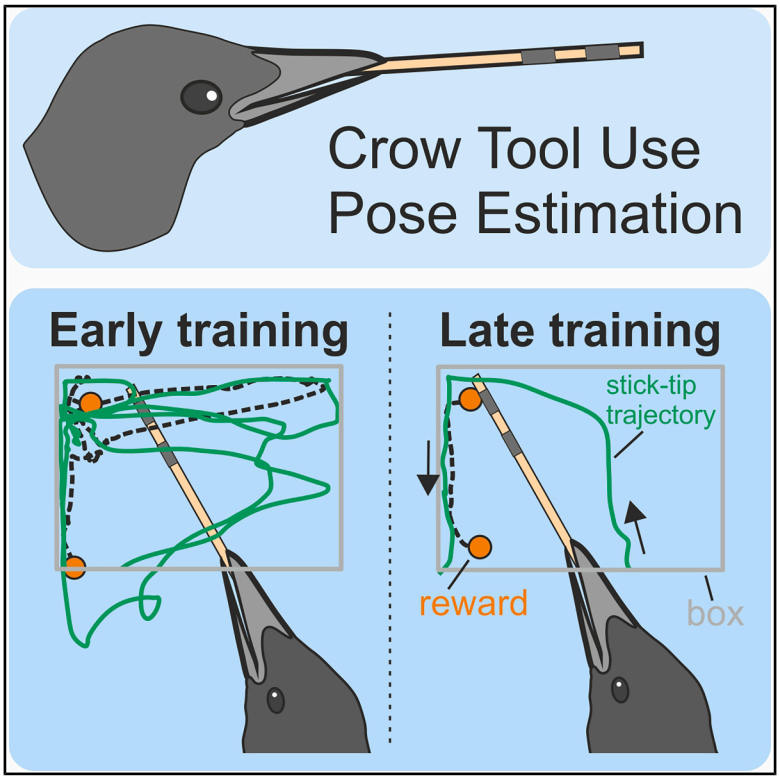
Report

Current Biology

Learned precision tool use in carrion crows

Graphical abstract



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In brief

Moll et al. show that carrion crows—which do not habitually use tools in the wild—can be trained to use a stick tool as an extension of their body. Trained crows flexibly adjust tool orientation and dexterously correct errors when the tool's working end loses control over the target.

Highlights

- Tool-naive carrion crows can learn to use stick tools
- Pose estimation shows that tool-use precision is refined by reinforcement learning
- Performance suggests crows integrate the tool into their peripersonal space

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Report

Learned precision tool use in carrion crows

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SUMMARY

Tool use is rare in the animal kingdom but relatively common among dexterous generalists such as primates, parrots, and corvid songbirds.[1] New Caledonian (NC) crows, known for their instinctive tool-making abilities, have long intrigued researchers; however, the motor-cognitive skills underlying these behaviors—such as the level of cause-and-effect understanding and precise yet flexible motor control—remain unresolved.[2–6] To investigate how learning shapes these skills, we studied carrion crows, an NC-crow-related corvid species with similar cognitive abilities but no tool-use-specific adaptations.[7,8] We trained three tool-naive carrion crows to use a beak-held stick to retrieve food pellets from a transparent Plexiglas crack in an automated apparatus. Utilizing computational pose estimation,[9] we tracked the crows' development of stick tool skills over thousands of trials. Our findings demonstrate that tool-naive carrion crows learn to handle tools with impressive skill, achieving dexterity similar to habitual tool users like NC crows. More notably, we observed that all the crows developed efficient, unique, and goal-directed movement patterns. Even after extensive training, the crows retained a remarkable level of flexibility, swiftly correcting errors and adjusting the orientation of the stick to maintain precise alignment. Our findings suggest that reinforcement learning alone can foster skilled tool use in dexterous, cognitively flexible corvids. This implies that only modest evolutionary changes—such as a predisposition to maneuver elongated objects when exploring crevices[7,10]—may be needed to transform dexterous generalists into habitual tool users.

RESULTS AND DISCUSSION

Crows and other members of the corvid family are songbirds with exceptionally large brains and advanced behaviors, including future planning and tool use.[4,11–18] Tool use is defined by Shumaker et al.[1] as "The external employment of an [ ] object to alter [ ] the form, position, or condition of another object [ ], when the user holds and directly manipulates the tool [ ] and is responsible for the proper and effective orientation of the tool."[1] Observations of tool-use behaviors have been documented in at least nine out of the 40–44 known crow and raven species.[15,19–22] However, regular tool use only occurs in two island-dwelling species: the New Caledonian (NC) and the Hawaiian crow.[4,22] Video recordings of NC crows demonstrate their refined, precise tool-use skills, implying that their tool-use-related decision-making relies on rapid, sensory feedback-driven responses rather than on a limited set of fixed action patterns.[2,3,5] Here, we asked whether similarly dexterous, tool-use-related motor-cognitive skills can be learned by tool-naive carrion crows (*Corvus corone*) in the absence of tool-use-specific adaptations.[15,18,23–25]

Tool-use skills are refined by trial-and-error learning

We trained three crows to use a beak-held stick to retrieve food pellets from a transparent Plexiglas box in an automated apparatus (Figures 1A and 1B; Video S1). We recorded the crows' behavior with two top-view video cameras at 200 Hz (Figure 1B). This high frame rate and stereo view allowed for precise, three-dimensional tracking of selected body and object part positions using the pose estimation software DeepLabCut[9] (Figure 1C).

At the start of each trial, a pellet was automatically placed at one of three fixed positions—"left," "middle," or "right"—at the far end of the Plexiglas box, out of reach of the crow's beak (Figure 1B, showing the initial pellet position "left"). The stick dispenser then presented the upper 1 cm of a 13-cm-long stick, which the crow pulled out (Figure 1C1). After this initial pull, the crow often better aligned the stick with its beak for a more secure grip (Figure 1C2, more details below). The crow then inserted the stick into the box through an open side facing the bird (cf. Figures 1A–1C) and maneuvered the stick tip toward the pellet. Using the stick, the crow guided the pellet to within reach of its beak—either to the proximal third of the box or completely out of it (Figures 1C3 and 1D). Importantly, if the pellet was moved out too quickly, it could fall off the elevated setup table, rendering it unreachable for the crow (cf. Figure 1A). Before consuming the pellet, all three crows returned the stick to the dispenser (Figure 1C4; Video S1). By actively pushing the stick back into the dispenser, they triggered a mechanism that fully retracted the stick and initiated the next trial.

Prior to performing the task autonomously, all three crows underwent a pre-training procedure (see STAR Methods). They were shaped by the experimenter to retrieve pellets from any position within the box and to initiate trials independently within 22–28 pre-training sessions (~30–90 min per session). At that point, the human trainer withdrew from the setup, and all

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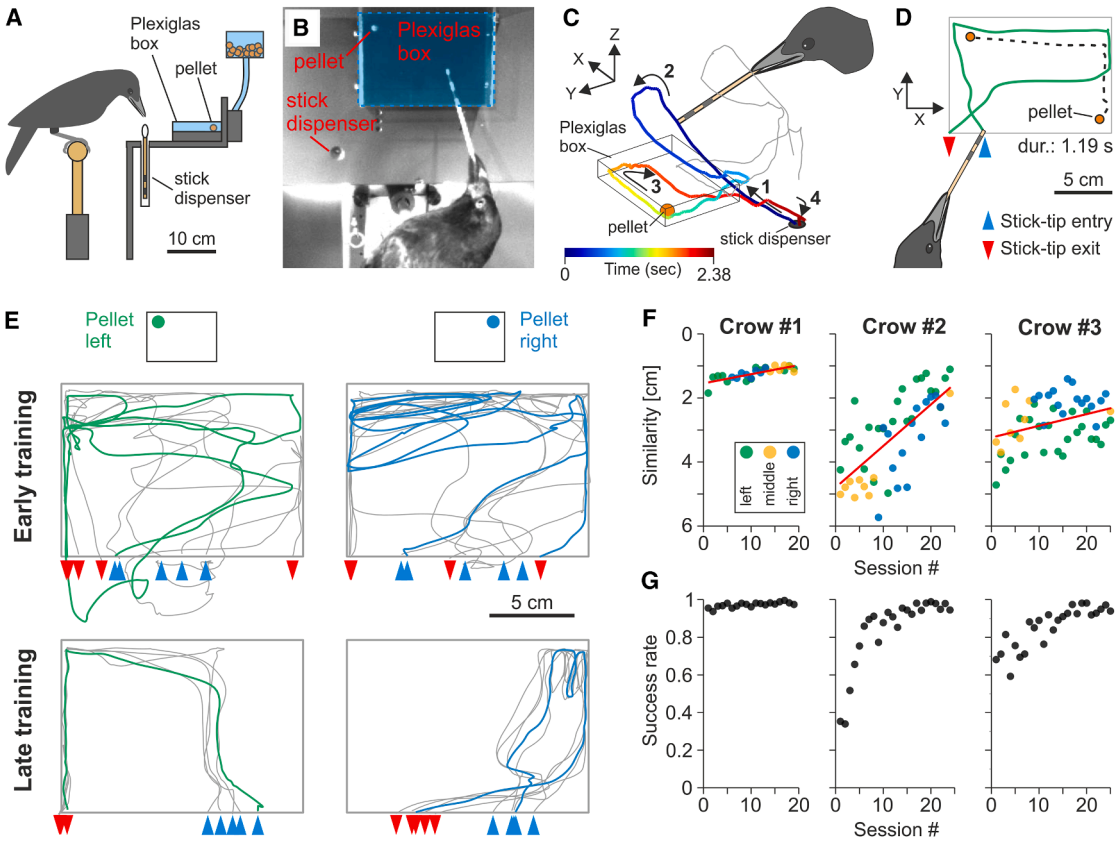

Figure 1. Carrion crows learn to use stick tools

(A) Schematic of the behavioral setup (side view). Note that the stick is returned to and fully retracted by the stick dispenser after each trial.

(B) High-speed camera view (top view) of a crow using a stick to access a pellet in the left rear corner of the Plexiglas box. The transparent box is graphically emphasized by a blue overlay.

(C) Example trial (crow 1, pellet position: left). Trajectories of the stick tip (colored) and beak tip (gray) are depicted from the moment the stick tip left the dispenser to the moment it was returned.

(D) Same trial as in (C) projected to the horizontal plane. Trajectories of the stick tip (green) and pellet (dotted line) from the moment the stick tip entered the box (blue triangle) until it exited (red triangle).

(E) Left column: green lines show single exemplary stick-tip trajectories from an early (top) and late training session (bottom) for trials where the pellet was positioned on the left. Corresponding trajectories from 4 additional trials are shown for comparison in both panels (gray). Gray rectangle represents the box. Right column: same as left column but for trials where the pellet was positioned on the right.

(F) Session medians of pairwise median Euclidean distances between trajectories, separately shown for each condition (i.e., pellet left, middle, or right). Note that similarity increases with decreasing Euclidean distance.

(G) Proportion of successful trials for each session.

See also Video S1.

subsequent sessions were recorded on video (for crows 2 and 3). For crow 1, video recording began later, as this crow had completed an additional 20 training sessions using earlier, semi-automated versions of the apparatus before recordings commenced.

To assess whether and how the crows' tool-use behavior improved in the absence of a human trainer, we analyzed the two-dimensional trajectory of the stick tip during pellet manipulation—specifically, from the moment the stick entered to the moment it exited the Plexiglas box (Figure 1D). In early sessions without a human trainer, crows frequently moved the pellet back and forth with large, imprecise stick movements before it came within reach, resulting in highly variable stick-tip trajectories (Figure 1E, top row). In contrast, during later sessions, the stick movements were more deliberate and consistently aimed toward the pellet, yielding pellet-position-specific trajectories with markedly lower inter-trial variability (Figure 1E, bottom row). To quantify this reduction in variability, we calculated the median pairwise Euclidean distances between all trajectories for each pellet position and session. These distances significantly decreased over sessions in all three crows (n = 9,147 trials over 19–25 sessions in 3 birds; trials per session: mean, 134.8, SD, 85.8) (gamma generalized linear mixed model [GLMM]: −0.019 ± 0.007, t = −2.63, p = 0.009) (Figure 1F). Interestingly, this improvement appeared to generalize across pellet positions. For instance, crow 2 exhibited high inter-trial similarity on "middle" pellet trials in the final session, despite having been exposed only to "left" and "right" positions during the preceding 15 sessions (Figure 1F, crow 2). As a result of these kinematic improvements, fewer pellets were lost due to falling off the table, leading

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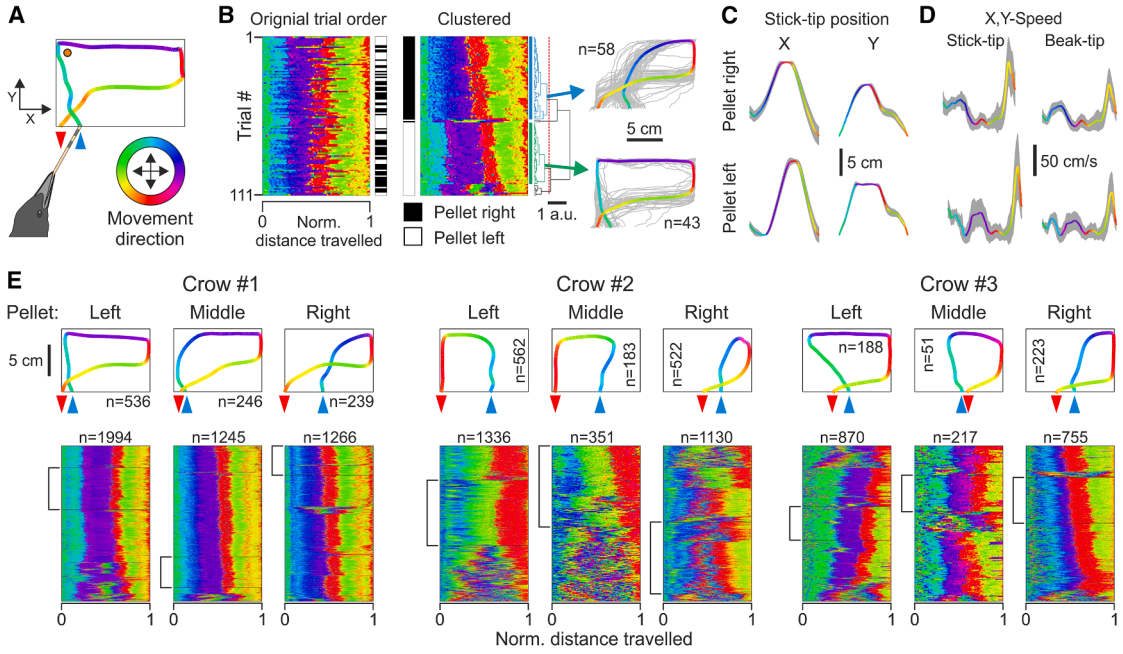

Figure 2. Crows develop unique movement patterns

(A) Example stick-tip trajectory color coded by movement direction.

(B) Hierarchical clustering revealed pellet-position-specific trajectories. Left: heatmap showing all trials of an exemplary session in original order. Each line represents the normalized stick-tip trajectory of a single trial from the moment the stick tip entered the box until it exited, color coded by movement direction. Black and white bar indicates pellet position for each trial. Middle: same heatmap as on the left but trials are ordered by pairwise spatial similarity using hierarchical clustering, resulting in the dendrogram shown. Right: applying a threshold (red dotted line) of 0.8 arbitrary units to the dendrogram resulted in two large clusters with pellet-position-specific stick-tip trajectories. Trajectories of individual trials are shown in gray overlaid by their average (bold color-coded line).

(C) Average stick-tip dynamics along the *x* and *y* axes (cf. A) for the two large clusters shown in (B). Gray shading indicates standard deviation.

(D) Corresponding average stick-tip and beak-tip speed profiles. Same trials as in (C). Gray shading indicates standard deviation.

(E) Heatmaps show stick-tip trajectories from all trials for each bird and pellet position, ordered by pairwise spatial similarity using hierarchical clustering. For each column, the most prevalent movement pattern, that is, the average trajectory of the largest cluster indicated by black brackets to the left of the heatmaps, is shown at the top.

to very high success rates in the final sessions (Figure 1G). Additionally, the time required for pellet manipulation significantly decreased over sessions (n = 9,164 trials over 19–25 sessions in 3 birds) (gamma GLMM: −0.008 ± 0.003, t = −2.37, p = 0.018). Taken together, these findings show that once task contingencies are understood, carrion crows can refine their tool use through trial-and-error learning alone.

Unique and efficient movement patterns

We observed that all three crows developed goal-directed movement strategies. These strategies differed systematically across pellet positions and between individuals, prompting us to determine the most commonly used movement pattern for each condition across all trials (n = 9,164, in 3 birds). To visualize and juxtapose the large set of stick-tip trajectories, we employed a color code representing movement direction (Figure 2A), allowing us to display each trajectory as a single line in a heatmap (Figure 2B).[26] For a typical session, we then applied hierarchical clustering to group trajectories based on their spatial similarity. This analysis revealed a strong correspondence between pellet position and trajectory type (Figure 2B), also reflected in low within-condition spatial variability (Figure 2C). Similarly, average speed profiles revealed condition-specific sub-movement patterns that closely matched between stick-tip and beak-tip trajectories, demonstrating precise, coordinated tool control (Figure 2D).

To extend these findings to our full dataset, we used the same hierarchical clustering criteria for all trials, separately for each bird and pellet position. In every case, the largest cluster captured the crow's most prevalent movement strategy, revealing striking inter-individual differences (Figure 2E). Interestingly, crows 1 and 3 each developed a side preference, always sliding out the pellet on the right (cf. Figures 1D and 3 for corresponding pellet trajectories). In contrast, crow 2 flexibly matched its exit side to the pellet position in "left" and "right" trials, despite sharing crow 3's pre-training history. Nonetheless, all crows consistently directed their movements toward the pellet, underscoring the efficiency of their tool-use strategies.

Swift error corrections

Although the crows' precision and consistency are impressive, it raises the question of how flexible their behavior is beyond the three learned pellet positions. Fortunately, occasional irregularities in pellet delivery offered a natural test. Sometimes the feeder delivered two pellets or none. In most cases, the crows promptly adapted—either retrieving both pellets (together or sequentially) before returning the stick or, if no pellet was present, returning the stick immediately without inserting it into

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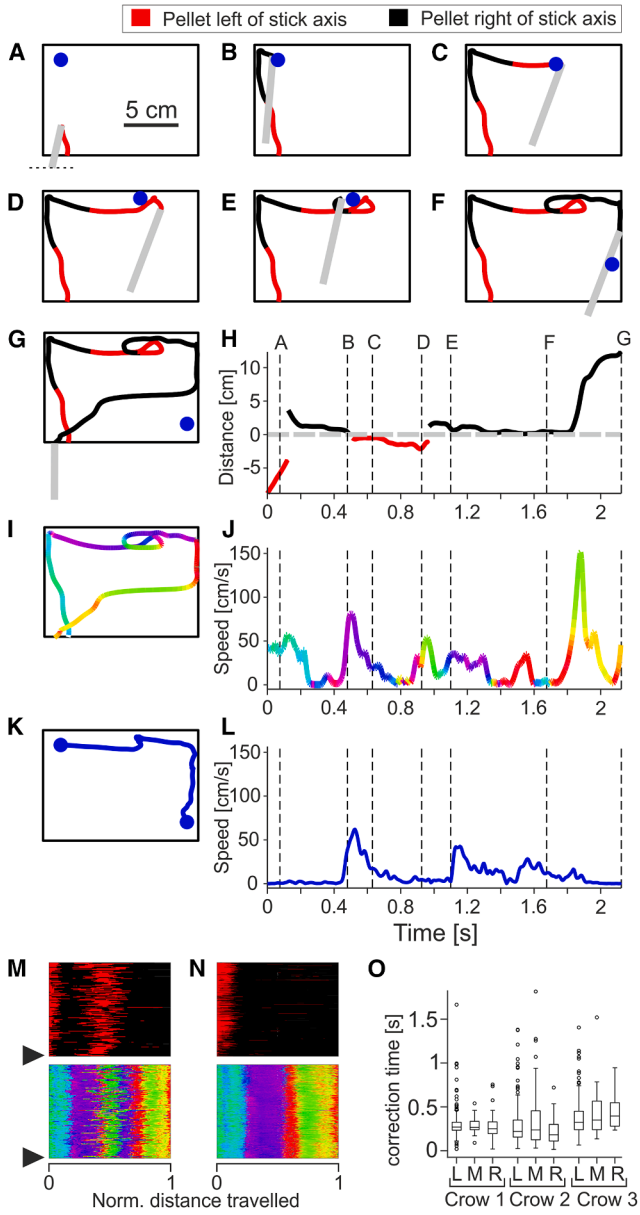

Figure 3. Performance errors are compensated by swift corrective movements

(A–G) Individual frames from one example trial (A–L) in which the crow momentarily lost control over the pellet (cf. C and D). (A)–(G) show the Plexiglas box (rectangle, top view), stick (gray), and pellet (blue). The stick-tip trajectory is shown in black and red. Trajectory sections during which the pellet was located on the left side of the stick axis are shown in red.

(H) Euclidean distance between the pellet and the closest point along the stick, from the moment the stick tip entered the box until it exited. Time points of individual example frames (A–G) are indicated by vertical dotted lines. Distances are shown as negative values for samples during which the pellet was located on the left side of the stick axis (red).

(I) Stick-tip trajectory color coded by movement direction (cf. Figure 2A).

(J) Stick-tip speed profile. Vertical dotted lines indicate example frames (A–G).

(K) Pellet trajectory.

(L) Pellet speed profile.

(M) Example trial from (A)–(L) indicated by black triangle in the context of similar correction trials (crow 1, n = 153 trials; selected based on hierarchical clustering results). Top: each line represents one normalized trial (red: pellet on left side of stick axis; black: pellet on right side of stick axis). Bottom: same trials as in top panel, color coded by movement direction.

(N) Same as (M) but for a cluster of trials with no corrective actions (crow 1, n = 536).

(O) Correction times for each bird and pellet position (crow 1, L: n = 305, M: n = 36, R: n = 51; crow 2, L: n = 170, M: n = 46, R: n = 38; crow 3, L: n = 128, M: n = 13, R: n = 24).

See also Video S2.

the box. Particularly revealing were their rapid reactions to small performance errors—such as when the stick lost contact with the pellet and continuing along the usual trajectory would have left the pellet behind (Figures 3A–3G; Video S2).

To quantify the crows' behavior during these "correction trials," we measured the Euclidean distance between the pellet and the stick from the moment the stick entered to when it exited the Plexiglas box (Figure 3H). In typical, non-correction trials, the pellet stayed on one side of the stick axis throughout manipulation, whereas in correction trials, it crossed over to the other side. To capture this, we additionally determined for each time point whether the pellet was positioned on the left or right side of the stick axis (indicated in red and black, respectively, in Figures 3A–3H).

In the example shown (Figures 3A–3L), the pellet initially remained on the right side of the stick axis (Figure 3B). The crow then accidentally moved the stick past the moving pellet, with the side switch marking the moment when control was lost (Figure 3C). The crow immediately responded by slowing the stick's movement to match the speed of the slowing pellet (Figures 3I–3L). When the pellet stopped moving, the crow swiftly reversed the stick's movement back past the pellet, with the side switch marking the moment when control was regained (Figure 3E). We defined the interval between losing and regaining control as the "correction time."

Based on our hierarchical clustering results (cf. Figure 2E), we identified 153 additional trials resembling this correction pattern in crow 1 (Figure 3M). In all these trials, the onset of the correction period (Figure 3M, top) was followed by a reversal of the stick tip's movement direction (Figure 3M, bottom, green color at ~0.5 normalized distance traveled), indicating a corrective action. Notably, this corrective action was absent in the corresponding cluster of non-correction trials (Figure 3N). We determined the median correction times across birds and pellet positions for all trials with a single performance error and found them to range between 183 and 395 milliseconds (Figure 3O, n = 811 trials in 3 birds). These rapid responses suggest that our crows continuously monitored the effects of their tool use and swiftly adjusted their actions accordingly.

Proper and effective tool orientation

At the start of each trial, when the crows pulled the stick from the dispenser (Figure 4A), the stick was often misaligned with the beak axis (Figure 4B). In the majority of these cases, the initial pull was followed by one or several brief tosses—momentary releases and re-grasps of the stick—to adjust its orientation within the beak and achieve a better grip. Only after these adjustments did the crows insert the stick into the box (Figure 4C; Video S3). In crows 1 and 2, adjustment movements were characterized by a quick downward motion of the beak tip (Figure 4D, "B"),

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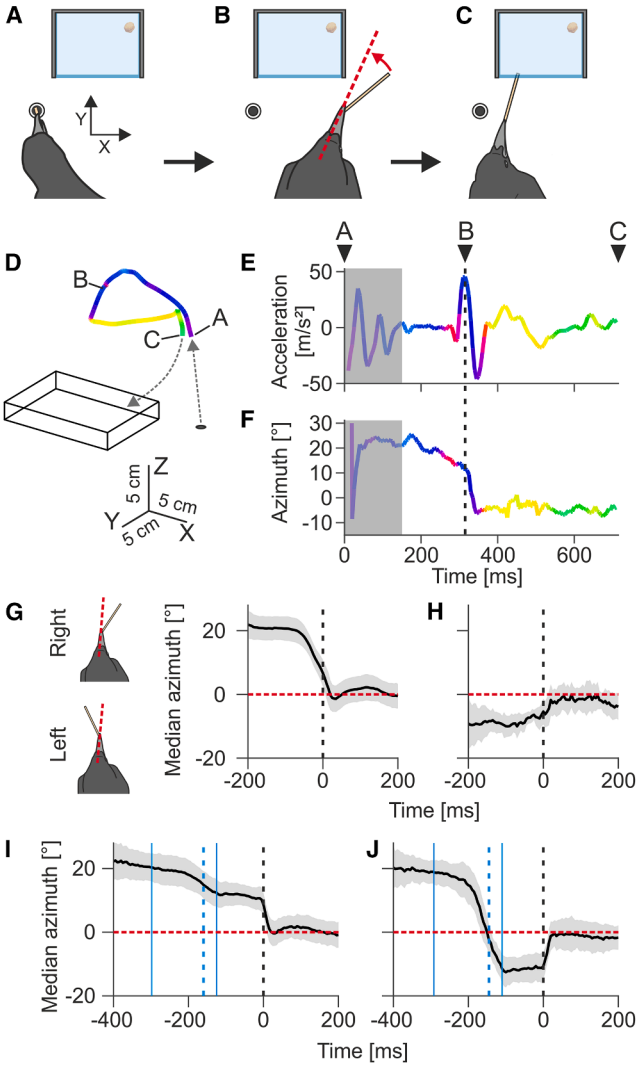

Figure 4. Crows ensure proper tool orientation

(A–C) After pulling the stick from the dispenser (A), crows often re-oriented it to align it with their beak's axis (red dotted line) (B), before inserting it into the Plexiglas box (C).

(D) Example trial showing the beak-tip trajectory from the moment the stick tip was detected until it was inserted into the box, color coded by movement direction (cf. Figure 2A). Capital letters refer to the events depicted in (A)–(C). Note that stick re-orientation B is accompanied by a downward movement of the beak tip, reflecting a toss, that is, the moment when the crow momentarily released and re-grasped the stick.

(E) Beak-tip acceleration profile for the trial period shown in (D). A prominent acceleration peak (black dotted line) indicates the time when the crow tossed the stick. The period immediately after the pull (0–150 ms) is indicated by a gray background and was not considered for toss detection.

(F) Angle between the beak axis and the stick axis for the trial period shown in (D). Positive values indicate a beak-stick-axis deviation to the right (cf. B). Note that the beak-stick-axis deviation drops at the time of the toss (black dotted line).

(G) Median beak-stick-axis deviation for single-toss trials with an initial deviation to the right, aligned to the toss acceleration peak (black dotted line) (crow 1, n = 2,364).

(H) Same as (G) for initial deviations to the left (crow 1, n = 28).

(I) Same as (G) but for trials with two consecutive tosses and a deviation to the right after the first toss (crow 1, n = 717). Blue dotted line indicates the median time of the first toss, relative to the second toss, with the solid blue lines indicating the 5th and 95th percentile of the data.

(J) Same as (I) but for trials with a deviation to the left after the first toss (crow 1, n = 176).

Gray shading indicates the median absolute deviation (MAD) in (G)–(J).

See also Video S3.

producing a distinct, high-amplitude peak in the beak-tip acceleration profile (Figure 4E, "B") (in crow 3, adjustment movements were too subtle to reliably detect them with our approach). In the displayed example, this adjustment reduced the beak-stick-axis deviation from ~20° to less than 5° (Figure 4F). Across similar single-toss trials, the median beak-stick-axis deviation decreased significantly after the toss: from 17.0° to 0.6° in crow 1 (Figure 4G) (median absolute deviation [MAD] = 4.3° and 4.9°, respectively; n = 2,364; paired Wilcoxon, $p < 0.001$) and from 10.1° to −0.2° in crow 2 (MAD = 5.5° and 6.4°; n = 242; paired Wilcoxon, $p < 0.001$). In trials where the stick initially deviated to the left, the absolute deviation also significantly decreased post-adjustment (Figure 4H) (paired Wilcoxon, crow 1: $n = 28$, $p < 0.01$; crow 2: $n = 684$, $p < 0.001$). Interestingly, when two adjustment movements occurred, the first often failed to achieve proper alignment—typically due to under- or over-correction (Figures 4I and 4J). In these cases, a second toss followed quickly, with a median latency of 155 ms in crow 1 (Figures 4I and 4J; MAD = 47.8 ms, n = 893) and 195 ms in crow 2 (MAD = 117.6 ms, n = 169). In rarer cases, such as when a dropped stick was retrieved from the table, the initial misalignment could approach 90°, prompting a fast series of successive adjustments that gradually brought the stick into correct alignment. Taken together, these results highlight the crows' remarkable flexibility in tool handling and their ability to finely control tool orientation through rapid, feedback-guided motor adjustments.

Implications for comparative cognition and neurobiology

Our study extends previous research into habitual and non-habitual corvid tool use by quantifying the behavior at a sub-movement level with high temporal and spatial resolution.[2,13,15,18,23–25,27,28] We show that carrion crows, despite lacking specific adaptations of habitual tool users like NC crows,[7,8,25,29] can learn to perform a complex tool-use task with dexterity, efficiency, and flexibility. Through progressive shaping and trial-and-error learning, they developed consistent, goal-directed movement strategies, corrected errors dynamically, and adjusted tool orientation with fine motor control.[25] These behaviors meet established criteria for animal tool use[1] and align with the concept of "tooling"—the transformation of the body into a body-plus-object system.[30] Collectively, they highlight the capacity of non-habitual tool users to employ stick tools as a functional extension of their body when provided with the right learning conditions.[31–33]

A striking characteristic of the crows' early tool-use behavior was their high motor variability, even after the solution space[34] had been narrowed during pre-training. Such variability is considered essential for reinforcement learning, providing the exploratory substrate from which effective strategies can be selected.[34–36] As aptly stated by Dhawale et al.[34]: "Motor

variability is to skill learning what genetic variation is to evolution: an essential component of a process that, through selection by consequence, shapes adaptive behaviors.[37]" Consistent with this framework, and with human motor learning,[38] we found that variability in movement trajectories gradually decreased as performance improved, suggesting reinforcement-driven refinement.

By the end of training, our crows demonstrated fine control over the working end of the tool, adjusting its orientation and position with precision to interact with the target—behavior that closely resembles that observed in habitual tool users such as NC crows[2,5,39] and notably differs from what has been reported in non-tool-using corvids like rooks.[15,40] This suggests that refined tool manipulation skills can emerge from domain-general mechanisms, such as associative learning,[41,42] chaining,[43] and sensorimotor feedback integration. However, the presence of such domain-general mechanisms does not rule out the involvement of higher cognitive processes that allow inferences about tool utility without direct sensorimotor feedback.[17,18,44–47] In addition to advanced learning and working memory capacities—both demonstrably present in carrion crows[48–53]—animals must possess an initial understanding that objects can be used as tools.[40] Such conceptual knowledge rarely arises spontaneously and is often shaped by an inherited motivation to use objects as extensions of the animal's body[7,10,29,54] and/or social learning.[55,56] Thus, the rarity of flexible tool use in the animal kingdom reflects the unlikely co-occurrence of at least three enabling factors: motivation followed by conceptual knowledge, high cognitive capacity, and fine motor control.[40,57]

The precision and flexibility exhibited by our crows suggest that they may treat the stick as a functional extension of their beak[58]—akin to the incorporation of tools into peripersonal space observed in non-human primates.[33,59] In primates, tool use is thought to alter the body schema, with neurons adapting to represent the working end of the tool rather than the hand.[33] Analogously, neurons in the crow brain may encode the dynamics of the stick tip during tool use and the beak tip otherwise. Such abstract neuronal representations may occur in higher associative areas like the nidopallium caudolaterale (NCL), which has been implicated in tool-related cognition.[21,60–63] Beyond its role as a multi-sensory hub, NCL is a key node in the avian "general motor system" and thus likely involved in controlling tool-use-related movements.[63–69] Our behavioral paradigm offers a promising scaffold for future studies investigating neuronal correlates of corvid tool use in the avian general motor system and beyond.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Felix W. Moll (felix.moll@uni-tuebingen.de).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Raw pose estimation data from all figures, including instructions required to reanalyze the data, were deposited on Mendeley at DOI: https://doi.org/10.17632/v3zh338ykc.1 and are publicly available as of the date of publication.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

F.W.M. and A.N. designed the research. F.W.M. and J.W. conducted the research. F.W.M. and J.W. analyzed data. F.W.M. wrote the initial draft of the manuscript. F.W.M. and A.N. edited and reviewed the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.08.033.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw pose estimation data	This paper	Mendeley Data: https://doi.org/10.17632/v3zh338ykc.1
Experimental models: Organisms/strains		
Carrion crows (Corvus corone)	Institute's breeding facility	N/A
Software and algorithms		
MATLAB	MathWorks	R2024b
DeepLabCut	Nath et al.[9]	github.com/DeepLabCut; version 2.3.5

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Animals

Three carrion crows (*Corvus corone*) (crow 1: male, 6 y; crow 2 and 3: female, 2 y) obtained from the institute's breeding facility were used. They were housed in spacious indoor aviaries (L x W x H: 3.6 x 2.4 x 3 m) in social groups of up to four individuals with daylight and a natural light-dark cycle under controlled temperature and air humidity conditions.[70] The crows were kept on a controlled feeding protocol and earned food as a reward during training and recording periods. Additional food was supplemented after the daily sessions if necessary. Water was always provided ad libitum. All procedures were conducted according to the national guidelines for animal experimentation and approved by the national authority, the Regierungspräsidium Tübingen, Germany.

METHOD DETAILS

Tool use task and video recordings

Behavioral sessions occurred in an operant conditioning chamber illuminated with LED strips (3000 K, Lepro, China) and two IR light sources (1PL-2019C, Tonton Security, China). The crows were strapped to a wooden perch using leather jesses and placed in front of an elevated platform (Figure 1A). They faced a transparent Plexiglas box (L x W x H: 14 x 10 x 2 cm) fixed to the platform, elevated by 2 cm from the platform and positioned 10 cm from the platform's front edge (Figure 1A).

At the beginning of each trial, a custom pellet feeder automatically released one pellet (NutriBird T16, Versele-Laga, Belgium) into one of three small chambers behind the opaque rear wall of the Plexiglas box (Figure 1A). A gate in this wall, fixed to a servo (servo 15 kg, Miuzei, China; driven by Arduino Uno R3, Italy), could be rotated upwards, connecting the Plexiglas box to the three chambers behind it. While the gate was opened, a custom, stepper motor (28BYJ-48 with ULN2003 driver board, Elegoo, China) driven 'pellet-slider' precisely moved the pellet from its chamber into one of three positions inside the box ('left', 'middle', or 'right'; i.e., 1.5 cm from the rear wall and 1.5, 7.0 or 12.5 cm from the left wall, respectively). In each session, one or two of the three available pellet position settings were used. When two positions were used, one of the two was randomly chosen for each trial (e.g., Figure 2B).

Once the pellet was in position, the rear wall gate was closed, and the upper 1 cm of a 13 cm wooden stick (Medical Applicator, Fuhrmann, Germany) was automatically presented through a 6 mm wide borehole on the left side of the Plexiglas box by a custom-built, motorized 'stick dispenser' (6 V, N20 micro gear motor, DollaTek, China) (Figure 1B). After pulling the stick from the dispenser, the crows needed to insert the stick into the box through its open front side and then use the stick to maneuver the pellet into reach (Figure 1B). To complete a trial and to initiate the next trial, the crows had to actively push the stick back into the dispenser, which triggered a mechanism that fully retracted the stick and released the next pellet.

Two cameras (GS3-U3-32S4M-C, FLIR, USA), equipped with wide-angle lenses (3.5mm, C Series, Edmund Optics, USA) were fixed 46 cm above the platform, parallel to the platforms front edge and 15 cm apart from each other, thus delivering a stereo top-view of the Plexiglas box (cf. Figure 1B). We triggered the synchronous acquisition of individual frames (562 x 512 pixels, shutter: 2 ms) at a rate of 200 Hz with an Arduino generated pulse train (Arduino Uno R3, Italy) that was fed into both cameras. These frames were saved to a local hard drive using the camera manufacturer's software (FlyCapture 2.13.3.61) and converted to videos after each session, using custom Python code. For each trial, video acquisition automatically started when the stick dispenser started to drive out the stick and ended 1 second after the returned stick was fully retracted.

Pre-training

We introduced all three crows to the set-up and the tool use task by progressive shaping.[31,71] Working closely with their human trainer, crows were rewarded for behaviors such as holding the stick in their beak; inserting it into handheld plastic tubes

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(diameters: 3 cm and 1.5 cm), a Plexiglas box, and the apparatus' stick dispenser; and for moving pellets with the stick. Pre-training ended once the crows had learned to successfully use the apparatus independent of their human trainer.

Trial-and-error sessions

After pre-training, crow 1 was recorded across 19 sessions over 53 days, crow 2 across 24 sessions over 59 days, and crow 3 across 25 sessions over 59 days. Crows never received more than one session per day.

Pose estimation

We selected a large set of representative video frames (n = 329, all birds, both cameras) and used them to manually annotate body parts and object parts of interest (i.e., beak-tip, beak-base, stick-tip, proximal stick-stripe, pellet, and box corners) with DeepLabCut's graphical user interface (DLC, version 2.3.5).[9] This training data-set was used to train a deep neural network with DLC (resnet50, 200 k iterations), which we then applied to all videos. To create a DLC 3D project, we calibrated our cameras by recording a brief video of an 11 x 8 checkerboard array (27.5 x 20 cm) that was moved and rotated continuously, covering the crows' action radius within the set-up. Frames of this video were fed into DLC's triangulation algorithms to reconstruct the trajectories of individual body and object parts in three dimensions with pose estimation data from both cameras. In a last step, we used custom Matlab software (Matlab R2024a) to smooth trajectories with a 10 sample (i.e., 50 ms) Gaussian window and to rotate trajectory coordinates to align them with the 3 axes of the conditioning chamber.

Success rate and trajectory similarity

To quantify movement trajectory similarity and task success rate, we focused our analysis on trials in which a single pellet was placed at one of the three designated positions (left, middle, or right) and the crow inserted the stick into the box. A trial was classified as successful if the crow was able to retrieve the pellet after returning the stick to the dispenser. Conversely, a trial was deemed unsuccessful if the pellet either fell off the platform or remained too deep inside the box to be reached by the crow's beak.

To compare stick-tip trajectories pairwise, we first trimmed each trajectory from the point at which the stick-tip entered the box first to the point it last exited (Figure 1D). We then projected all trimmed trajectories to the horizontal plane and resampled them to 500 evenly spaced points using Matlab's 'interparc()' function with spline interpolation (Matlab R2024b). For each pair of trajectories, we computed the Euclidean distance between corresponding points and used the median of these distances as a measure of spatial similarity. This process was repeated for all trajectory pairs within a session, and session-level similarity was quantified as the median of these pairwise medians. In very rare cases, the pellet accidentally ended up in a position that was otherwise not tested during a given session (i.e., a pellet accidentally ended up in the middle position, although all other trials during this session were left or right trials)—these particular trials were excluded from our pairwise distance analysis.

Statistical analysis of performance

We used a generalized linear mixed-effects model (GLMM) to assess whether performance (i.e., pairwise trajectory distances and pellet manipulation time) improved across sessions. The model was fit in Matlab (R2024b) using the 'fitglme()' function. The model included fixed effects for session number and task condition, with random intercepts and random slopes for session by subject. To account for positively skewed performance distributions, the model used a gamma distribution with a log link function.

Hierarchical clustering

To identify recurring movement patterns, we grouped trimmed stick-tip trajectories based on their pairwise spatial similarity using hierarchical clustering. Dendrograms were constructed in Matlab (R2024b) with the 'linkage()' function (linkage method: 'complete', distance metric: 'spearman'). To capture dominant trajectory motifs for individual crows, clustering was performed separately for each task condition (i.e., pellet position) across all sessions. Clusters were defined by applying a fixed threshold of 0.8 arbitrary units (a.u.) to the resulting dendrograms. To visualize individual, normalized trials as lines in a heat-map after clustering, we used resampled, trimmed trajectories (see above), and computed the direction of movement for each pair of samples (cf. Figures 2A and 2B).[26]

Pellet manipulation errors

To identify instances when the stick erroneously lost control over the pellet during pellet manipulation, we calculated the minimal Euclidean distance between the pellet and the stick axis for all frames, starting from the moment the stick-tip first entered the box until it last exited. For each frame, we also determined whether the pellet was on the preferred or non-preferred side of the stick axis, relative to typical trials, where the pellet remained on one side of the stick axis throughout the manipulation.

Using custom Matlab code, we defined error events as periods in which the distance between the pellet's center to the closest point along the stick exceeded 4 mm for more than 15 ms to the non-preferred side, followed by a movement that brought the pellet back to the preferred side. Only trials with a single switch to the non-preferred side were retained for further analysis.

While this approach effectively identified trials with performance errors, it also produced false positives. For example, the algorithm flagged instances where the pellet temporarily crossed to the non-preferred side but was already within the crow's beak reach, rendering a corrective movement unnecessary. To address this, a second analysis step involved a human observer reviewing the algorithmically identified video sections. Using custom Matlab code, the observer either accepted or rejected these sections based

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on manual inspection. To quantify the duration of corrective movement events (i.e., 'corrections time'), we determined the time between the moment the pellet position switched to the non-preferred side of the stick axis until it returned to the preferred side for all events.

Tool orientation estimation

To identify instances when our crows adjusted stick tool orientation prior to pellet manipulation, we considered the trial period between the time just after the stick was pulled from the dispenser (i.e., 30 frames after the stick-tip was first detected) until the moment the stick-tip first entered the box. During this period, crows 1 and 2 notably tossed the stick to orient it in their beak. To flag these tosses, we computed the beak-tip acceleration, considering all 3 dimensions of the beak tip trajectory. Tosses were effectively identified by moments of rapid beak-tip acceleration followed by rapid deceleration, with a peak to trough difference of > 30 m/s^2. To distinguish toss related acceleration peaks from peaks resulting from the beak being rapidly moved toward the box, we applied k-means clustering ('kmeans()', Matlab R2024b) to all acceleration peak related beak-tip positions in space. This allowed us to restrict our analysis to acceleration events within the toss cluster, while excluding events linked to the stick being quickly moved into the box. Crow 3 was excluded from the tool orientation analysis, as its potential orientation movements were too subtle to be reliably detected with our approach.

To quantify how tool orientation was changed by toss events, we determined the angle between the beak-axis (i.e., the line through the beak-base and beak-tip) and the stick-axis, after projecting both axes to the horizontal plane for each frame (cf. Figure 4B). For trials in which the average beak-stick-axis deviation exceeded ±5° (i.e., with the stick oriented either to the left or right of the beak axis) in a 90 ms window before the toss event (-100 to -10 ms, pre-toss), we also determined the average beak-stick-axis deviation in a 90 ms window after the toss event (10 to 100 ms, post-toss). Left and right deviation trials were analyzed separately. In trials with two consecutive tosses, average pre- and post-toss beak-stick-axis deviations were determined in the same manner for both tosses.