. G. Homberger. Reprinted with permission.

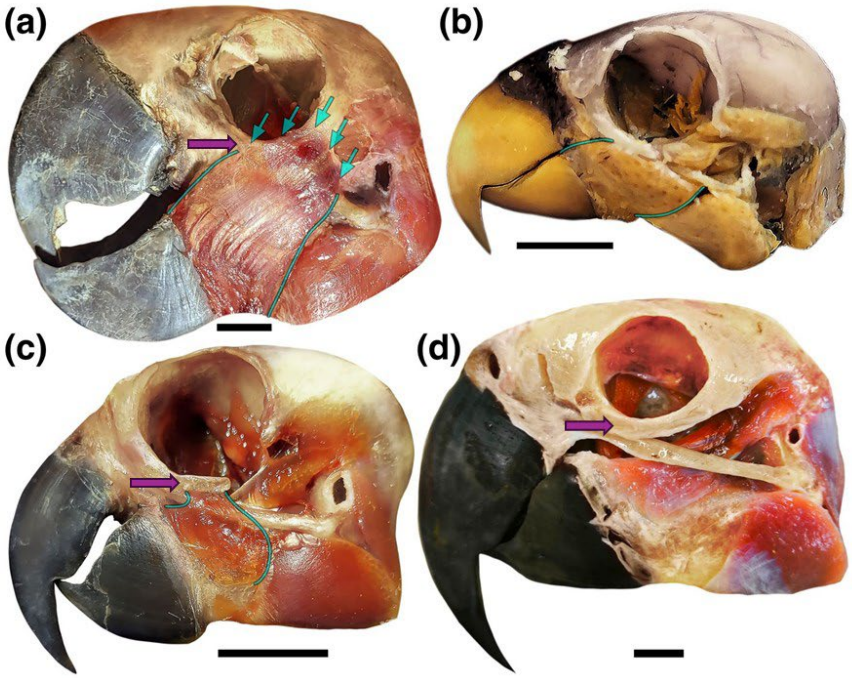
Beak movements are facilitated by multiple evolutionary gains and losses of structures in parrots (see Table 1). One notable skeletal innovation in parrots is the craniofacial hinge, a joint-like structure within the prokinetic avian skull (Zusi, 1993) that permits independent movement of the upper beak relative to the braincase. While the upper beak is part of the skull in many birds, craniofacial hinges are present in a few other avian lineages besides parrots. Nevertheless, this

structure in parrots has evolved through distinct developmental and evolutionary pathways (Tokita, 2003). In psittacines, this hinge, in conjunction with additional novel musculoskeletal adaptations (Homberger, 2017), enables greater deflection of the maxilla and allows for a more independent movement (Tokita, 2003; Young et al., 2023). Recent studies suggest that the evolution of cranial kinesis and related skeletal-muscular adaptations in parrots was driven by both dietary demands and the beak's functional role in locomotion (Dickinson et al., 2024; Young et al., 2022, 2023). In this evolutionarily novel form of locomotion, called "tripedal" or "beakiation," parrots repurpose their beak as a functional third limb, demonstrating surprising parallels with primate brachiation. By employing a cyclical pattern of alternating movements between their two hindlimbs and the beak, they propel themselves along a substrate. The beak not only acts as a stabilizing hook but also generates propulsive and tangential forces, effectively functioning like a true limb (Dickinson et al., 2023; Young et al., 2022, 2023).

A study on the early evolution of the avian skull found that most of the avian lineages lost key structures involved in powerful jaw closure in contrast to their dinosaur ancestors (Bhullar et al., 2016). However, some of these features were somewhat conserved or re-developed in the parrot lineages (Carril et al., 2014, 2015; Tokita, 2004; Tokita et al., 2007). One such novel feature of the parrot skull is the suborbital arch, which is present in some, but not all, parrot species (Faillace et al., 2025) (see Figure 5). This bony structure lies ventral to the orbit, framing the eye socket completely. It serves as both an attachment and reinforcement site for the *M. pseudomasseter* (PSM), a jaw muscle unique to parrots (Homberger, 2003) (see Figure 5). The presence of the suborbital arch shifts the muscle's attachment site more laterally and rostrally, producing a diagonal pull on the lower mandible rather than a purely posterior one (Homberger, 2003).

Figure 5

Lateral view of head dissections of four parrots



Note. Lateral views illustrating three developmental stages of the *M. pseudomasseter* (outlined in teal) across different parrot species. The PSM is highly developed in *Cacatua moluccensis* (a) and *Trichoglossus haematodus* (b), poorly developed in *Aratinga solstitialis* (c), and entirely absent in *Ara ararauna* (d). Blue arrowheads in (a) indicate the extensive insertion of the PSM along the fused suborbital arch and zygomatic process. Purple arrowheads indicate presence of the bony suborbital arch. Scale bar = 1 cm. Adapted from "Variation in Parrot Jaw Musculature," by A. C. L. Faillace, A. Berger, M. I. S. Santana, & A. Hartstone-Rose, 2025, *The Anatomical Record*, *1–15* (https://doi.org/10.1002/ar.25667). CC BY-NC-ND. Reprinted with permission.

The *M. pseudomasseter* functions as a jaw adductor across parrot species which possess it, in some species supported through its attachment to the suborbital arch (see Figure 5), and facilitates both forward (Burton, 1974) and transverse (Homberger, 2003) movements of the mandible, thereby adding additional DoFs and contributing to the high bite forces characteristic of parrots (Burton, 1974; Harrison et al., 2024; Zusi, 1993). Among parrots, cockatoos (Family:

Cacatuidae) exhibit the most strongly developed PSM (Faillace et al., 2025), along with a prominently developed suborbital arch.

The *M. ethmomandibularis* (EM) is another muscle unique to parrots and is consistently present across all known species (see Table 1). Functionally, it serves as a powerful jaw-closing (adductor) muscle and, owing to its rostral attachment on the interorbital septum, also facilitates forward translation of the lower jaw in addition to elevation (Burton, 1974). Together, the PSM and EM provide additional DoFs to the lower mandible, enabling transverse and forward movements in addition to vertical jaw closure.

Parrots have lost the *M. pseudotemporalis profundus*, a muscle found in many other bird lineages (Burton, 1974) which typically works in coordination with others to lower the upper jaw by retracting the quadrate bone (see Table 1). Burton (1974) proposed that in parrots, the quadrate bone's repositioning, shifted downward and backward, diminished the mechanical advantage of the *M. pseudotemporalis profundus*, ultimately leading to its evolutionary loss. In its place, the novel *M. ethmomandibularis* (EM), appears to have evolved to compensate for its functional deficit while additionally providing more surface area for other muscle attachments (Zusi, 1993). Combined with the uniquely deep and antero-posteriorly elongated medial condyle of the quadrate, which facilitates sliding movements of the lower jaw along its articulation, these adaptations enable a distinctive antero-posterior jaw action (Burton, 1974), adding to the DoFs of the lower mandible.

In most other birds, the postorbital ligament (PO), a collagenous band connecting the skull to the lower mandible, functions to mechanically couple movements of the upper and lower jaws (Bout & Zweers, 2002; Homberger, 2017). While not unique to parrots, the loss of this ligament in their lineage has contributed to a decoupled, independent jaw movement (Bout & Zweers, 2002; Meekangvan et al., 2006). As a result, parrots are capable of side-to-side movements of the lower

mandible, an ability facilitated by the absence of the postorbital ligament, the unique morphology of the quadrate bone, and the presence of novel jaw muscles (Homberger, 2017).

Parrot tongue mobility has long fascinated scientists; as early as the 1860s, researchers dissected and compared parrot tongues (Giebel, 1862; Nitzsch, 1895). Their movements are so distinctive that hyoid skeleton kinetics have been thoroughly studied in only a few bird species, including parrots (Homberger, 1980, 1986, 2017). The hyoid skeleton is a complex skeletal structure within the tongues of birds that facilitates tongue movement by providing attachment sites for various muscles and its morphology can vary considerably across the avian lineage (Homberger & Meyers 1989; Jung et al., 2017; Korzoun et al., 2001).

The bone at the very tip of the tongue, called the paraglossum, is paired in parrots, whereas it is fused in most other birds. This gives the parrot tongue tip a bulbous, thumb-like appearance (Homberger, 2017), which is used to manipulate objects precisely within the oral cavity, such as pushing and securing objects toward the maxilla, a version of the precision grip (O'Hara et al., 2021). Posterior to the paraglossum lies the basihyal, which is significantly broader in parrots compared to other birds. Additionally, parrots possess unique upward and forward projections on either side of the basihyal, known as the parahyal processes. These structures likely evolved to provide additional attachment sites for muscles of the lingual apparatus, supporting the highly refined and versatile tongue movements characteristic of parrots.

Parrots possess a complex lingual musculature comprising 13 distinct muscles, two of which are considered novel and are primarily situated at the tongue tip (Homberger, 1986). Most of the lingual muscles in parrots show more subdivisions than do their homologues in other birds. These muscles collectively facilitate extensive multidirectional movement of the tongue within the oral cavity (Homberger, 1986). While these structures are not evolutionarily homologous to mammalian tongue muscles, parrots remain the only avian group known to exhibit intrinsic tongue

musculature functionally similar to that of mammals (Erdogan & Iwasaki, 2014; Knospe, 1992). However, due to the internal skeletal support provided by the hyoid apparatus and the heavily keratinized lingual nail (Homberger, 1986), we propose that the parrot tongue tip shows greater functional convergence to a primate thumb.

The parrot tongue tip, in particular, comprises muscular adaptations that render dexterous movements achievable (see Table 1). A novel tongue muscle in parrots, the *M. mesoglossus*, connects the paraglossum to the basihyal within the hyoid apparatus (Burton, 1974; Homberger, 1986), controls dorsal flexion, and may contribute to elevation and stabilization of the tongue tip. In some species, such as in members of the genus *Cacatua*, the *M. mesoglossus* is fully developed as muscle tissue, while in others it is partially or entirely replaced by dense connective tissue (Mudge, 1903). In *Nestor notabilis*, for example, the *M. mesoglossus* is absent and replaced by an elongated tendon (Mudge, 1903), likely due to lower ecological reliance on seed processing in their diet (Jackson, 1960; Diamond & Bond, 1991). The saddle-shaped joint between the paraglossum and basihyal allows the lingual body to move vertically and slightly laterally, driven by the action of two antagonistic muscles (Homberger, 2017).

The *M. supraglossus* is another novel intrinsic tongue muscle, whose contraction produces multiple effects: It extends the paraglossale, narrows both the lingual tip and the central region of the tongue, flattens the dorsal surface of the tongue tip, and tilts the area enclosed by the lingual nail dorsally (Homberger, 2017). Additionally, the M. ceratoglossus acts across a single joint to rotate the paraglossum and lingual body downward (Homberger, 2017). The development of the *M. ceratoglossus* varies among parrot species and appears to be particularly well-developed in *Cacatua* (Homberger, 1986; Mudge, 1903).

The lingual apparatus, the structural support system of the tongue, functions as a tensegrity-based system, in which the hyoid skeleton provides structural rigidity, while flexibility

and dynamic control are mediated by surrounding connective fasciae and extrinsic muscles. In parrots, the hyoid horns, the anterior elements of the hyoid skeleton that connect to the larynx, are anchored via fluid-filled hyoid sheaths, which are integrated into the surrounding fascial network (Homberger, 2017). As such, the parrot tongue represents a complex of hydraulic and hydrostatic structures that work together to provide both mechanical strength and flexibility. Between the tongue muscles and the lingual nail (the specialized epithelium at the tip of the tongue), are vascular structures that operate on a hydrostatic principle, allowing the tongue surface to malleably adjust to the shape of contacted objects. This functional flexibility is supported by regionally differentiated keratinization of the lingual epithelium: less keratinized areas enable folding and deformation in sync with muscular movements, while highly keratinized regions, such as the tip, can exert targeted force without yielding, much like a primate thumb (Homberger, 1986).

Sensory and Neural Adaptations

The upper and lower bills of parrots contain dense concentrations of mechanoreceptors, known as Herbst corpuscles, particularly along the inner surfaces of the bill tip, allowing for object exploration via haptic feedback without relying on visual input, unlike in most other birds (Demery et al., 2011; Lessner et al., 2023; Martin & Martin, 2021). Additionally, the innervation of the beak and tongue apparatus in parrots is markedly different from that of other bird species and mammals (Wild, 1981, 2015; Wild et al., 1997).

In birds, the hypoglossal nerve (cranial nerve XII) is the main motor nerve controlling the tongue and the tracheal and syringeal muscles involved in vocalization (Orosz, 2007). Most species have two hypoglossal roots, but the Galah (*Cacatua roseicapilla*) has three, with this root system being the thickest of all cranial nerves (Wild, 1981). Notably, in parrots the hypoglossal nerve remains unusually large even after innervating all major tongue muscles, as it also supplies the novel intrinsic muscle *M. mesoglossus* (Wild, 1981).

In parrots, the trigeminal nerve, with its associated trigeminal motor nucleus, contains a higher number of motor neurons than in quails (Tokita & Nakayama, 2014). Both the hypoglossal and trigeminal systems are highly developed, but their specialization appears directed toward manipulative precision and coordination, rather than tactile exploration as seen in tactile-foraging species such as ducks or shorebirds, which possess specialized mechanoreceptors in their beaks (Iwaniuk & Wylie, 2020).

In line with this, the principal sensory nucleus of the trigeminal nerve (PrV), the brain region responsible for processing trigeminal sensory input, is notably enlarged in parrots, especially in a member of the genus *Cacatua* (Gutiérrez-Ibáñez et al., 2009). PrV receives not only trigeminal but also glossopharyngeal and hypoglossal afferents, integrating sensory information from the beak and tongue. This expanded connectivity likely underlies the observed enlargement of PrV in parrots (Gutiérrez-Ibáñez et al., 2009), reflecting increased sensory demands from the entire orofacial region. Notably, projections from the glossopharyngeal nerve to PrV appear unique to parrots, while hypoglossal projections to PrV have also been reported in the zebra finch (Faunes & Wild, 2017).

Wild (1981) also identified a large population of sensory neurons in the jugular ganglion associated with the hypoglossal nerve, particularly from its lingual branch. This suggests a predominantly tactile, rather than proprioceptive, sensory function. Furthermore, the convergence of glossopharyngeal (cranial nerve IX) and hypoglossal afferents onto trigeminal sensory nuclei supports the hypothesis that parrots employ a highly integrated “tongue-and-beak” feeding strategy, one that relies on fine motor control during food manipulation. The hypoglossal nucleus itself shows a clear somatotopic organization, with distinct regions responsible for the control of tongue and syrinx muscles. This spatial arrangement reflects both shared and specialized neural

circuits that support the dual demands of precise feeding and complex vocal behavior in parrots (Wild, 1981).

Finally, parrots exhibit a unique somatosensory pathway that bypasses the thalamus. Tactile information from the body is transmitted from the spinal cord to a brainstem nucleus (*nucleus subprincipalis*) and then projected directly to the forebrain region known as the *nucleus basorostralis* (Bas). This results in a complete somatotopic body map within Bas, including disproportionately large areas representing the feet and beak, whereas in most birds, Bas primarily encodes input from the head and beak only (Wild, 2015; Wild et al., 1997, 2001). This map is analogous to the primary sensory cortex (SI) in mammals, but its sensory input arrives via different neural pathways.

These findings suggest that both afferent and efferent structures, originally dedicated to vocalization and food processing, have been evolutionarily repurposed in parrots, at least in the Goffin's cockatoo, to also support fine motor control of the tongue and beak during tool use. This mirrors the way the prokinetic skull has been co-opted to facilitate climbing. Parrots thus seem to demonstrate not only remarkable behavioral flexibility but also significant morphological adaptability.

Table 1

Morphological Novelties of the Parrot Beak and Tongue

Morphological novelty	(Secondary) Craniofacial hinge	Suborbital arch	*M. pseudomasseter*	*M. ethmomandibularis*
Type	Skeletal (skull)	Skeletal (skull)	Muscular (jaw)	Muscular (jaw)
Function	More independent movement of upper beak; allows for wide opening; likely involved in locomotion	Attachment & reinforcement site for *M. pseudomasseter*	Strong jaw adductor; allows for lateral and forward movements of mandible	Strong jaw adductor; allows for forward movement of mandible

Evolutionary origin	Either from prokinetic or rhynchokinetic skull; 'pseudoprokinesis'	Ossification of subocular ligament beneath eye socket; independent development of *M. pseudomasseter*; multiple independent developments or secondary losses within Psittaciformes	Independent development of suborbital arch; recurrence through heterochrony/heterotopy; derivative of *M. adductor mandibulae externus*	Derivative *of M. pterygoideus dorsalis*; recurrence through heterochrony/heterotopy
Presence within parrot lineages	In all	In some	Not all / underdeveloped in some	In all
Methods and references	Anatomical & developmental (Tokita, 2003); biomechanical (Young et al., 2023)	Anatomical & developmental (Tokita, 2003, 2004); phylogenetic (Tokita et al., 2007; Carril et al., 2015); paleontological (Carril et al., 2014); anatomical & biomechanical (Carril et al., 2015; Homberger, 2003; Zusi, 1993; Faillace et al., 2025)	Phylogenetic (Tokita et al., 2007; Carril et al., 2015); developmental (Tokita, 2004; Carril et al., 2016); paleontological (Carril et al., 2014); anatomical & biomechanical (Carril et al., 2015; Homberger, 2003; Zusi, 1993; Faillace et al., 2025)	Developmental (Tokita, 2004; Carril et al., 2016); paleontological (Carril et al., 2014); anatomical & biomechanical (Carril et al., 2015; Burton, 1974; Zusi, 1993; Homberger, 2017, 2003; Faillace et al., 2025); phylogenetic (Carril et al., 2015)

Note. Italics indicate muscle names in accordance with anatomical nomenclature.

[a] Present either as muscle or as underdeveloped tissue.

Bird Brain

The avian brain provides the neuroanatomical basis for understanding dexterity in parrots, illustrating how complex motor control and sensory integration, functions akin to those of the mammalian neocortex, are achieved through the organization of the avian pallium.

Since Bernstein's seminal work, our understanding of avian brain function has advanced significantly (see Emery, 2005, and Güntürkün et al., 2021, for reviews). The once-dismissive term *bird brain* is now scientifically outdated. A growing body of research has shown that avian cognition, particularly in corvids and parrots, can rival that of primates across a range of high-level behavioral tasks (Balakhonov, 2017; Güntürkün & Bugnyar, 2016; Lambert et al., 2019; Pika et al., 2020; Rössler & Auersperg, 2022). In fact, behavioral evidence for complex cognition in birds preceded widespread neuroscientific acceptance. For example, Irene Pepperberg began her pioneering studies on symbolic communication and abstract concept learning in the grey parrot Alex in the 1970s (summarized in Pepperberg, 2000), at a time when prevailing models of avian neuroanatomy still indicated that bird brains lacked cortical structures (Edinger, 1908; Reiner et al., 2004.

This paradigm shifted in the late 20th century and was decisively redefined by the Avian Brain Nomenclature Consortium (2000–2002, Duke University). Drawing on comparative, developmental, and molecular evidence, the consortium introduced a now widely accepted terminology recognizing extensive pallial and subpallial subdivisions in the avian telencephalon (Reiner et al., 2004), providing a more accurate foundation for understanding avian neural architecture and cognition.

A major focus of this shift has been the nidopallium caudolaterale (NCL), a pallial structure now recognized as functionally analogous (though not anatomically homologous) to the prefrontal cortex (PFC) in mammals. The PFC is central to higher-order cognition in mammals, including working memory, attention, planning, decision-making, voluntary motor control, and tool use. Although birds lack a layered neocortex, the NCL supports similar executive functions and shows comparable dopaminergic modulation and pre-thalamic connectivity (Güntürkün, 2005; Güntürkün & Bugnyar, 2016; Jarvis et al., 2005). Located in the caudolateral nidopallium, this region enables

many of the behaviors once considered exclusive to primates, such as future planning, inferential reasoning, and flexible problem-solving.

Notably, research suggests that structurally distinct brain architectures, such as the nuclear pallium in birds and the layered cortex in mammals, can give rise to convergent cognitive solutions. This likely reflects shared biochemical and network-level constraints across vertebrates, leading to convergent evolution of cognitive capacities under similar selective pressures (Güntürkün, 2005; Güntürkün et al., 2021).

From an evolutionary perspective, the mammalian neocortex and avian pallium both derive from ancestral pallial structures shared by their last common ancestor (Montiel et al., 2015). In mammals, the dorsal pallium evolved into a six-layered neocortex (Reiner et al., 2005), whereas the avian pallium retained a nuclear organization. Despite this, it contains at least four major, molecularly distinct cell populations arranged in columnar-like functional units, paralleling canonical circuits of the mammalian cortex (Jarvis et al., 2013; Zaremba et al., 2025).

Similar findings come from neuroanatomy: Important regions of the avian pallium, such as the hyperpallium (including the Wulst) and the dorsal ventricular ridge (DVR), have radially and tangentially organized fibers that resemble the columnar and laminar architecture of the mammalian neocortex (Stacho et al., 2020). Additionally, sensory zones in the DVR project to higher order associative and motor areas via long-range connections that mirror the structure of mammalian cortical circuits (Stacho et al., 2020). Among these, only the Wulst, which is mostly involved in visual processing, is widely considered homologous to the mammalian visual cortex (Stacho et al., 2020). While the DVR is not homologous to the neocortex, it performs functionally analogous roles in sensory processing and association (Reiner et al., 2005). Recent work using genetic tagging has shown that excitatory (CaMKII-positive) and inhibitory (GAD1-positive) neurons in the avian brain exhibit distinct firing properties and connectivity

patterns that strongly resemble functions of mammalian cortical circuits (Spool et al., 2021). This suggests that the excitatory–inhibitory architecture underlying cognition is conserved across amniotes (Ball & Balthazart, 2021), despite major anatomical differences. Moreover, neurochemical studies have shown that dopaminergic input to the nidopallium caudolaterale (NCL) is crucial for working memory, much like dopamine's role in the mammalian PFC (Güntürkün, 2005; von Eugen et al., 2020).

Paleoneuroanatomical data from Ksepka et al. (2020) suggests that early birds and non-avian dinosaurs had similar relative brain sizes, with no major increase associated with the origin of flight. Instead, significant shifts in brain–body allometry occurred after the Cretaceous–Paleogene mass extinction. Modern lineages like parrots and corvids achieved large relative brain sizes. Parrots did so primarily by reducing body size, and corvids via increases in both brain and body size (Ksepka et al., 2020).

Parrots and corvids are evolutionary outliers among birds. They exhibit high neuron densities in the pallial telencephalon that are two to four times greater than in similarly sized primates and show unique adaptations in connectivity and brain organization (Kverkova et al., 2022; Olkowicz et al., 2016). Higher neuron counts and dense synaptic networks support enhanced integration and parallel processing, especially in associative areas like the nidopallium (Güntürkün, 2021). Tool-using species such as New Caledonian crows and Goffin’s cockatoos also have a highly folded cerebellum and high telencephalon–cerebellum connectivity, facilitating fine motor control and goal-directed behavior (Gutiérrez-Ibáñez et al., 2018).

Parrots in particular possess disproportionately large medial spiriform nuclei (SpM), pre-thalamic structures that connect the telencephalon with the cerebellum. The circuit is functionally similar to the pontine nuclei in primates, which send cortical signals to the cerebellum for coordination and movement prediction (Gutiérrez-Ibáñez et al., 2018). The enlarged SpM may

facilitate parrots' enhanced motor planning and vocal control, which are both essential for tool use and vocal mimicry.

Parrots, alongside songbirds and hummingbirds, are capable of vocal learning. Jarvis (2013) showed that vocal learning evolved through the duplication and specialization of motor pathways. Parrots uniquely possess the AAC (anterior arcopallium), a forebrain region encoding vocal features like pitch and harmonics in a way that resembles the human speech motor cortex (Yang & Long, 2025). Unlike songbirds, which form distinct neural patterns for each vocal element, parrots use overlapping ensembles to represent acoustically similar sounds, supporting flexible vocal imitation. These findings align with the "motor theory" of vocal learning, which suggests that language evolved from pre-existing motor systems (Feenders et al., 2008). The avian vocal system, especially in parrots, is closely linked to the lingual and jaw motor systems used in both vocalization and object manipulation suggesting that convergent neural architectures may support both functions (Homberger, 2017; Wild, 1981).

Conclusion

We propose that parrots, using the Goffin's cockatoo as a particularly illustrative example, may represent valuable models for dexterity research. When analyzing the current body of knowledge on parrot morphology and Goffin behavior in particular, it becomes evident that they fulfill the four core components that outline dexterity:

1. Motor Coordination: Goffin's cockatoos exhibit remarkable motor coordination, flexibly using tools both in captivity and in the wild (Auersperg et al., 2012; O'Hara et al., 2021). They employ a variety of tool types (Laumer et al., 2017, 2020), manufacture tools for different purposes (Auersperg et al., 2016) and use tool sets (including composite tools) in sequential order to achieve a single goal (Osuna-Mascaro et al., 2021, 2022). They display diverse individual techniques, problem-solving styles, and movement patterns across

these tasks. Particularly striking is their multifunctional beak-and-tongue apparatus. While it is originally an adaptation for seed dehusking it is functionally repurposed into a dexterous *facial hand* capable of solving complex object-related tasks. Unlike New Caledonian crows, which hold tools laterally across the base of the bill (Eibl-Eibesfeldt, 1962; Hunt et al., 1996; Rutz et al., 2016), Goffin's switch between power, precision and compound-like grips, resembling the versatility observed in primates and even human infants. We propose that future research should investigate the degrees of freedom of the beak-and-tongue apparatus in psittacine models such as kea and Goffin's cockatoos. However, it is already evident that the combination of at least three distinct grip types and a highly mobile tongue capable of multi-directional movement affords a high degree of functional flexibility. What distinguishes parrots, particularly cockatoos, from other avian tool users like crows is the combination of strength and versatility afforded by their unique cranio-lingual morphology (Homberger, 1986).

2. Goal-Oriented Tool Use and (possibly) Causal Inference**:** Goffin's demonstrate goal-directed tool use and behaviors suggestive of causal understanding. They manufacture and adjust tool lengths (Auersperg et al., 2018), keep tools safe for future use in costly contexts (Auersperg et al., 2017), transport tool sets in advance to solve specific problems (Osuna-Mascaro et al., 2022), and use composite tools and sets in correct sequential order (Osuna-Mascaro et al., 2021, 2022). While the depth of their technical reasoning skills still needs more investigation, their behaviors imply functional apprehension and at least simple forms of anticipatory planning. Through the convergent evolution of brain structures associated with higher cognition and motor control (Gutiérrez-Ibáñez et al., 2018; Olkowicz et al., 2016), parrots have developed capacities that support complex problem-solving,

whether in cracking nuts in the wild (O'Hara et al., 2021) or manipulating puzzle boxes in laboratory settings (Auersperg et al., 2012, 2014a).

3. Learning and Flexibility**:** The role of learning and flexibility is evident in nearly every tool-use experiment with Goffins. Task completion time decreases with experience, often in a ratchet-like fashion (Auersperg et al., 2013). Goffins exhibit strong trial-and-error learning, emulation-based social learning (Auersperg et al., 2014a), and high problem-solving flexibility. They adapt strategies when previously successful methods fail (Colbourne et al., unpublished) and consistently display inter-individual variation in techniques.
4. Mastering Complex Dexterity: The most challenging characteristics of dexterity to assess, adequacy, resourcefulness, and accuracy, remain largely underexplored in most animals. Most studies focus on outcome measures like speed or success. Future research should aim to design tasks with maximal degrees of freedom for interaction, allowing subjects to express their full motor capabilities. The goal would be to test whether, through learning, subjects can identify and refine the most efficient motor solution, aligning with Bernstein's (1996) concept of dexterity as a cognitively driven process.

Sugasawa et al. (2021) proposed that object manipulation in primates and non-primates could be more effectively compared by classifying grip types not by morphological features, such as which digits are involved, but by functional criteria, such as force vectors that reflect the dynamic interaction between the manipulator and the object. We support this perspective and suggest that, since object manipulation is a key component of dexterity, dexterity research as a whole could benefit from such function-based categorizations. This approach would facilitate more meaningful comparisons between dexterous animals, regardless of whether they possess hands.

Although Bernstein (1996, p. 91) once described birds as "ill-suited for the accumulation of personal experiences, for mastering new, complex motor skills, and particularly for displaying dexterity during unexpected, unpredictable motor problems," the evidence from parrots, and Goffin's cockatoos in particular, suggests otherwise. Far from being ill-suited for dexterity, parrots may be the most compelling non-primate example of Bernstein's core principles realized in nature. In fact, they seem to emerge as living proof that dexterity is not the sole domain of animals with hands.

References

Adolph, K. E., & Hoch, J. E. (2019). Motor development: Embodied, embedded, enculturated, and enabling. *Annual Review of Psychology*, *70*, 141–164. https://doi.org/10.1146/annurev-psych-010418-102836

Alba, D. M., Moyà-Solà, S., & Köhler, M. (2003). Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. *Journal of Human Evolution*, *44*(2), 225–254. https://doi.org/10.1016/s0047-2484(02)00207-5

Almécija, S., & Sherwood, C. C. (2017). Hands, brains, and precision grips: Origins of tool use behaviors. In J. H. Kaas (Ed.), *Evolution of nervous systems* (2nd ed., Vol. 4, pp. 299–315). Academic Press. https://doi.org/10.1016/B978-0-12-804042-3.00085-3

Almécija, S., Smaers, J. B., & Jungers, W. L. (2015). The evolution of human and ape hand proportions. *Nature Communications*, *6*, 7717. https://doi.org/10.1038/ncomms8717

Anderson, C. V., & Deban, S. M. (2010). Ballistic tongue projection in chameleons maintains high performance at low temperature. *Proceedings of the National Academy of Sciences*, *107*(12), 5495–5499. https://doi.org/10.1073/pnas.0910778107

Araújo, D., & Davids, K. (2011). What exactly is *acquired* during skill acquisition? *Journal of Consciousness Studies, 18*(3-4), 7–23.

Auersperg, A. M. I., Gajdon, G. K., & Huber, L. (2010). Kea, *Nestor notabilis*, produce dynamic relationships between objects in a second-order tool use task. *Animal Behaviour*, *80*(5), 783–789. https://doi.org/10.1016/j.anbehav.2010.08.007

Auersperg, A. M. I., von Bayern, A. M. P., Gajdon, G. K., Huber, L., & Kacelnik, A. (2011). Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi-access box paradigm. *PLoS ONE*, *6*(6), e20231. https://doi.org/10.1371/journal.pone.0020231

Auersperg, A. M. I., Szabo, B., von Bayern, A. M. P., & Kacelnik, A. (2012). Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo. *Current Biology*, *22*(21), R903–R904. https://doi.org/10.1016/j.cub.2012.09.00

Auersperg, A. M. I., Kacelnik, A., & von Bayern, A. M. P. (2013). Explorative learning and functional inferences on a five-step means–means–end problem in Goffin's cockatoos (*Cacatua goffiniana*). *PLoS ONE*, *8*(7), e68979. https://doi.org/10.1371/journal.pone.0068979

Auersperg, A. M. I., von Bayern, A. M. P., Weber, S., Szabadvari, A., Bugnyar, T., & Kacelnik, A. (2014a). Social transmission of tool use and tool manufacture in Goffin cockatoos (*Cacatua goffini*). *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20140972. https://doi.org/10.1098/rspb.2014.0972

Auersperg, A. M., Oswald, N., Domanegg, M., Gajdon, G. K., & Bugnyar, T. (2014b). Unrewarded object combinations in captive parrots. *Animal Behavior and Cognition*, *1*(4), 470–488. https://doi.org/10.12966/abc.11.05.2014

Auersperg, A. M. I., Borasinski, S., Laumer, I., & Kacelnik, A. (2016). Goffin's cockatoos make the same tool type from different materials. *Biology Letters*, *12*(11), 20160689. https://doi.org/10.1098/rsbl.2016.0689

Auersperg, A. M. I., Köck, C., Pledermann, A., O'Hara, M., & Huber, L. (2017). Safekeeping of tools in Goffin's cockatoos (*Cacatua goffiniana*). *Animal Behaviour*, *128*, 125–133. https://doi.org/10.1016/j.anbehav.2017.04.010

Auersperg, A. M. I., Köck, C., O'Hara, M., & Huber, L. (2018). Tool-making cockatoos adjust the lengths but not the widths of their tools to function. *PLoS ONE*, *13*(11), e0205429. https://doi.org/10.1371/journal.pone.0205429

Backman, C., Gibson, S. C. D., & Parsons, J. (1992). Assessment of hand function: The relationship between pegboard dexterity and applied dexterity. *Canadian Journal of Occupational Therapy*, *59*(4), 208–213. https://doi.org/10.1177/000841749205900406

Baker, J., Barton, R. A., & Venditti, C. (2024). The coevolution of encephalization and manual dexterity in hominins and other primates. *bioRxiv*. https://doi.org/10.1101/2024.09.17.613411

Balakhonov, D., & Rose, J. (2017). Crows rival monkeys in cognitive capacity. *Scientific Reports*, *7*(1), 8809. https://doi.org/10.1038/s41598-017-09400-0

Ball, G. F., & Balthazart, J. (2021). Evolutionary neuroscience: Are the brains of birds and mammals really so different? *Current Biology*, *31*(13), R840–R842. https://doi.org/10.1016/j.cub.2021.05.004

Bann, S. D., Khan, M. S., & Darzi, A. W. (2003). Measurement of surgical dexterity using motion analysis of simple bench tasks. *World Journal of Surgery*, *27*(4), 390–394. https://doi.org/10.1007/s00268-002-6769-7

Bardo, A., Borel, A., Meunier, H., Guéry, J.-P., & Pouydebat, E. (2016). Behavioral and functional strategies during tool use tasks in bonobos. *American Journal of Physical Anthropology*, *161*(1), 125–140. https://doi.org/10.1002/ajpa.23015

Bardo, A., Cornette, R., Borel, A., & Pouydebat, E. (2017). Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology*, *164*. https://doi.org/10.1002/ajpa.23323

Bardo, A., Vigouroux, L., Kivell, T. L., & Pouydebat, E. (2018). The impact of hand proportions on tool grip abilities in humans, great apes and fossil hominins: A biomechanical analysis using musculoskeletal simulation. *Journal of Human Evolution*, *125*, 106–121. https://doi.org/10.1016/j.jhevol.2018.10.001

Bastos, A. P. M., Horváth, K., Webb, J. L., et al. (2021). Self-care tooling innovation in a disabled kea (*Nestor notabilis*). *Scientific Reports*, *11*, 18035. https://doi.org/10.1038/s41598-021-97086-w

Bernstein, N. A. (1996). Dexterity and its development. In M. L. Latash & M. T. Turvey (Eds.), *Dexterity and its development* (pp. 1–244). Lawrence Erlbaum Associates.

Bhullar, B.-A. S., Hanson, M., Fabbri, M., Pritchard, A., Bever, G. S., & Hoffman, E. (2016). How to make a bird skull: Major transitions in the evolution of the avian cranium, paedomorphosis, and the beak as a surrogate hand. *Integrative and Comparative Biology*, *56*(3), 389–403. https://doi.org/10.1093/icb/icw069

Bongaardt, R., & Meijer, O. (2000). Bernstein's theory of movement behavior: Historical development and contemporary relevance. *Journal of Motor Behavior, 32*(1), 57–71. https://doi.org/10.1080/00222890009601360

Bout, R., & Zweers, G. (2002). The role of cranial kinesis in birds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *131*(1), 197–205. https://doi.org/10.1016/S1095-6433(01)00470-6

Bright, J. A., Marugán-Lobón, J., Rayfield, E. J., et al. (2019). The multifactorial nature of beak and skull shape evolution in parrots and cockatoos (Psittaciformes). *BMC Evolutionary Biology*, *19*, 104. https://doi.org/10.1186/s12862-019-1432-1

Brusatte, S. L., O'Connor, J. K., & Jarvis, E. D. (2015). The origin and diversification of birds. *Current Biology*, *25*(19), R888–R898. https://doi.org/10.1016/j.cub.2015.08.003

Burton, P. J. K. (1974). Jaw and tongue features in Psittaciformes and other orders with special reference to the anatomy of the Tooth-billed pigeon (*Didunculus strigirostris*). *Journal of Zoology*, *174*(2), 255–276. https://doi.org/10.1111/j.1469-7998.1974.tb03156.x

Call, J. (2013). Three ingredients for becoming a creative tool user. In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 3–20). Cambridge University Press.

Carril, J., Degrange, F. J., & Tambussi, C. P. (2014). Jaw muscle reconstruction of the Late Pliocene Psittaciform *Nandayus vorohuensis* from Argentina. *Ameghiniana, 51*(4), 361–365. https://doi.org/10.5710/AMGH.25.03.2014.2223

Carril, J., Degrange, F. J., & Tambussi, C. P. (2015). Jaw myology and bite force of the monk parakeet (Aves, Psittaciformes). *Journal of Anatomy*, *227*(1), 34–44. https://doi.org/10.1111/joa.12330

Carril, J., Ronderos, J. R., Tambussi, C. P., & Chiale, M. C. (2016). Jaw myogenesis in the monk parakeet: evidence of developmental reprogramming in the emergence of novel muscles in Psittaciformes (Aves). *Zoology*, *119*(6), 534–540. https://doi.org/10.1016/j.zool.2016.06.006

Cenni, A., Nord, C., Christie, J. B. A., Wandia, I. N., & Leca, J.-B. (2024). How does object play shape tool use emergence? Integrating observations and field experiments in longtailed macaques. *Animal Behaviour, 218*, 239–254. https://doi.org/10.1016/j.anbehav.2024.09.001

Chatagny, P., Badoud, S., Kaeser, M., Gindrat, A.-D., Savidan, J., Fregosi, M., Moret, V., Roulin, C., Schmidlin, E., & Rouiller, E. (2013). Distinction between hand dominance and hand preference in primates: A behavioral investigation of manual dexterity in nonhuman primates (macaques) and human subjects. *Brain and Behavior, 3*(5), 575–595. https://doi.org/10.1002/brb3.160

Christel, M. (1993). Grasping techniques and hand preferences in Hominoidea. In H. Preuschoft & D. J. Chivers (Eds.), *Hands of primates* (pp. 91–108). Springer, Vienna. https://doi.org/10.1007/978-3-7091-6914-8_7

Christel, M. I., & Fragaszy, D. (2000). Manual function in *Cebus apella*: Digital mobility, preshaping, and endurance in repetitive grasping. *International Journal of Primatology, 21*(4), 697–719. https://doi.org/10.1023/A:1005521522418

Corti, E. J., Johnson, A. R., Riddle, H., Gasson, N., Kane, R., & Loftus, A. M. (2017). The relationship between executive function and fine motor control in young and older adults. *Human Movement Science, 51*, 41–50. https://doi.org/10.1016/j.humov.2016.11.001

Costes, P., Soppelsa, J., Houssin, C., Boulinguez-Ambroise, G., Pacou, C., Gouat, P., Cornette, R., & Pouydebat, E. (2024). Effect of the habitat and tusks on trunk grasping techniques in African savannah elephants. *Ecology and Evolution, 14*(4), e11317. https://doi.org/10.1002/ece3.11317

Crast, J., Fragaszy, D., Hayashi, M., & Matsuzawa, T. (2009). Dynamic in-hand movements in adult and young juvenile chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology, 138*(3), 274–285. https://doi.org/10.1002/ajpa.20925

Darian-Smith, I., Galea, M. P., Darian-Smith, C., Sugitani, M., Tan, A., & Burman, K. (1996). The anatomy of manual dexterity: The new connectivity of the primate sensorimotor thalamus and cerebral cortex. *Advances in Anatomy, Embryology, and Cell Biology, 133*, 1–140.

Davare, M., Kraskov, A., Rothwell, J. C., & Lemon, R. N. (2011). Interactions between areas of the cortical grasping network. *Current Opinion in Neurobiology, 21*(4), 565–570. https://doi.org/10.1016/j.conb.2011.05.021

de Wit, M. M., de Vries, S., van der Kamp, J., & Withagen, R. (2017). Affordances and neuroscience: Steps towards a successful marriage. *Neuroscience & Biobehavioral Reviews, 80*, 622–629. https://doi.org/10.1016/j.neubiorev.2017.07.008

Deich, J. D., Houben, D., Allan, R. W., & Zeigler, H. P. (1985). “On-line” monitoring of jaw movements in the pigeon. *Physiology & Behavior, 35*(2), 307–311. https://doi.org/10.1016/0031-9384(85)90354-3

Demery, Z. P., Chappell, J., & Martin, G. R. (2011). Vision, touch and object manipulation in Senegal parrots (*Poicephalus senegalus*). *Proceedings of the Royal Society B: Biological Sciences, 278*(1722), 3687–3693. https://doi.org/10.1098/rspb.2011.0374

Diamond, J., & Bond, A. B. (1991). Social behavior and the ontogeny of foraging in the kea (*Nestor notabilis*). *Ethology, 88*(2), 128–144. https://doi.org/10.1111/j.1439-0310.1991.tb00268.x

Dickinson, E., Young, M. W., & Granatosky, M. C. (2024). Beakiation: How a novel parrot gait expands the locomotor repertoire of living birds. *Royal Society Open Science, 11*(1), 231397. https://doi.org/10.1098/rsos.231397

Diedrichsen, J., & Kornysheva, K. (2015). Motor skill learning between selection and execution. *Trends in Cognitive Sciences, 19*(4), 227–233. https://doi.org/10.1016/j.tics.2015.02.003

Edinger, L. (1908). The relations of comparative anatomy to comparative psychology. *Journal of Comparative Neurology and Psychology, 18*, 437–457.

Eibl-Eibesfeldt, I. (1961). Über den Werkzeuggebrauch des Spechtfinken *Camarhynchus pallidus*. *Zeitschrift für Tierpsychologie, 18*(3), 343–346. https://doi.org/10.1111/j.1439-0310.1961.tb00424.x

Eibl-Eibesfeldt, I., & Sielmann, H. (1962). Beobachtungen am Spechtfinken *Cactospiza pallida* (Sclater und Salvin). *Journal für Ornithologie, 103*, 92–101. https://doi.org/10.1007/BF01670851

Elangovan, N. (2022). *Analysis and evaluation of the dexterity, grasping, and manipulation capabilities of human and robot hands* [Doctoral dissertation, Indian Institute of Technology]. ResearchGate.

983 Emery, N. J. (2005). Cognitive ornithology: The evolution of avian intelligence. *Philosophical*
984 *Transactions of the Royal Society B: Biological Sciences, 361*(1465), 23–43.
985 https://doi.org/10.1098/rstb.2005.1736
986 Emery, N. J., & Clayton, N. S. (2009). Tool use and physical cognition in birds and mammals.
987 *Current Opinion in Neurobiology, 19*(1), 27–33. https://doi.org/10.1016/j.conb.2009.02.003
988 Erdoğan, S., & Iwasaki, S. (2014). Function-related morphological characteristics and specialized
989 structures of the avian tongue. *Annals of Anatomy, 196*(2–3), 75–87.
990 https://doi.org/10.1016/j.aanat.2013.09.005
991 Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by
992 central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon:
993 Techniques and individual differences. *American Journal of Primatology, 79*(8), e22672.
994 https://doi.org/10.1002/ajp.22672
995 Faillace, A. C. L., Berger, A., Santana, M. I. S., & Hartstone-Rose, A. (2025). Variation in parrot jaw
996 musculature. *The Anatomical Record*, *1–15*. https://doi.org/10.1002/ar.25667
997 Faunes, M., & Wild, J. M. (2017). The sensory trigeminal complex and the organization of its primary
998 afferents in the zebra finch (*Taeniopygia guttata*). *The Journal of Comparative Neurology,*
999 *525*(13), 2820–2831. https://doi.org/10.1002/cne.24249
1000 Feenders, G., Liedvogel, M., Rivas, M., Zapka, M., Horita, H., Hara, E., Wada, K., Mouritsen, H., &
1001 Jarvis, E. D. (2008). Molecular mapping of movement-associated areas in the avian brain: A
1002 motor theory for vocal learning origin. *PLoS ONE*, *3*(3), e1768.
1003 https://doi.org/10.1371/journal.pone.0001768
1004 Figueiredo, S., Machado, L., Lousada, A. D. P., Castelo, L. S., Fardilha, M. L., & Sa, A. (2016).
1005 Physicians versus surgeons: A pilot study on hand dexterity within a controlled population.
1006 *Acta Orthopaedica Belgica*, *82*(3), 456–461.

Forshaw, J. M., & Knight, F. (2010). *Parrots of the world: An identification guide (Princeton Field Guides)*. Princeton University Press.

Fragaszy, D. M., & Crast, J. (2016). Functions of the hand in primates. In T. Kivell, P. Lemelin, B. Richmond, & D. Schmitt (Eds.), *The evolution of the primate hand* (pp. 313–344). Springer. https://doi.org/10.1007/978-1-4939-3646-5_12

Fragaszy, D. M., & Mangalam, M. (2018). Tooling. In H. J. Brockmann et al. (Eds.), *Advances in the study of behavior* (Vol. 50, pp. 177–241). Academic Press. https://doi.org/10.1016/bs.asb.2018.01.001

Frye, B., Valure, P., Craft, S., Baxter, M., Scott, C., Wise-Walden, S., Bissinger, D., Register, H., Copeland, C., Jorgensen, M., Justice, J., Kritchevsky, S., Register, T., & Shively, C. (2021). Temporal emergence of age-associated changes in cognitive and physical function in vervets (*Chlorocebus aethiops sabaeus*). *GeroScience*, *43*, 1035–1053. https://doi.org/10.1007/s11357-021-00338-w

García, S., Strüber, D., Brugali, D., Di Fava, A., Schillinger, P., Pelliccione, P., & Berger, T. (2019). Variability modeling of service robots: Experiences and challenges. *Proceedings of the 13th International Workshop on Variability Modelling of Software-Intensive Systems*, 1–6. https://doi.org/10.1145/3302333.3302350

Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In J. G. Else & P. C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour* (Vol. 3, pp. 93–104). Cambridge University Press.

Giebel, C. (1862). Zur Anatomie der Papageien nach Chr. Nitzsch's Untersuchungen mitgetheilt. *Zeitschrift für die gesammten Naturwissenschaften*, *19*, 133–152.

Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature, 201*, 1264–1266. https://doi.org/10.1038/2011264a0

Goodman, M., Hayward, T., & Hunt, G. R. (2018). Habitual tool use innovated by free-living New Zealand kea. *Scientific Reports, 8*, 13935. https://doi.org/10.1038/s41598-018-32363-9

Grant, P. R. (1999). *Ecology and evolution of Darwin's finches*. Princeton University Press.

Gruber, R., Schiestl, M., Boeckle, M., Frohnwieser, A., Miller, R., Gray, R. D., Clayton, N. S., & Taylor, A. H. (2019). New Caledonian crows use mental representations to solve metatool problems. *Current Biology, 29*(4), 686–692.e3. https://doi.org/10.1016/j.cub.2019.01.008

Güntürkün, O. (2005). Avian and mammalian "prefrontal cortices": Limited degrees of freedom in the evolution of the neural mechanisms of goal-state maintenance. *Brain Research Bulletin, 66*(4–6), 311–316. https://doi.org/10.1016/j.brainresbull.2005.02.004

Güntürkün, O. (2012). The convergent evolution of neural substrates for cognition. *Psychological Research, 76*(2), 212–219. https://doi.org/10.1007/s00426-011-0377-9

Güntürkün, O., & Bugnyar, T. (2016). Cognition without cortex. *Trends in Cognitive Sciences, 20*(4), 291–303. https://doi.org/10.1016/j.tics.2016.02.001

Güntürkün, O., von Eugen, K., Packheiser, J., & Pusch, R. (2021). Avian pallial circuits and cognition: A comparison to mammals. *Current Opinion in Neurobiology, 71*, 29–36. https://doi.org/10.1016/j.conb.2021.08.007

Gutiérrez-Ibáñez, C., Iwaniuk, A. N., & Wylie, D. R. (2009). The independent evolution of the enlargement of the principal sensory nucleus of the trigeminal nerve in three different groups of birds. *Brain, Behavior and Evolution*, *74*(4), 280–294. https://doi.org/10.1159/000270904

Gutiérrez-Ibáñez, C., Iwaniuk, A. N., & Wylie, D. R. (2018). Parrots have evolved a primate-like telencephalic-midbrain-cerebellar circuit. *Scientific Reports, 8*, 9960. https://doi.org/10.1038/s41598-018-28301-4

Gutiérrez-Ibáñez, C., Němec, P., Paré, M., Wylie, D. R., & Lefebvre, L. (2025). How do big brains evolve? *Trends in Ecology & Evolution, 40*(6), 554–562. https://doi.org/10.1016/j.tree.2025.03.008

Harrison, S. L., Sutton, G. P., Herrel, A., & Deeming, D. C. (2025). Estimated and in vivo measurements of bite force demonstrate exceptionally large bite forces in parrots (Psittaciformes). *Journal of Anatomy, 246*, 299–315. https://doi.org/10.1111/joa.14144

Holzhaider, J., Hunt, G., & Gray, R. (2010). Social learning in New Caledonian crows. *Learning & Behavior, 38*, 206–219. https://doi.org/10.3758/LB.38.3.206

Homberger, D. G. (1980). Funktionell-morphologische Untersuchungen zur Radiation der Ernährungs- und Trinkmethoden der Papageien (Psittaci). *Bonner Zoologische Monographien, 13*, 1–192.

Homberger, D. G. (1986). The lingual apparatus of the African grey parrot, *Psittacus erithacus* Linné (Aves: Psittacidae): Description and theoretical mechanical analysis. *Ornithological Monographs, 39*, iii–233. https://doi.org/10.2307/40166788

Homberger, D. G., & Meyers, R. A. (1989). Morphology of the lingual apparatus of the domestic chicken, *Gallus gallus*, with special attention to the structure of the fasciae. *The American Journal of Anatomy, 186*(3), 217–257. https://doi.org/10.1002/aja.1001860302

Homberger, D. (2003). The comparative biomechanics of a prey-predator relationship: The adaptive morphologies of the feeding apparatus of Australian black-cockatoos and their foods as a basis for the reconstruction of the evolutionary history of the Psittaciformes. In V. L. Bels, J.-P. Gasc, & A. Casinos (Eds.), *Vertebrate biomechanics and evolution* (pp. 203–228). BIOS Scientific Publishers.

Homberger, D. (2017). The avian lingual and laryngeal apparatus within the context of the head and jaw apparatus, with comparisons to the mammalian condition: Functional morphology and

biomechanics of evaporative cooling, feeding, drinking, and vocalization. In J. N. Maina (Ed.), *The biology of the avian respiratory system: Evolution, development, structure and function* (pp. 27–97). Springer International Publishing. https://doi.org/10.1007/978-3-319-44153-5_2

Hunt, G. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature, 379*, 249–251. https://doi.org/10.1038/379249a0

Hunt, G. R., & Gray, R. D. (2002). Species-wide manufacture of stick-type tools by New Caledonian crows. *Emu, 102*, 349–353.

Hunt, G. R., & Gray, R. D. (2004). The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society B: Biological Sciences, 271*(Suppl 3), S88–S90. https://doi.org/10.1098/rsbl.2003.0085

Hunt, G. R., Gray, R. D., & Taylor, A. H. (2013). Why is tool use rare in animals? In C. M. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 89–118). Cambridge University Press.

Iwaniuk, A. N., & Hurd, P. L. (2005). The evolution of cerebrotypes in birds. *Brain, Behavior and Evolution, 65*(4), 215–230. https://doi.org/10.1159/000084313

Iwaniuk, A., Lefebvre, L., & Wylie, D. (2009). The comparative approach and brain–behaviour relationships: A tool for understanding tool use. *Canadian Journal of Experimental Psychology, 63*, 150–159. https://doi.org/10.1037/a0015678

Iwaniuk, A. N. (2017). The evolution of cognitive brains in non-mammals. In S. Watanabe, M. A. Hofman, & T. Shimizu (Eds.), *Evolution of the brain, cognition, and emotion in vertebrates* (pp. 101–124). Springer Japan. https://doi.org/10.1007/978-4-431-56559-8_5

Iwaniuk, A. N., & Wylie, D. R. (2020). Sensory systems in birds: What we have learned from studying sensory specialists. *Journal of Comparative Neurology, 528*(16), 2902–2918. https://doi.org/10.1002/cne.24896

Jackson, J. R. (1960). Keas at Arthurs Pass. *Notornis, 9*(2), 39–58.

Jarvis, E. D., Güntürkün, O., Bruce, L. *et al*. Avian Brain Nomenclature Consortium. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience, 6*(2), 151–159. https://doi.org/10.1038/nrn1606

Jarvis, E. D., Yu, J., Rivas, M. V., Horita, H., Feenders, G., Whitney, O., Jarvis, S. C., Jarvis, E. R., Kubikova, L., Puck, A. E. P., Siang-Bakshi, C., Martin, S., McElroy, M., Hara, E., Howard, J., Pfenning, A., Mouritsen, H., Chen, C.-C., & Wada, K. (2013). Global view of the functional molecular organization of the avian cerebrum: Mirror images and functional columns. *The Journal of Comparative Neurology, 521*(16), 3614–3665. https://doi.org/10.1002/cne.23404

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements* (p. xii, 283). Clarendon Press/Oxford University Press.

Joseph, T., Brown, O. I., Khalid, S., Giannoudi, M., Sagar, R. C., Bunola-Hadfield, E., Chapman, S. J., Slater, T. A., Straw, S., & Drozd, M. (2024). Dexterity assessment of hospital workers: Prospective comparative study. *BMJ, 387*, e081814. https://doi.org/10.1136/bmj-2024-081814

Jung, J.-Y., Naleway, S. E., Yaraghi, N. A., Herrera, S., Sherman, V. R., Bushong, E. A., Ellisman, M. H., Kisailus, D., & McKittrick, J. (2016). Structural analysis of the tongue and hyoid apparatus in a woodpecker. *Acta Biomaterialia, 37,* 1–13. https://doi.org/10.1016/j.actbio.2016.03.030

Kaeser, M., Chatagny, P., Gindrat, A.-D., Savidan, J., Badoud, S., Fregosi, M., Moret, V., Roulin, C., Schmidlin, E., & Rouiller, E. (2014). Variability of manual dexterity performance in non-

human primates (*Macaca fascicularis*). *International Journal of Comparative Psychology, 27*, 295–325. https://doi.org/10.46867/ijcp.2014.27.02.04

Karakostis, F. A., Haeufle, D., Anastopoulou, I., Moraitis, K., Hotz, G., Tourloukis, V., & Harvati, K. (2021). Biomechanics of the human thumb and the evolution of dexterity. *Current Biology, 31*(6), 1317–1325.e8. https://doi.org/10.1016/j.cub.2020.12.041

Kenward, B., Weir, A. A. S., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature, 433*(7022), 121–121. https://doi.org/10.1038/433121a

Kenward, B., Rutz, C., Weir, A., & Kacelnik, A. (2006). Development of tool use in New Caledonian crows: Inherited action patterns and social influences. *Animal Behaviour, 72*, 1329–1343. https://doi.org/10.1016/j.anbehav.2006.04.007

Kier, W. M. (2012). The diversity of hydrostatic skeletons. *The Journal of Experimental Biology, 215*(Pt 8), 1247–1257. https://doi.org/10.1242/jeb.056549

Kim, K., Jeon, H.-A., Seo, J., Park, J., Won, J., Yeo, H.-G., Jeon, C.-Y., Huh, J.-W., Kim, Y.-H., Hong, Y., Choi, J.-W., & Lee, Y. (2020). Evaluation of cognitive function in adult rhesus monkeys using the finger maze test. *Applied Animal Behaviour Science, 224*, 104945. https://doi.org/10.1016/j.applanim.2020.104945

King, B. J. (1986). Extractive foraging and the evolution of primate intelligence. *Human Evolution, 1*, 361–372. https://doi.org/10.1007/BF02436709

Kinoshita, M., Matsui, R., Kato, S., Hasegawa, T., Kasahara, H., Isa, K., Watakabe, A., Yamamori, T., Nishimura, Y., Alstermark, B., Watanabe, D., Kobayashi, K., & Isa, T. (2012). Genetic dissection of the circuit for hand dexterity in primates. *Nature, 487*(7406), 235–238. https://doi.org/10.1038/nature11206

Kivell, T. L. (2021). Human evolution: Thumbs up for efficiency. *Current Biology, 31*(6), R289–R291. https://doi.org/10.1016/j.cub.2021.02.021

Kivell, T. L., Baraki, N., Lockwood, V., Williams-Hatala, E. M., & Wood, B. A. (2023). Form, function and evolution of the human hand. *American Journal of Biological Anthropology, 181*(S76), 6–57. https://doi.org/10.1002/ajpa.24667

Klump, B. C., Sugasawa, S., St Clair, J. J. H., et al. (2015). Hook tool manufacture in New Caledonian crows: Behavioural variation and the influence of raw materials. *BMC Biology, 13*, 97. https://doi.org/10.1186/s12915-015-0204-7

Klump, B. C., Cantat, M., & Rutz, C. (2019). Raw-material selectivity in hook-tool-crafting New Caledonian crows. *Biology Letters, 15*(2), 20180836. https://doi.org/10.1098/rsbl.2018.0836

Knospe, C. (1992). Gibt es eine innere Zungenmuskulatur beim Papagei? *Anatomia, Histologia, Embryologia, 21*(1), 65–67. https://doi.org/10.1111/j.1439-0264.1992.tb00320.x

Korzoun, L., Erard, C., & Gasc, J.-P. (2001). Distinctive morphofunctional features of the bill and hyoid apparatus of turacos (Aves, Musophagidae): Relations with frugivory. *Comptes rendus de l'Académie des sciences. Série III, Sciences de la vie, 324*, 965–977.

Ksepka, D. T., Balanoff, A. M., Smith, N. A., Bever, G. S., Bhullar, B.-A. S., Bourdon, E., Braun, E. L., Burleigh, J. G., Clarke, J. A., Colbert, M. W., Corfield, J. R., Degrange, F. J., De Pietri, V. L., Early, C. M., Field, D. J., Gignac, P. M., Gold, M. E. L., Kimball, R. T., Kawabe, S., … Smaers, J. B. (2020). Tempo and pattern of avian brain size evolution. *Current Biology, 30*(11), 2026–2036.e3. https://doi.org/10.1016/j.cub.2020.03.060

Kverková, K., Marhounová, L., Polonyiová, A., Kocourek, M., Zhang, Y., Olkowicz, S., Straková, B., Pavelková, Z., Vodička, R., Frynta, D., & Němec, P. (2022). The evolution of brain neuron numbers in amniotes. *Proceedings of the National Academy of Sciences of the United States of America, 119*(11), e2121624119. https://doi.org/10.1073/pnas.2121624119

Lakjer, T. (1926). *Studien über die Trigeminus-versorgte Kaumuskulatur der Sauropsiden*. Reitzel.

Lambert, P. J., Stiegler, A., Rössler, T., Lambert, M. L., & Auersperg, A. M. I. (2021). Goffin's cockatoos discriminate objects based on weight alone. *Biology Letters, 17*(9), 20210250. https://doi.org/10.1098/rsbl.2021.0250

Latash, M. L. (2009). Coordination. In M. D. Binder, N. Hirokawa, & U. Windhorst (Eds.), *Encyclopedia of neuroscience* (pp. 886–888). Springer. https://doi.org/10.1007/978-3-540-29678-2_1269

Laumer, I., Bugnyar, T., & Auersperg, A. (2016). Flexible decision-making relative to reward quality and tool functionality in Goffin cockatoos (*Cacatua goffiniana*). *Scientific Reports, 6*, 28380. https://doi.org/10.1038/srep28380

Laumer, I. B., Bugnyar, T., Reber, S. A., & Auersperg, A. M. I. (2017). Can hook-bending be let off the hook? Bending/unbending of pliant tools by cockatoos. *Proceedings of the Royal Society B: Biological Sciences, 284*(1862), 20171026. https://doi.org/10.1098/rspb.2017.1026

Laumer, I. B., Jelbert, S. A., Taylor, A. H., et al. (2021). Object manufacture based on a memorized template: Goffin's cockatoos attend to different model features. *Animal Cognition, 24*, 457–470. https://doi.org/10.1007/s10071-020-01435-7

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution, 63*(4), 233–246. https://doi.org/10.1159/000076784

Lefebvre, L. (2013). Brains, innovations, tools and cultural transmission in birds, non-human primates, and fossil hominins. *Frontiers in Human Neuroscience, 7*, 245. https://doi.org/10.3389/fnhum.2013.00245

Lemon, R. N. (2008). An enduring map of the motor cortex. *Experimental Physiology, 93*(7), 798–802. https://doi.org/10.1113/expphysiol.2007.039081

Lesnik, J. J., Sanz, C. M., & Morgan, D. B. (2015). The interdigital brace and other grips for termite nest perforation by chimpanzees of the Goualougo Triangle, Republic of Congo. *American Journal of Physical Anthropology, 157*(2), 252–259. https://doi.org/10.1002/ajpa.22706

Lessner, E., Echols, M., Paul-Murphy, J., Speer, B., & Holliday, C. (2023). Grey parrot (*Psittacus erithacus*) beak papillae and nerves identified using novel 2-D and 3-D imaging modalities. *American Journal of Veterinary Research, 84*, 1–7. https://doi.org/10.2460/ajvr.23.03.0059

Li, Z.-M. (2006). Functional degrees of freedom. *Motor Control, 10*(4), 301–310. https://doi.org/10.1123/mcj.10.4.301

Liu, M., Xiong, C.-H., & Hu, D. (2016). Assessing the manipulative potentials of monkeys, apes and humans from hand proportions: Implications for hand evolution. *Proceedings of the Royal Society B: Biological Sciences, 283*, 20161923. https://doi.org/10.1098/rspb.2016.1923

Lonsdorf, E. V., & Sanz, C. M. (2022). Behavioral and cognitive perspectives on the evolution of tool use from wild chimpanzees. *Current Opinion in Behavioral Sciences, 46*, 101144. https://doi.org/10.1016/j.cobeha.2022.101144

Macfarlane, N. B. W., & Graziano, M. S. A. (2009). Diversity of grip in *Macaca mulatta*. *Experimental Brain Research, 197*(3), 255–268. https://doi.org/10.1007/s00221-009-1909-z

Mangalam, M., & Fragaszy, D. M. (2016). Transforming the body-only system into the body-plus-tool system. *Animal Behaviour, 117*, 115–122. https://doi.org/10.1016/j.anbehav.2016.04.016

Mangalam, M., & Fragaszy, D. M. (2018). Reply to 'tool use and dexterity: Beyond the embodied theory'. *Animal Behaviour, 139*, e5–e8. https://doi.org/10.1016/j.anbehav.2018.03.017

Mangalam, M., Cuadra, C., & Singh, T. (2021). Sensory redundancy and perceptual invariance in force production and object manipulation. *Current Opinion in Physiology, 19*, 148–155. https://doi.org/10.1016/j.cophys.2020.11.002

Martin, G. R., & Martin, R. O. (2021). Psittaciformes sensory systems. In J. Vonk & T. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 1704–1711). Springer. https://doi.org/10.1007/978-3-319-47829-6_1704-1

Marzke, M. W. (1997). Precision grips, hand morphology, and tools. *American Journal of Physical Anthropology, 102*(1), 91–110. https://doi.org/10.1002/(SICI)1096-8644(199701)102:1<91::AID-AJPA8>3.0.CO;2-G

Marzke, M. W. (2013). Tool making, hand morphology and fossil hominins. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1630), 20120414. https://doi.org/10.1098/rstb.2012.0414

Matsui, H., Hunt, G., Oberhofer, K., et al. (2016). Adaptive bill morphology for enhanced tool manipulation in New Caledonian crows. *Scientific Reports, 6*, 22776. https://doi.org/10.1038/srep22776

McEntire, C. R. S., Choudhury, G. R., Torres, A., Steinberg, G. K., Redmond, D. E., & Daadi, M. M. (2016). Impaired arm function and finger dexterity in a nonhuman primate model of stroke. *Stroke, 47*(4), 1109–1116. https://doi.org/10.1161/STROKEAHA.115.012506

McGrew, W. C. (2013). Is primate tool use special? Chimpanzee and New Caledonian crow compared. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1630), 20120422. https://doi.org/10.1098/rstb.2012.0422

Meekangvan, P., Barhorst, A., Burton, T. D., Chatterjee, S., & Schovanec, L. (2006). Nonlinear dynamical model and response of avian cranial kinesis. *Journal of Theoretical Biology, 240*(1), 32–47. https://doi.org/10.1016/j.jtbi.2005.08.027

Metcalf, C. D., Irvine, T. A., Sims, J. L., Wang, Y. L., Su, A. W. Y., & Norris, D. O. (2014). Complex hand dexterity: A review of biomechanical methods for measuring musical performance. *Frontiers in Psychology, 5*, 414. https://doi.org/10.3389/fpsyg.2014.00414

Mioduszewska, B., O'Hara, M., Haryoko, T., Auersperg, A., Huber, L., & Prawiradilaga, D. (2019). Notes on ecology of wild Goffin's cockatoo in the late dry season with emphasis on feeding ecology. *TREUBIA, 45*, 85–102. https://doi.org/10.14203/treubia.v45i0.3706

Montiel, J. F., Vasistha, N. A., Garcia-Moreno, F., & Molnár, Z. (2015). From sauropsids to mammals and back: New approaches to comparative cortical development. *The Journal of Comparative Neurology, 524*(3), 630–645. https://doi.org/10.1002/cne.23871

Morasso, P. (2022). A vexing question in motor control: The degrees of freedom problem. *Frontiers in Bioengineering and Biotechnology, 9*, 783501. https://doi.org/10.3389/fbioe.2021.783501

Mudge, G. P. (1903). On the myology of the tongue of parrots, with a classification of the order, based upon the structure of the tongue. *Transactions of the Linnean Society of London*, 16, 211–278.

Napier, J. R. (1960). Studies of the hands of living primates. *Proceedings of the Zoological Society of London, 134*(4), 647–657. https://doi.org/10.1111/j.1469-7998.1960.tb05606.x

Napier, J. R. (1961). Prehensility and opposability in the hands of primates. In *Symposium of the Zoological Society of London* (Vol. 5, pp. 115–132).

Napier, J. (1962). Fossil hand bones from Olduvai Gorge. *Nature, 196*(4853), 409–411. https://doi.org/10.1038/196409a0

Navalón, G., Bright, J. A., Marugán-Lobón, J., & Rayfield, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution, 73*(3), 422–435. https://doi.org/10.1111/evo.13655

Nitzsch, C. L. (1859). Anatomische Notizen über die Papageien. *Zeitschrift für die gesammten Naturwissenschaften*, *13*, 118–125.

O'Hara, M., Mioduszewska, B., Mundry, R., Yohanna, Haryoko, T., Rachmatika, R., Prawiradilaga, D. M., Huber, L., & Auersperg, A. M. I. (2021). Wild Goffin's cockatoos flexibly manufacture and use tool sets. *Current Biology, 31*(20), 4512–4520.e6. https://doi.org/10.1016/j.cub.2021.08.009

Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences, 113*(26), 7255-7260. https://doi.org/10.1073/pnas.1517131113

Olsen, A. M. (2017). Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Functional Ecology, 31*(10), 1985–1995. https://doi.org/10.1111/1365-2435.12890

Olson, R. A., Montuelle, S. J., Chadwell, B. A., Curtis, H., & Williams, S. H. (2021). Jaw kinematics and tongue protraction-retraction during chewing and drinking in the pig. *Journal of Experimental Biology, 224*(7), jeb239509. https://doi.org/10.1242/jeb.239509

Osiurak, F., & Danel, S. (2018). Tool use and dexterity: Beyond the embodied theory. *Animal Behaviour, 139*, e1–e4. https://doi.org/10.1016/j.anbehav.2018.03.016

Osuna-Mascaró, A., & Auersperg, A. (2018). On the brink of tool use? Could object combinations during foraging in a feral Goffin's cockatoo (*Cacatua goffiniana*) result in tool innovations? *Animal Behavior and Cognition, 5*, 105–115. https://doi.org/10.26451/abc.05.02.05.2018

Osuna-Mascaró, A. J., Ortiz, C., Stolz, C., Musgrave, S., Sanz, C. M., Morgan, D. B., & Fragaszy, D. M. (2021). Dexterity and technique in termite fishing by chimpanzees (*Pan troglodytes troglodytes*) in the Goualougo Triangle, Republic of Congo. *American Journal of Primatology, 83*(1), e23215. https://doi.org/10.1002/ajp.23215

Osuna-Mascaró, A. J., Mundry, R., Tebbich, S., et al. (2022). Innovative composite tool use by Goffin's cockatoos (*Cacatua goffiniana*). *Scientific Reports, 12*, 1510. https://doi.org/10.1038/s41598-022-05529-9

Overington, S. E., Morand-Ferron, J., Boogert, N. J., & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour, 78*(4), 1001–1010. https://doi.org/10.1016/j.anbehav.2009.06.033

Padberg, J., Franca, J. G., Cooke, D. F., Soares, J. G. M., Rosa, M. G. P., Fiorani, M., Gattass, R., & Krubitzer, L. (2007). Parallel evolution of cortical areas involved in skilled hand use. *Journal of Neuroscience, 27*(38), 10106–10115. https://doi.org/10.1523/JNEUROSCI.2632-07.2007

Parker, S. T. (2015). Re-evaluating the extractive foraging hypothesis. *New Ideas in Psychology, 37*, 1–12. https://doi.org/10.1016/j.newideapsych.2014.11.001

Patti, A., Vicari, D. S. S., Giustino, V., Figlioli, F., Seidita, G. M., Monella, A. C. M., Oddo, A., Paoli, A., Drid, P., Thomas, E., & Bianco, A. (2025). The impact of sports experience on manual dexterity performances in school-age children. *Heliyon, 11*(1), e41421. https://doi.org/10.1016/j.heliyon.2024.e41421

Pepperberg, I. M. (2000). *The Alex studies: Cognitive and communicative abilities of grey parrots*. Harvard University Press.

Pika, S., Sima, M. J., Blum, C. R., Herrmann, E., & Mundry, R. (2020). Ravens parallel great apes in physical and social cognitive skills. *Scientific Reports, 10*(1), 20617. https://doi.org/10.1038/s41598-020-77060-8

Pizzimenti, M. A., Darling, W. G., Rotella, D. L., McNeal, D. W., Herrick, J. L., Ge, J., Stilwell-Morecraft, K. S., & Morecraft, R. J. (2007). Measurement of reaching kinematics and prehensile dexterity in nonhuman primates. *Journal of Neurophysiology, 98*(2), 1015–1029. https://doi.org/10.1152/jn.00354.2007

Poirier, F. (1988). Dexterity as a valid measure of hand function. *Occupational Therapy in Health Care, 4*(3–4), 69–83. https://doi.org/10.1080/J003v04n03_07

Rahman, A., & Al-Jumaily, A. (2013). Design and development of a bilateral therapeutic hand device for stroke rehabilitation. *International Journal of Advanced Robotic Systems, 10*(12), 405. https://doi.org/10.5772/56809

Rat-Fischer, L., Plunkett, K., von Bayern, A. M. P., & Kacelnik, A. (2024). Object play and problem solving in infancy: Insights into tool use. *Journal of Experimental Child Psychology, 244*, 105957. https://doi.org/10.1016/j.jecp.2024.105957

Reiner, A., Perkel, D. J., Mello, C. V., & Jarvis, E. D. (2004). Songbirds and the revised avian brain nomenclature. *Annals of the New York Academy of Sciences, 1016*, 77–108. https://doi.org/10.1196/annals.1298.013

Reiner, A., Yamamoto, K., & Karten, H. J. (2005). Organization and evolution of the avian forebrain. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology, 287A*(1), 1080–1102. https://doi.org/10.1002/ar.a.20253

Rössler, T., Mioduszewska, B., O'Hara, M., Huber, L., Prawiradilaga, D. M., & Auersperg, A. M. I. (2020). Using an innovation arena to compare wild-caught and laboratory Goffin's cockatoos. *Scientific Reports, 10*(1), 8681. https://doi.org/10.1038/s41598-020-65223-6

Rössler, T., & Auersperg, A. M. (2022). Recent developments in parrot cognition: A quadrennial update. *Animal Cognition, 26*(1), 199–228. https://doi.org/10.1007/s10071-022-01733-2

Rutz, C., Bluff, L. A., Reed, N., Troscianko, J., Newton, J., Inger, R., Kacelnik, A., & Bearhop, S. (2010). The ecological significance of tool use in New Caledonian crows. *Science, 329*(5998), 1523–1526. https://doi.org/10.1126/science.1192053

Rutz, C., Sugasawa, S., van der Wal, J. E. M., Klump, B. C., & St Clair, J. J. H. (2016). Tool bending in New Caledonian crows. *Royal Society Open Science, 3*(8), 160439.

https://doi.org/10.1098/rsos.160439

Sanz, C. M., & Morgan, D. B. (2007). Chimpanzee tool technology in the Goualougo Triangle, Republic of Congo. *Journal of Human Evolution, 52*(4), 420–433. https://doi.org/10.1016/j.jhevol.2006.11.001

Sanz, C. M., Call, J., & Boesch, C. (Eds.). (2013). *Tool use in animals: Cognition and ecology*. Cambridge University Press. https://doi.org/10.1017/CBO9780511894800

Sato, R., Kodama, S., Okawa, J., Murakami, K., Ono, T., & Hori, K. (2024). Tongue and jaw movement assessed by 3D motion capture during gum chewing. *Frontiers in Physiology, 15*, 1409005. https://doi.org/10.3389/fphys.2024.1409005

Sheard, C., Street, S. E., Evans, C., Lala, K. N., Healy, S. D., & Sugasawa, S. (2023). Beak shape and nest material use in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences, 378*(1884), 20220147. https://doi.org/10.1098/rstb.2022.0147

Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: The use and manufacture of tools by animals*. Johns Hopkins University Press.

Sobinov, A., & Bensmaia, S. (2021). The neural mechanisms of manual dexterity. *Nature Reviews Neuroscience, 22*, 263–278. https://doi.org/10.1038/s41583-021-00528-7

Spinozzi, G., Truppa, V., & Laganà, T. (2004). Grasping behavior in tufted capuchin monkeys (*Cebus apella*): Grip types and manual laterality for picking up a small food item. *American Journal of Physical Anthropology, 125*(1), 30–41. https://doi.org/10.1002/ajpa.10362

Spool, J. A., Macedo-Lima, M., Scarpa, G., Morohashi, Y., Yazaki-Sugiyama, Y., & Remage-Healey, L. (2021). Genetically identified neurons in avian auditory pallium mirror core principles of their mammalian counterparts. *Current Biology, 31*(13), 2831–2843.e6. https://doi.org/10.1016/j.cub.2021.04.039

Stacho, M., Herold, C., Rook, N., Wagner, H., Axer, M., Amunts, K., & Güntürkün, O. (2020). A cortex-like canonical circuit in the avian forebrain. *Science, 369*(6511), eabc5534. https://doi.org/10.1126/science.abc5534

Steinberg, F., & Bock, O. (2013). Influence of cognitive functions and behavioral context on grasping kinematics. *Experimental Brain Research, 225*(3), 387–397. https://doi.org/10.1007/s00221-012-3379-y

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Sugasawa, S., Klump, B. C., St Clair, J. J. H., & Rutz, C. (2017). Causes and consequences of tool shape variation in New Caledonian crows. *Current Biology, 27*(24), 3885–3890.e4. https://doi.org/10.1016/j.cub.2017.11.028

Sugasawa, S., Webb, B., & Healy, S. D. (2021). Object manipulation without hands. *Proceedings of the Royal Society B: Biological Sciences, 288*(1943), 20203184. https://doi.org/10.1098/rspb.2020.3184

Tan, A. W. Y. (2017). From play to proficiency: The ontogeny of stone-tool use in coastal-foraging long-tailed macaques (*Macaca fascicularis*) from a comparative perception-action perspective. *Journal of Comparative Psychology, 131*(2), 89–114. https://doi.org/10.1037/com0000068

Tariciotti, L., Mattioli, L., Viganò, L., Gallo, M., Gambaretti, M., Sciortino, T., Gay, L., Conti Nibali, M., Gallotti, A., Cerri, G., Bello, L., & Rossi, M. (2024). Object-oriented hand dexterity and grasping abilities, from the animal quarters to the neurosurgical OR: A systematic review of the underlying neural correlates in non-human, human primate and recent findings in awake brain surgery. *Frontiers in Integrative Neuroscience, 18*, 1324581. https://doi.org/10.3389/fnint.2024.1324581

Tebbich, S., & Bshary, R. (2004). Cognitive abilities related to tool use in the woodpecker finch, Cactospiza pallida. *Animal Behaviour, 67*(4), 689–697. https://doi.org/10.1016/j.anbehav.2003.08.003

Tebbich, S., Stankewitz, S., & Teschke, I. (2012). Investigating the relationship between feeding ecology, flexibility and neophobia in two species of Darwin's finches. *Ethology, 118*, 135–146.

Tokita, M. (2003). The skull development of parrots with special reference to the emergence of a morphologically unique craniofacial hinge. *Zoological Science, 20*(7), 749–758. https://doi.org/10.2108/zsj.20.749

Tokita, M. (2004). Morphogenesis of parrot jaw muscles: Understanding the development of an evolutionary novelty. *Journal of Morphology, 259*(1), 69–81. https://doi.org/10.1002/jmor.10172

Tokita, M., Kiyoshi, T., & Armstrong, K. N. (2007). Evolution of craniofacial novelty in parrots through developmental modularity and heterochrony. *Evolution & Development, 9*(6), 590–601. https://doi.org/10.1111/j.1525-142X.2007.00199.x

Tokita, M., & Nakayama, T. (2014). Development of the trigeminal motor neurons in parrots: Implications for the role of nervous tissue in the evolution of jaw muscle morphology. *Journal of Morphology, 275*(2), 191–205. https://doi.org/10.1002/jmor.20208

Troscianko, J., von Bayern, A., Chappell, J., et al. (2012). Extreme binocular vision and a straight bill facilitate tool use in New Caledonian crows. *Nature Communications, 3*, 1110. https://doi.org/10.1038/ncomms2111

Tsuchida, J., Kawasaki, K., Sankai, T., Kubo, N., Terao, K., Koyama, T., Makino, J., & Yoshikawa, Y. (2003). New type of puzzle-task finger maze learning in *Macaca fascicularis*. *International Journal of Primatology, 24*(2), 261–270. https://doi.org/10.1023/A:1023040931101

Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: Representation of action in human anterior intraparietal sulcus. *NeuroImage, 36*(Suppl 2), T77–T86. https://doi.org/10.1016/j.neuroimage.2007.03.026

von Bayern, A. M., Heathcote, R. J., Rutz, C., & Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Current Biology, 19*(22), 1965–1968. https://doi.org/10.1016/j.cub.2009.10.037

von Bayern, A. M. P., Danel, S., Auersperg, A. M. I., et al. (2018). Compound tool construction by New Caledonian crows. *Scientific Reports, 8*, 15676. https://doi.org/10.1038/s41598-018-33458-z

von Eugen, K., Tabrik, S., Güntürkün, O., & Ströckens, F. (2020). A comparative analysis of the dopaminergic innervation of the executive caudal nidopallium in pigeon, chicken, zebra finch, and carrion crow. *The Journal of Comparative Neurology, 528*(17), 2929–2955. https://doi.org/10.1002/cne.24878

Weir, A. A., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science, 297*(5583), 981. https://doi.org/10.1126/science.1073433

Wild, J. M. (1981). Identification and localization of the motor nuclei and sensory projections of the glossopharyngeal, vagus, and hypoglossal nerves of the cockatoo (*Cacatua roseicapilla*), Cacatuidae. *The Journal of Comparative Neurology, 203*(3), 351–377. https://doi.org/10.1002/cne.902030304

Wild, J. M., Reinke, H., & Farabaugh, S. M. (1997). A non-thalamic pathway contributes to a whole body map in the brain of the budgerigar. *Brain Research, 755*(1), 137–141. https://doi.org/10.1016/s0006-8993(97)00026-7

Wild, J. M., & Zeigler, H. P. (1999). Neural control of the avian jaw and its role in consummatory behaviour. In N. J. Adams & R. H. Slotow (Eds.), *Proceedings of the 22nd International Ornithological Congress, Durban* (pp. 777–783). Johannesburg: BirdLife South Africa.

Wild, J. M. (2015). The avian somatosensory system: A comparative view. In C. G. Scanes (Ed.), *Sturkie's avian physiology* (6th ed., pp. 55–69). Academic Press. https://doi.org/10.1016/B978-0-12-407160-5.00005-1

Wild, J. M. (2022). The avian somatosensory system: A comparative view. In C. G. Scanes & S. Dridi (Eds.), *Sturkie's avian physiology* (7th ed., pp. 123–137). Academic Press. https://doi.org/10.1016/B978-0-12-819770-7.00018-9

Won, J., Yi, K. S., Choi, C.-H., Jeon, C.-Y., Seo, J., Kim, K., Yeo, H.-G., Park, J., Kim, Y. G., Jin, Y. B., Koo, B.-S., Lim, K. S., Lee, S., Kim, K. J., Choi, W. S., Park, S.-H., Kim, Y.-H., Huh, J.-W., Lee, S.-R., … Lee, Y. (2020). Assessment of hand motor function in a non-human primate model of ischemic stroke. *Experimental Neurobiology, 29*(4), 300–313. https://doi.org/10.5607/en20023

Wright, T., Schirtzinger, E., Eberhard, J., Graves, G., Sanchez, J., Capelli, S., Muller, H., Scharpegge, J., Chambers, G., & Fleischer, R. (2008). A multilocus molecular phylogeny of the parrots (Psittaciformes): Support for a Gondwanan origin during the Cretaceous. *Molecular Biology and Evolution, 25*(10), 2141–2156.

Yang, Z., & Long, M. A. (2025). Convergent vocal representations in parrot and human forebrain motor networks. *Nature, 640*, 427–434. https://doi.org/10.1038/s41586-025-08695-8

Yong, J., MacDermid, J. C., & Packham, T. (2020). Defining dexterity—Untangling the discourse in clinical practice. *Journal of Hand Therapy, 33*(4), 517–519. https://doi.org/10.1016/j.jht.2019.11.001

Young, M. W., Dickinson, E., Flaim, N. D., & Granatosky, M. C. (2022). Overcoming a “forbidden phenotype”: The parrot's head supports, propels and powers tripedal locomotion. *Proceedings of the Royal Society B: Biological Sciences, 289*, 20220245. https://doi.org/10.1098/rspb.2022.0245

Young, M. W., Wilken, A. T., Manafzadeh, A. R., Schurr, A. F., Bastian, A., Dickinson, E., & Granatosky, M. C. (2023). The dual function of prokinesis in the feeding and locomotor systems of parrots. *Journal of Experimental Biology, 226*(24), jeb246659. https://doi.org/10.1242/jeb.24665

Zaremba, B., Fallahshahroudi, A., Schneider, C., Schmidt, J., Sarropoulos, I., Leushkin, E., Berki, B., Van Poucke, E., Jensen, P., Senovilla-Ganzo, R., Hervas-Sotomayor, F., Trost, N., Lamanna, F., Sepp, M., García-Moreno, F., & Kaessmann, H. (2025). Developmental origins and evolution of pallial cell types and structures in birds. *Science, 387*(6735), eadp5182. https://doi.org/10.1126/science.adp5182

Zeigler, H. P., Levitt, P. W., & Levine, R. R. (1980). Eating in the pigeon (*Columba livia*): Movement patterns, stereotypy, and stimulus control. *Journal of Comparative and Physiological Psychology, 94*(5), 783–794. https://doi.org/10.1037/h0077818

Zhong, S., Su, L., Xu, M., Loke, D., Yu, B., Zhang, Y., & Zhao, R. (2024). Recent advances in artificial sensory neurons: Biological fundamentals, devices, applications, and challenges. *Nano-Micro Letters, 17*(1), 61. https://doi.org/10.1007/s40820-024-01550-x

Zullo, L., Di Clemente, A., & Maiole, F. (2022). How octopus arm muscle contractile properties and anatomical organization contribute to arm functional specialization. *The Journal of Experimental Biology, 225*(6), jeb243163. https://doi.org/10.1242/jeb.243163

Zusi, R. L. (1993). Patterns of diversity in the avian skull. In J. Hanken & B. K. Hall (Eds.), *The skull* (Vol. 2, pp. 391–437). University of Chicago Press.

1477