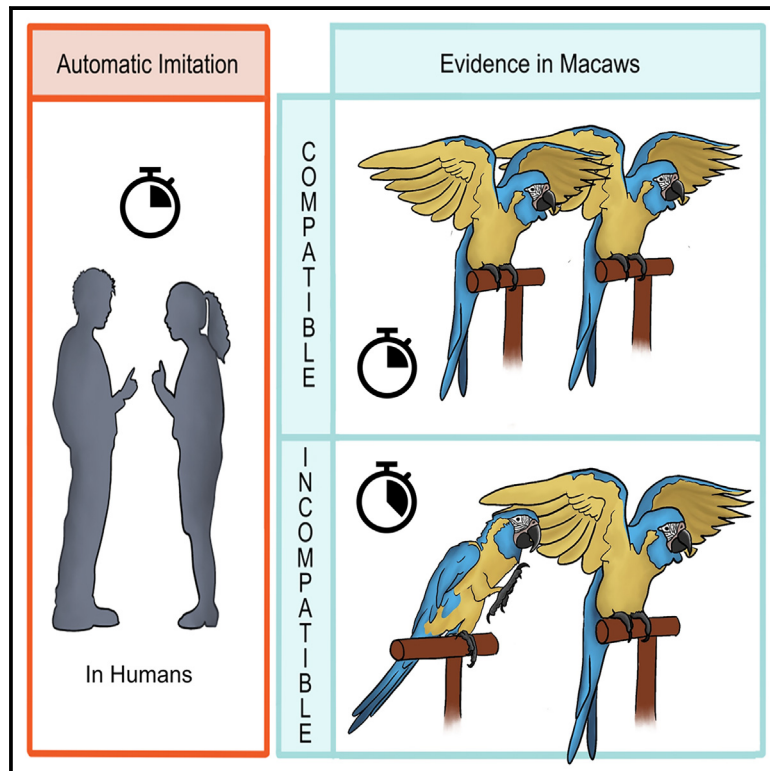# Automatic imitation of intransitive actions in macaws

Graphical abstract

Authors

Esha Haldar, Padmini Subramanya,
Auguste M.P. von Bayern

Correspondence

iesha.haldar@gmail.com (E.H.),
auguste.bayern@bi.mpg.de (A.M.P.v.B.)

In brief

Behavioral neuroscience; Applied
sciences; Animal science

Highlights

- Macaws show automatic imitation of conspecifics for intransitive actions

- Macaws made more correct responses taking lesser response time to copy others

- Macaws performed poorly when producing incompatible actions with demonstrations

- Macaws learnt to inhibit automatic imitation effect eventually

CellPress

iScience

Article

Automatic imitation of intransitive actions in macaws

Esha Haldar,[1,2,3,5,*] Padmini Subramanya,[3,4] and Auguste M.P. von Bayern[1,3,*]

[1]Max Planck Institute for Biological Intelligence, Seewiesen 82319, Germany
[2]Division of Evolutionary Biology, Ludwig-Maximilians-Universität, 82152 Munich, Germany
[3]Comparative Cognition Research Station, Loro Parque Fundacion, Puerto de La Cruz, 38400 Tenerife, Spain
[4]Department of Biology, University of Bremen, Bremen 28359, Germany
[5]Lead contact
*Correspondence: iesha.haldar@gmail.com (E.H.), auguste.bayern@bi.mpg.de (A.M.P.v.B.)
https://doi.org/10.1016/j.isci.2024.111514

SUMMARY

Automatic imitation is the involuntary tendency of humans to copy others' actions even when counterproductive. We examined the automatic imitation of *intransitive* actions in blue-throated macaws (*Ara glaucogularis*), employing a stimulus-response-compatibility task. After training seven macaws to perform two different actions with legs and wings upon specific hand commands, the subjects were divided into a compatible and incompatible group. We rewarded the subjects for performing the same action as the conspecific model in the compatible group and the opposite action in the incompatible group. Involuntarily imitating the demonstrated actions, the incompatible group made more errors than the compatible group and took longer to eventually respond correctly. The study provides evidence for the automatic imitation of intransitive actions in non-human animals— parrots, suggesting that arbitrary action imitation facilitated by a mirror-neuron system in parrot brain may be adaptive in the ever-changing complex social environment of parrots and possibly drive cultural evolution.

INTRODUCTION

Human cultural evolution is underpinned by the ability of humans to imitate. Conscious imitative learning of cultural conventions promotes the generational practice of traditions and rituals in ethnic groups.[1,2] Nonconscious imitation of gestures and arbitrary actions, on the other hand, facilitates group coalescing by promoting affiliative, prosocial attitudes toward group members.[3–6] For example, in a study[7] using a virtual social game (Cyberball) female human participants were either excluded from the game by fellow ingroup members (females) or by outgroup members (males). They then interacted with a female or a male "new" participant, a confederate. Female participants who were excluded by an ingroup (females) mimicked the female confederate more than the male (outgroup) confederate and this increase in mimicry was successful as the confederate reported increased affiliation with the excluded female participant.[3,7] Thus, as described by Lakin,[4] nonconscious imitation acts as a "social glue," which facilitates group cohesion and leads to faster spread of cultural practices. Although the two types of imitation are fundamentally different, both conscious and nonconscious imitation require equal attention[8] and need to be investigated for their adaptive benefits. The former has been studied extensively in many non-human animal species, whereas the nonconscious imitation of arbitrary actions lacks investigation, leaving a gap in the understanding of the spread of cultural conventions in animals.

The involuntary tendency to copy others' perceived actions, even when it interferes with one's own action execution has been interchangeably termed "motor mimicry," "mirror-effects" and recently "automatic imitation"[8]. Neurologically, it has been attributed to the mirror-neuron system[9–17] present in the brains of humans and monkeys,[15] which fires during the observation and execution of the same action thus resulting in *mirror effects*. Studies have reported that the unintentional mimicking of gestures or *motor mimicry* increased cooperation and prosocial attitudes between participants during social interactions.[3–6] Since then, the involuntary effect of action observation on action execution has been studied in controlled laboratory settings and was termed *automatic imitation*.[8,18]

To date, the most widely used paradigm to investigate automatic imitation in humans has been the stimulus-response-compatibility (SRC) task.[19,20] In SRC tasks, the compatibility of a visual stimulus with an action determines the accuracy of the action execution.[19] This compatibility effect is measured by response time or error rate in action execution, i.e., the higher the compatibility between perception and action, the lower the response time and error rate.[9,19,20] For example, when Brass and colleagues[19] asked one group of participants to always lift their index finger and another group to always tap the same finger while observing video stimuli of lifting and tapping of index fingers, participants' response time was much longer when the action and the video stimulus were incompatible than when they were compatible. According to Heyes such a stimulus

Table 1. Details of the subjects in the two experimental groups

Experimental groups	Individuals	Age (years)/Sex (M or F)
Compatible	Morty	4/M
Compatible	Long John	8/M
Compatible	Rick	4/M
Incompatible	Sherlock	15/M
Incompatible	Thor	13/M
Incompatible	Pepper	2/F
Incompatible	Watson	13/F

Also see Tables S1 and S2 for details on demonstrators.

response compatibility (SRC) effect evidences *automatic imitation*.[8]

Studies of automatic imitation distinguish between two types of actions: i) *intransitive* or non-object oriented actions and ii) *transitive* or object-oriented actions with a defined "goal." Tapping or lifting of fingers,[19] or opening and closing of a hand,[21] constitute intransitive actions that do not involve any objects or goals. In contrast, goal-directed transitive actions are directed at a physical, visible target, object or goal,[22–24] such as touching a dot on paper, pressing a lever, pecking a manipulandum and so forth. To date, a plethora of literature on the automatic imitation of intransitive and transitive actions in humans exists (see e.g., meta-analysis by Cracco and colleagues[18] comprising 161 studies). However, only three studies have addressed and reported automatic imitation in non-human animals, namely in capuchin monkeys (*Sapajus* spp.), dogs (*Canis familiaris*), and budgerigars (*Melopsittacus undulatus*), and all of them involved transitive, object-oriented actions.[25–27] The study on automatic imitation in capuchin monkeys revealed very weak compatibility, hence the automatic imitation effect, in an SRC task.[25] The other two non-human animal studies revealed a pronounced automatic imitation effect for a pecking vs. stepping action on a manipulandum in the budgerigars[27] and for opening a door with the head vs. the paw in the case of dogs.[26] But due to the lack of any experimental evidence, it remains unknown whether the automatic imitation of intransitive actions is prevalent in non-human animals.

Parrots are an important model taxon for investigating the automatic imitation of intransitive actions. They are highly social, often living in complex fission fusion societies[28] and typically exhibit long-term pair bonds[28,29] as well as slow development and extended parental care[30] that provides ample social learning opportunities.[30–32] They possess large brains relative to their body size in addition to high neuron densities[33] and belong to the few vocally learning animal taxa possessing excellent vocal imitation abilities.[33–36] Some species of parrots also show gestural communication involving intransitive behaviors.[37,38] The parrot species already tested in transitive action imitation, budgerigars, imitated actions in a goal-directed problem solving task[39] and showed automatic imitation of pecking and stepping behavior on a manipulandum.[27]

In the current study, our goal was, therefore, to investigate whether blue-throated macaws (*Ara glaucogularis*) show automatic imitation when executing intransitive actions while observing a conspecific demonstrator perform either compatible (i.e., matching) or incompatible (i.e., non-matching) actions. We trained $n = 7$ macaws (Table 1) to perform two intransitive actions, i.e., "lift leg" and "flap wings," reliably on command using a specific hand signal for each action. After the subjects reached a discrimination criterion of 80% correct responses in two consecutive sessions consisting of 30 trials each, we divided them into a compatible and an incompatible group. The compatible group received rewards for performing the same actions as the demonstrator and the incompatible group received rewards for performing non-matching actions as the demonstrator (lift leg for wing and vice-versa). In the first test (cued-response test) the subjects received hand signals from an experimenter which indicated the action to be performed, concurrent with the conspecific demonstrations. The rationale of the first test was to cue the correct action by providing the respective command to the subject in order to facilitate the reward contingency learning in the two groups. In the second test (non-cued response test), the subjects were hand signaled to act by a "do it now" command, without specifying the action to be performed. The second test was conducted with a neutral "do it command" instead of the two action commands forcing the subject to pay attention to the conspecific demonstrator rather than concentrate on the experimenter's hand command and ignoring the action demonstrated in parallel. If macaws are indeed susceptible to an automatic imitation effect, the action stimuli matching the response will facilitate the compatible group's performance, whereas the stimuli not matching the response will hinder the incompatible group's performance. The compatible group should therefore gain more rewards and commit fewer errors than the incompatible group. Overall, this study aimed to investigate the automatic imitation of intransitive actions and thus evaluate behavioral evidence for the role of mirror systems in intransitive action imitation in non-human animals.

RESULTS

Acquisition training phase

All subjects (Table 1) were trained and tested for the acquisition and discrimination of "lift leg" and "flap wings" with specific hand signals. The subjects reached the discrimination criterion of 80% correct responses within five sessions each consisting of 30 trials. The mean (±S.E.) of correct responses in the last two sessions of the compatible group was 0.92 (±0.021) and for those assigned to the incompatible group was 0.92 (±0.028). A one-way ANOVA revealed no significant difference ($F_{(1, 5)}$ = [0.033], $p = 0.86$, Tukey's HSD Test: 95% C. I = [-0.08, 0.1]) between the two groups. Thus, subjects in both compatible and incompatible groups were able to perform "lift leg" and "flap wings" reliably on specific hand commands.

Test 1: Cued response

In the cued response test and the consecutive non-cued response test, the subjects were tested for automatic imitation with demonstrations from a conspecific (Figure 1). The demonstrator performed the actions in response to hand commands from an experimenter who was obscured from the view of the subject by an opaque curtain (Figure 1). In this test, the subjects also received
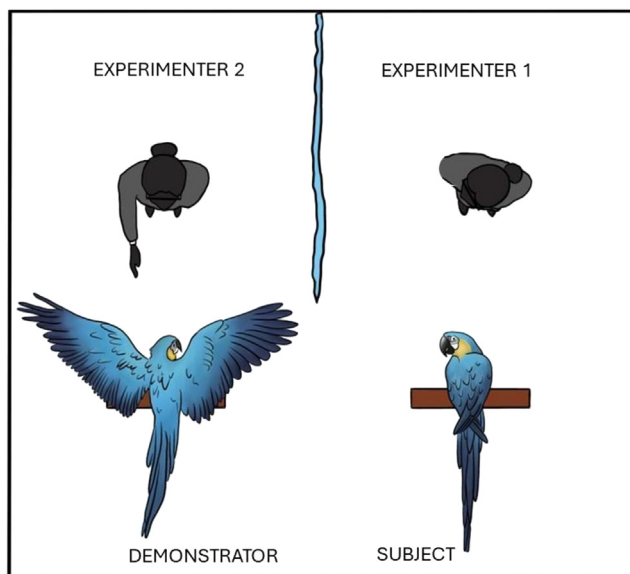
Figure 1. Illustration of the experimental setup
Experimenter 1 interacts with the subject on the right side and experimenter 2 interacts with the demonstrator on the left, with an opaque curtain passing between the two experimenters, such that experimenter 2 is visually obscured from the subject and experimenter 1 on the right.

hand commands from the other experimenter to execute the correct action (see Video S1) after seeing the demonstrator perform either the same (compatible group) or the non-matching action (incompatible group) (Figure 2). All the subjects in the compatible group reached the 80% response criterion in two sessions (for Rick, two out of four sessions had to be excluded because the demonstrator was not motivated to participate after 2–3 trials instead of 20 trials in the session) whereas the incompatible group reached the criterion within six sessions (Mean = 4.5, S.E = ±0.7). Considering nonnormal distribution of the data, a non-parametric Wilcoxon rank-sum test revealed a significant difference between

the mean number of sessions taken by the two groups (W = 0, p = 0.04) as illustrated in Figure 3. The mean of correct responses in each session is shown in Figure 4 for both the groups. A one-way ANOVA conducted to compare the mean of correct responses (across total sessions) between the groups revealed that the performance of the compatible group did not differ significantly from that of the incompatible group ($F_{(1, 5)}$ = [4.56], p = 0.08, Tukey's HSD test: 95% C. I = [-0.24, 0.02]).

Test 2: Non-cued response
In the non-cued test, the subjects received a "do it now" command (Figure 2) from the experimenter without specifying any action to be performed (see Video S2). For assessing the differences between the compatible and incompatible groups in the non-cued response test, the number of sessions required for each subject to reach the 80% criterion in two consecutive sessions was calculated along with the mean of correct responses and mean of incorrect responses in each session. Figure 3 shows the graph comparing the mean number of sessions required by the compatible (Mean = 4.0, S. E = ±0.5) and the incompatible (Mean = 13.0, S. E = ±0.7) groups for reaching the 80% correct response criterion. The compatible group took significantly fewer sessions to make 80% correct responses than the incompatible group (One way ANOVA: $F_{(1, 5)}$ = [110.5], p < 0.001, Tukey's HSD test: 95% C. I = [6.5, 11.4]). The mean of the correct response rate in each session for the compatible and incompatible groups is shown in Figure 5. A one-way ANOVA conducted to compare the mean of correct response rate across all sessions showed that the compatible group performed a significantly higher number of correct actions than the incompatible group ($F_{(1, 5)}$ = [51.04], p < 0.001). Tukey's HSD Test found a similar significant difference between the two groups (p = 0.1, 95% C.I. = [-0.6, 4.52]) revealing automatic imitation influencing the execution of counter imitative responses. Only one subject in the compatible group (Rick: Mean number of correction trials (NbCT) = 0.09; it refused to perform wings initially for an unknown reason) and three out of four
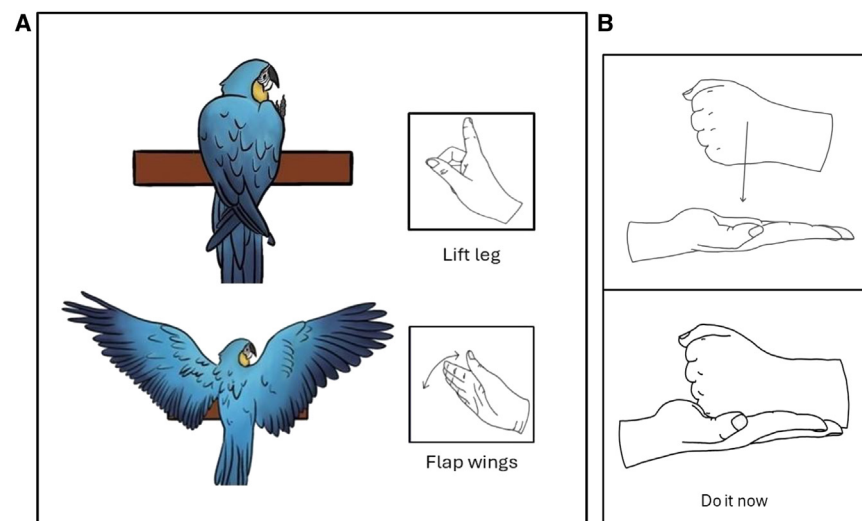

Figure 2. Illustration of the hand commands corresponding to the intransitive actions
(A) The pointed index finger corresponds to "lift leg" and to and fro motion of the palm corresponds to "Flap wings."
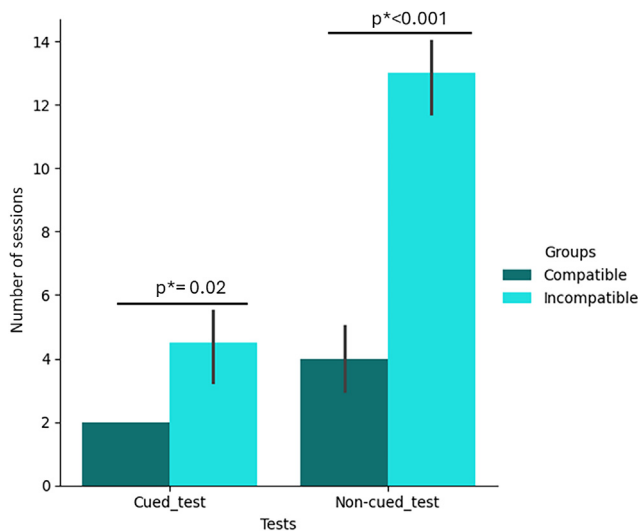(B) The hand signal corresponds to the "do it now" command in the *non-cued test*.

Figure 3. Plot depicts the mean number of sessions taken by *N* = 3 subjects in the compatible (teal blue) group and *N* = 4 subjects in the incompatible (light blue) group in the cued and non-cued response test

The compatible group took significantly fewer sessions than the incompatible group to reach the 80% correct response criterion in both the cued-response test (Wilcoxon rank-sum test: $W = 0$, $p = 0.04$)) and the non-cued response test (One way ANOVA: $F_{(1, 5)} = [110.5]$, $p < 0.001$). The threshold for statistical significance used was $p < 0.05$ and denoted in figure with (p^*).
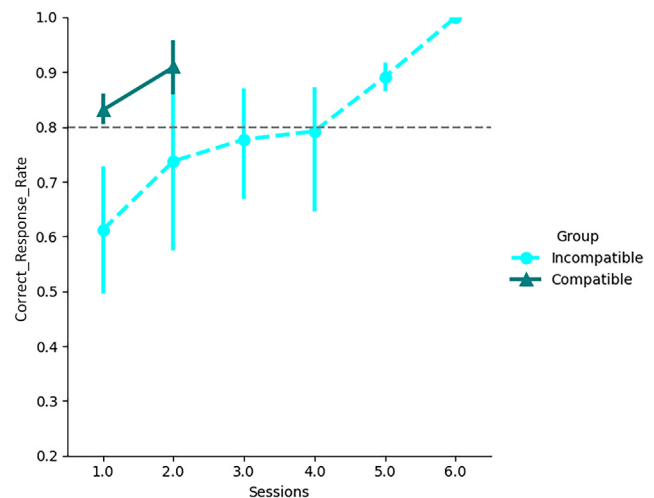

Figure 4. Plot depicts the mean correct response rate in each session of the cued response test

The compatible group (teal blue) of $N = 3$ subjects reached the learning criterion of 80% correct responses (gray dashed line) within two sessions (40 trials) and the incompatible group (light blue) of $N = 4$ subjects reached the criterion in six sessions (120 trials). The correct response rate of the two groups did not vary significantly (One way ANOVA: $F_{(1, 5)} = [4.56]$, $p = 0.08$).

subjects in the incompatible group (Pepper: Mean NbCT 0.02, Thor: Mean NbCT = 0.06 and Watson: Mean NbCT = 0.03) received the correction trials. The incompatible group finally achieved 80% correct responses throughout the last two of 14 sessions (Mean = 13.0, S.E = ±0.7) and then reliably performed the action that did not match the demonstrated one significantly more than copying the demonstrator's action (ANOVA for correct vs. incorrect actions in last two sessions within incompatible group: $F_{(1, 6)} = [4276.98]$, $p < 0.001$, 95% C.I = [-0.64, −0.6]).

Effect of action stimuli on automatic imitation

Differential responsiveness of a species to the two action stimuli can bias the result of an SRC task, for example, if one demonstrated action elicits more imitative responses than the other, such as is the case with contagious behaviors. A two-way ANOVA was used to analyze whether the type of action, i.e., "flap wings" or "lift leg," and the interaction of action type and groups had any differential effect on imitative responses in the non-cued response test. We considered the correct rewarded responses (imitative) of the compatible group and the incorrect responses (imitative) of the incompatible group as the imitative responses. An ANOVA with action type ("lift leg" or "flap wings") as within-subjects factor and groups (compatible or incompatible) as between-subjects factor, revealed no significant effect of "lift leg" or "flap wings" on the imitative responses of the seven subjects (except lift leg for an amputee bird is not counted, see Supplemental document S1) ($F_{(1,9)} = 3.075$, $p = 0.11$) and no significant effect of action type-group interaction ($F_{(1,9)} = 0.03$, $p = 0.85$), excluding differential contagiousness of these two behaviors to induce imitation in macaws.

Latency of correct response

The time difference between "do it now" command and the onset of the action in the non-cued test was considered as "latency of response" or "response time" (RT). Figure 6 shows the mean latency of correct response across each session for both groups. We expected that the mean latency of correct responses would be longer for the incompatible group than for the compatible group, as they needed to inhibit the automatic imitation effect to produce the counter-imitative responses. We fitted a generalized linear model with a mean latency of correct response as the dependent variable predicted by session number and groups. The fitted model was highly significant ($R^2 = 0.14$, $F_{(2, 61)} = 6.39$, $p = 0.003$) with both sessions and incompatible groups correctly predicting the mean latency of "correct" responses. The mean response time for correct actions decreased with session number ($\beta = -0.038$, $p = 0.003$) for both groups but overall, it was higher for the incompatible group ($\beta = 0.37$, $p = 0.004$) than the compatible group.

DISCUSSION

The present study provides evidence for the automatic imitation of intransitive actions in macaws, previously unreported in non-human animals. A strong compatibility effect in macaws was found for the two intransitive actions "lift leg" and "flap wings" in the SRC task. The compatible group made significantly more correct responses than the incompatible group in the non-cued response test. The incompatible group performed poorly by copying the actions of the demonstrator involuntarily, making incorrect unrewarded responses repeatedly. Thus, despite the costliness, the automatic imitation tendency affected the performance of the incompatible group. Previous studies in
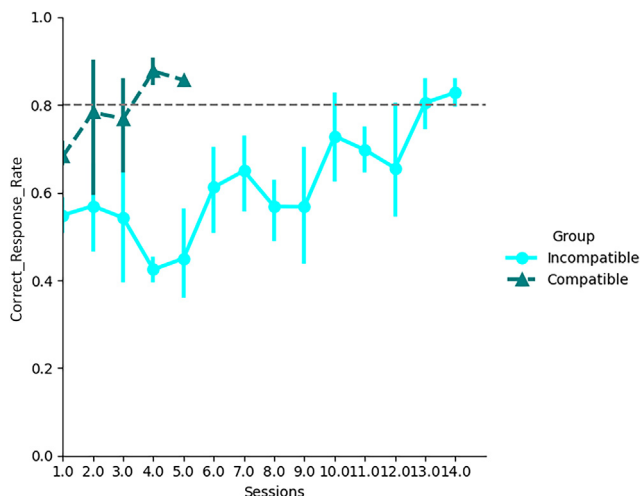
Figure 5. Plot depicts the mean correct response rate in each session of the non-cued response test

The compatible group (teal blue) of $N = 3$ subjects reached the learning criterion of 80% correct responses (gray dashed line) within five sessions (100 trials) and the incompatible group (light blue) of $N = 4$ subjects, reached the criterion in fourteen sessions (280 trials). The correct response rate of the compatible group was significantly higher (One way ANOVA: $F(1, 5) = [51.04]$, $p < 0.001$) than that of the incompatible group.

humans had shown automatic imitation effects for simple intransitive actions such as hand opening and closing actions,[10,21] arm movements,[9] index finger tapping and lifting[19,20] and so forth. Our findings that blue-throated macaws, a parrot species, are subject to automatic imitation effects while performing simple bodily movements implies that intransitive behaviors may be learned through imitation in parrots which may serve to foster affiliative bonds and group cohesion, possibly even leading to the learning of cultural conventions.

In humans, neurobiologically, automatic imitation has been attributed to neural circuits that include mirror neurons,[9–13,16–18] which are excited both during the observation and the execution of the same action. Although automatic imitation in parrots, as corroborated by our study, is not direct evidence of a mirror neuron system, it advocates for its presence in the neural circuitry of parrots. Parrots are excellent vocal learners imitating novel vocalizations throughout their lifetime.[33,40] They are also well known for auditory-motor entrainment or the ability to synchronize body movements with music beats.[41–43] Since mirror neurons are present in auditory and vocal circuits of songbirds,[40,43,44] the taxonomic sister group of parrots,[45] which are well-known for their auditory-vocal learning capacities, the presence of mirror-neurons for visual-motor pathways in the parrot brain seems plausible.

The cued-response test was conducted to ensure the subjects learned the reward contingency in each group. Here, the subjects were given the hand command for the correct response in parallel to the demonstration in both groups. We expected that in the incompatible group, the non-matching hand signal given simultaneously with the demonstrations would impact on the subjects' performance due to stimulus response incompati-

bility. However, only a moderate automatic imitation effect was detectable. The incompatible group took significantly more sessions than the compatible group to reach the learning criterion, but the correct response rate between the two groups did not vary significantly. The reason could be that when the response was cued by the hand commands, the macaws may have shifted their focus away from the conspecific demonstrator and toward the experimenter who gave the hand commands. But when the hand commands specifying the actions had been removed in the subsequent non-cued response test, the subjects had to shift their focus back to the demonstrator to figure out the correct responses. For the compatible group, matching demonstrations and responses resulted in rewards, whereas in the incompatible group, the non-matching demonstrations apparently caused interference and provoked imitative responses, revealing a pronounced automatic imitation effect.

Subjects in both the compatible and the incompatible group were given the "do it now" command in the non-cued test which was devoid of any cues for any particular action. For the compatible group, learning to produce the same action as the demonstrator in response to the newly introduced command was likely facilitated by automatic imitation as evidenced by their immediate good performance (correct response rate mean of 65% already in the first session). But for the incompatible group, learning the reward contingency meant inhibiting the automatic imitation response, as well as figuring out the correct response strategy. If the subjects had adopted learning by exclusion[46] strategy, subjects would have assigned the new "do it now" command to some novel "third" action. However, this is not supported by our observations as we could not observe any "third" action during the tests apart from "lift leg" and "flap wings" (except for some isolated events of "fluff" or "body shake" that occurred occasionally in both groups as part of their natural repertoire). Alternatively, the subjects might have assigned the "do it now" command to either of the two actions and performed only one action ("lift leg" or "flap wings") predominantly. This is supported by the finding that the incompatible group displayed a mean response rate of 48% in the first non-cued test session, meaning that the birds performed at chance level throughout the initial sessions. But with correction trials and increasing training in the course of the test, the subjects eventually learned to perform the incompatible actions in response to the demonstrations and reliably produced the counter-imitative responses in the final sessions.

The incompatible group took a significantly longer time (14 sessions) to meet the learning criterion of 80% correct responses in two consecutive sessions than the compatible group (within 5 sessions). They eventually reached it within 14 sessions (280 trials), reliably producing counter-imitative responses in the final stage. The finding that the parrots in the incompatible group eventually overcame the automatic imitation effect aligns with previous studies in humans and the previous budgerigar and dog studies. The budgerigars and dogs overcame the automatic imitation effect and learned to perform the opposite actions over time.[26,27] Similarly, human participants could be trained to carry out incompatible sensorimotor tasks. For example, Catmur and colleagues[17] required study participants to lift their index finger while watching a little finger movement and vice-versa. Following the training, the
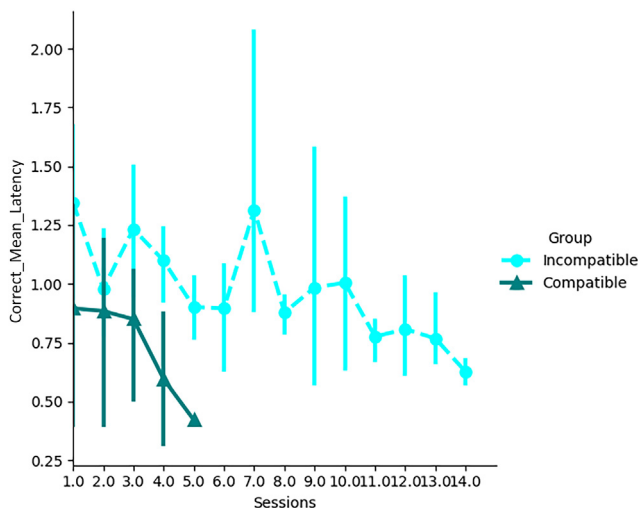
Figure 6. Plot depicts the mean latency of correct response time (RT) for each session of the non-cued response test for compatible (_N_ = 3) and incompatible (_N_ = 4) groups

The mean latency (Y axis) for correct responses of both the compatible (teal blue) and the incompatible (light blue) group declined (GLM: β = -0.038, _p_ = 0.003) with the number of sessions (X axis), but overall, the mean latency was higher for the incompatible group than the compatible group (GLM: β = 0.37, _p_ = 0.004).

muscle responsiveness of the fingers increased considerably during the observation of incompatible actions. These findings are consistent with Associative Sequence Learning theory,[8] which suggests that automatic imitation is programmed through acting and then associating with visual observations of the same motor pattern. Accordingly, automatic imitation effects are not innate but are instead generated through sensorimotor experience during ontogeny which can be reversed by training.[13,17]

The strength of the imitative tendency in the non-cued test was not affected by type of action, suggesting that macaws have no innate predisposition toward imitating either of these behaviors upon observation. This renders a contagiousness-like[47] confounding effect on our data unlikely and corroborates the automatic imitation effect we report.

The mean latency of correct response or correct response time (RT) was significantly higher for the incompatible group than for the compatible group in the non-cued test. SRC studies in humans consider longer response time (RT) or higher latency of action execution as an important parameter to reveal an automatic imitation effect in incompatible trials.[20] Our findings are congruent with such studies implying that the macaws in the incompatible group needed longer to inhibit the automatic response and then correctly produce the incompatible action unlike the compatible group, which automatically responded with correct actions. However, the response time decreased over the course of the test for both groups, indicating increased responsiveness of the subjects (i.e., an increased imitative tendency in the compatible group and counter-imitative tendency in the incompatible group) after considerable sensorimotor exposure and cumulative training over the course of the test.

Automatic intransitive action imitation in naturalistic situations is frequently observed in humans during social interactions and has been shown to increase affiliation,[3] feelings of closeness[48] between the mimicker and the mimicked. Mimicry of facial expressions and movement imitation during social plays has been observed in primates,[49] sun bears[50] (despite being solitary living species), and dolphins[51] which leads to affiliative communication between conspecifics. A similar pattern is observed in parrots mediated through audio-vocal pathways given that several parrot species mimic contact calls of particular individuals.[52–54] For example, orange-headed conures (_Aratinga canicularis_) imitate contact calls of conspecifics to interact with specific individuals in a social network[54] and to gain affiliation.[55] Automatic imitation may augment affiliative interaction resulting in pair-bonding in parrots or acceptance of individuals in social groups, however, more behavioral data on social interactions are required to substantiate this hypothesis. The use of conspecific demonstrators in our study instead of videos[27] of conspecifics or human demonstrators,[26] increased the ecological validity of the task and reflected in the positive findings, which suggest that motor mimicry may have evolved independently in various distantly related taxa but may indeed provide adaptive benefits in this species. Little is known about the behavior of wild blue-throated macaws and the ecology and life history of the species; however, it is known that outside the breeding season they form fission-fusion foraging flocks[56] like most parrot species, which constantly brings about the formation of new subgroups. This may require fast adaptation to new group constellations, fast synchronization, and bonding with the new group members, possibly facilitated by motor mimicry.

Overall, the present study provides evidence for the automatic imitation of intransitive actions in non-human animals, which in humans forms a crucial part of cultural evolution. Our findings that parrots are subject to the involuntary copying of intransitive actions, imply that in addition to excelling in vocal imitation and rhythmic synchrony, parrots have evolved motor imitation skills and may imitate conspecific gestures. This raises the hypothesis that the imitation of movements may be adaptive in parrots facilitating social bonding and group cohesion and possibly in the transmission of cultural conventions, which remains to be tested by future studies.

Limitations of the study

One limitation of the study was the small available sample of trained blue-throated macaws, which precluded an analysis of age or gender effects. As Blue-throated macaws (_Ara glaucogularis_) are critically endangered species, their availability in captivity is also limited.

AUTHOR CONTRIBUTIONS

E.H conceived the study. E.H and A.V.B designed and coordinated the study. E.H and P.S collected and analyzed the data, E.H wrote the article. A.V.B commented and edited the article. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Macaw subjects
  - Macaw demonstrators
  - Housing conditions
  - Ethical standards
- METHOD DETAILS
  - Experimental setup
  - Actions and commands
  - General procedure
  - Acquisition training phase
  - Test 1: Cued response
  - Test 2: Non-cued response
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Data scoring
  - Statistical analysis

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.111514.

REFERENCES

1. Jagiello, R., Heyes, C., and Whitehouse, H. (2022). Tradition and invention: The bifocal stance theory of cultural evolution. Behav. Brain Sci. 45, e249. https://doi.org/10.1017/S0140525X22000383.

2. Legare, C.H., Wen, N.J., Herrmann, P.A., and Whitehouse, H. (2015). Imitative flexibility and the development of cultural learning. Cognition 142, 351–361. https://doi.org/10.1016/j.cognition.2015.05.020.

3. Chartrand, T.L., and Van Baaren, R. (2009). Chapter 5 Human Mimicry. In Advances in Experimental Social Psychology (Elsevier), pp. 219–274. https://doi.org/10.1016/S0065-2601(08)00405-X.

4. Lakin, J.L., and Chartrand, T.L. (2003). Using Nonconscious Behavioral Mimicry to Create Affiliation and Rapport. Psychol. Sci. 14, 334–339. https://doi.org/10.1111/1467-9280.14481.

5. Chartrand, T.L., and Lakin, J.L. (2013). The Antecedents and Consequences of Human Behavioral Mimicry. Annu. Rev. Psychol. 64, 285–308. https://doi.org/10.1146/annurev-psych-113011-143754.

6. Van Baaren, R.B., Holland, R.W., Kawakami, K., and Van Knippenberg, A. (2004). Mimicry and Prosocial Behavior. Psychol. Sci. 15, 71–74. https://doi.org/10.1111/j.0963-7214.2004.01501012.x.

7. Lakin, J.L., Chartrand, T.L., and Arkin, R.M. (2008). I Am Too Just Like You: Nonconscious Mimicry as an Automatic Behavioral Response to Social Exclusion. Psychol. Sci. 19, 816–822. https://doi.org/10.1111/j.1467-9280.2008.02162.x.

8. Heyes, C. (2011). Automatic imitation. Psychol. Bull. 137, 463–483. https://doi.org/10.1037/a0022288.

9. Kilner, J.M., Paulignan, Y., and Blakemore, S.J. (2003). An Interference Effect of Observed Biological Movement on Action. Curr. Biol. 13, 522–525. https://doi.org/10.1016/S0960-9822(03)00165-9.

10. Press, C., Bird, G., Walsh, E., and Heyes, C. (2008). Automatic imitation of intransitive actions. Brain Cognit. 67, 44–50. https://doi.org/10.1016/j.bandc.2007.11.001.

11. Bastiaansen, J.A.C.J. (2009). Evidence for mirror systems in emotions. Phil. Trans. R. Soc. B 364, 2391–2404.

12. Blakemore, S.-J., and Frith, C. (2005). The role of motor contagion in the prediction of action. Neuropsychologia 43, 260–267. https://doi.org/10.1016/j.neuropsychologia.2004.11.012.

13. Cook, R., Bird, G., Catmur, C., Press, C., and Heyes, C. (2014). Mirror neurons: From origin to function. Behav. Brain Sci. 37, 177–192. https://doi.org/10.1017/S0140525X13000903.

14. Iacoboni, M. (2009). Imitation, Empathy, and Mirror Neurons. Annu. Rev. Psychol. 60, 653–670. https://doi.org/10.1146/annurev.psych.60.110707.163604.

15. Ferrari, P.F., Bonini, L., and Fogassi, L. (2009). From monkey mirror neurons to primate behaviours: possible 'direct' and 'indirect' pathways. Phil. Trans. R. Soc. B 364, 2311–2323. https://doi.org/10.1098/rstb.2009.0062.

16. Mukamel, R., Ekstrom, A.D., Kaplan, J., Iacoboni, M., and Fried, I. (2010). Single-Neuron Responses in Humans during Execution and Observation of Actions. Curr. Biol. 20, 750–756. https://doi.org/10.1016/j.cub.2010.02.045.

17. Catmur, C., Walsh, V., and Heyes, C. (2009). Associative sequence learning: the role of experience in the development of imitation and the mirror system. Phil. Trans. R. Soc. B 364, 2369–2380. https://doi.org/10.1098/rstb.2009.0048.

18. Cracco, E., Bardi, L., Desmet, C., Genschow, O., Rigoni, D., De Coster, L., Radkova, I., Deschrijver, E., and Brass, M. (2018). Automatic imitation: A meta-analysis. Psychol. Bull. 144, 453–500. https://doi.org/10.1037/bul0000143.

19. Brass, M., Bekkering, H., Wohlschläger, A., and Prinz, W. (2000). Compatibility between Observed and Executed Finger Movements: Comparing Symbolic, Spatial, and Imitative Cues. Brain Cognit. 44, 124–143. https://doi.org/10.1006/brcg.2000.1225.

20. Brass, M., Bekkering, H., and Prinz, W. (2001). Movement observation affects movement execution in a simple response task. Acta Psychol. *106*, 3–22.

21. Stürmer, B., Aschersleben, G., and Prinz, W. (2000). Correspondence effects with manual gestures and postures: A study of imitation. J. Exp. Psychol. Hum. Percept. Perform. *26*, 1746–1759. https://doi.org/10.1037/0096-1523.26.6.1746.

22. Chiavarino, C., Bugiani, S., Grandi, E., and Colle, L. (2013). Is Automatic Imitation Based on Goal Coding or Movement Coding?: A Comparison of Goal-Directed and Goal-Less Actions. Exp. Psychol. *60*, 213–225. https://doi.org/10.1027/1618-3169/a000190.

23. Bouquet, C.A., Shipley, T.F., Capa, R.L., and Marshall, P.J. (2011). Motor Contagion: Goal-Directed Actions Are More Contagious than Non-Goal-Directed Actions. Exp. Psychol. *58*, 71–78. https://doi.org/10.1027/1618-3169/a000069.

24. Wohlschläger, A., and Bekkering, H. (2002). Is human imitation based on a mirror-neurone system? Some behavioural evidence. Exp. Brain Res. *143*, 335–341. https://doi.org/10.1007/s00221-001-0993-5.

25. O'Sullivan, E.P., Claidière, N., and Caldwell, C.A. (2017). Action-matching biases in monkeys (Sapajus spp.) in a stimulus–response compatibility task: Evaluating experience-dependent malleability. J. Comp. Psychol. *131*, 337–347.

26. Range, F., Huber, L., and Heyes, C. (2011). Automatic imitation in dogs. Proc. Biol. Sci. *278*, 211–217. https://doi.org/10.1098/rspb.2010.1142.

27. Mui, R., Haselgrove, M., Pearce, J., and Heyes, C. (2008). Automatic imitation in budgerigars. Proc. Biol. Sci. *275*, 2547–2553. https://doi.org/10.1098/rspb.2008.0566.

28. A.U. Luescher, ed. (2006). Manual of Parrot Behavior, 1st ed. (Wiley). https://doi.org/10.1002/9780470344651.

29. Ikkatai, Y., and Seki, Y. (2023). Affiliation, Synchronization, and Rhythm Production by Birds. In Acoustic Communication in Animals, Y. Seki, ed. (Springer Nature Singapore), pp. 125–138. https://doi.org/10.1007/978-981-99-0831-8_8.

30. Lambert, M.L., Jacobs, I., Osvath, M., and von Bayern, A. (2019). Birds of a feather? Parrot and corvid cognition compared. Beyond Behav. *156*, 505–594. https://doi.org/10.1163/1568539X-00003527.

31. Slagsvold, T., and Wiebe, K.L. (2011). Social learning in birds and its role in shaping a foraging niche. Phil. Trans. R. Soc. B *366*, 969–977. https://doi.org/10.1098/rstb.2010.0343.

32. Coussi-Korbel, S., and Fragaszy, D.M. (1995). On the relation between social dynamics and social learning. Anim. Behav. *50*, 1441–1453. https://doi.org/10.1016/0003-3472(95)80001-8.

33. Chakraborty, M., Walløe, S., Nedergaard, S., Fridel, E.E., Dabelsteen, T., Pakkenberg, B., Bertelsen, M.F., Dorrestein, G.M., Brauth, S.E., Durand, S.E., and Jarvis, E. (2015). Core and Shell Song Systems Unique to the Parrot Brain. PLoS One *10*, e0118496. https://doi.org/10.1371/journal.pone.0118496.

34. Tramacere, A., Wada, K., Okanoya, K., Iriki, A., and Ferrari, P.F. (2019). Auditory-Motor Matching in Vocal Recognition and Imitative Learning. Neuroscience *409*, 222–234. https://doi.org/10.1016/j.neuroscience.2019.01.056.

35. Carouso-Peck, S., Goldstein, M.H., and Fitch, W.T. (2021). The many functions of vocal learning. Phil. Trans. R. Soc. B *376*, 20200235. https://doi.org/10.1098/rstb.2020.0235.

36. Benedict, L., Charles, A., Brockington, A., and Dahlin, C.R. (2022). A survey of vocal mimicry in companion parrots. Sci. Rep. *12*, 20271. https://doi.org/10.1038/s41598-022-24335-x.

37. Moura, L.N., Silva, M.L., Garotti, M.M.F., Rodrigues, A.L.F., Santos, A.C., and Ribeiro, I.F. (2014). Gestural communication in a new world parrot. Behav. Process. *105*, 46–48. https://doi.org/10.1016/j.beproc.2014.03.003.

38. Bertin, A., Beraud, A., Lansade, L., Blache, M.-C., Diot, A., Mulot, B., and Arnould, C. (2018). Facial display and blushing: Means of visual communication in blue-and-yellow macaws (Ara Ararauna)? PLoS One *13*, e0201762. https://doi.org/10.1371/journal.pone.0201762.

39. Heyes, C., and Saggerson, A. (2002). Testing for imitative and nonimitative social learning in the budgerigar using a two-object/two-action test. Anim. Behav. *64*, 851–859. https://doi.org/10.1006/anbe.2003.2002.

40. Chakraborty, M., and Jarvis, E.D. (2015). Brain evolution by brain pathway duplication. Phil. Trans. R. Soc. B *370*, 20150056. https://doi.org/10.1098/rstb.2015.0056.

41. Patel, A.D., Iversen, J.R., Bregman, M.R., and Schulz, I. (2009). Studying Synchronization to a Musical Beat in Nonhuman Animals. Ann. N. Y. Acad. Sci. *1169*, 459–469. https://doi.org/10.1111/j.1749-6632.2009.04581.x.

42. Schachner, A. (2010). Auditory-motor entrainment in vocal mimicking species: Additional ontogenetic and phylogenetic factors. Commun. Integr. Biol. *3*, 290–293. https://doi.org/10.4161/cib.3.3.11708.

43. Prather, J.F., Peters, S., Nowicki, S., and Mooney, R. (2008). Precise auditory–vocal mirroring in neurons for learned vocal communication. Nature *451*, 305–310. https://doi.org/10.1038/nature06492.

44. Keller, G.B., and Hahnloser, R.H.R. (2009). Neural processing of auditory feedback during vocal practice in a songbird. Nature *457*, 187–190. https://doi.org/10.1038/nature07467.

45. Kuhl, H., Frankl-Vilches, C., Bakker, A., Mayr, G., Nikolaus, G., Boerno, S.T., Klages, S., Timmermann, B., and Gahr, M. (2021). An Unbiased Molecular Approach Using 3′-UTRs Resolves the Avian Family-Level Tree of Life. Mol. Biol. Evol. *38*, 108–127. https://doi.org/10.1093/molbev/msaa191.

46. Zaine, I., Domeniconi, C., and De Rose, J.C. (2016). Exclusion performance and learning by exclusion in dogs. J. Exp. Anal. Behav. *105*, 362–374. https://doi.org/10.1002/jeab.209.

47. Tolman, C.W., and Wilson, G.F. (1965). Social feeding in domestic chicks. Anim. Behav. *13*, 134–142. https://doi.org/10.1016/0003-3472(65)90083-7.

48. Van Baaren, R., Janssen, L., Chartrand, T.L., and Dijksterhuis, A. (2009). Where is the love? The social aspects of mimicry. Phil. Trans. R. Soc. B *364*, 2381–2389. https://doi.org/10.1098/rstb.2009.0057.

49. Palagi, E., Norscia, I., Pressi, S., and Cordoni, G. (2019). Facial mimicry and play: A comparative study in chimpanzees and gorillas. Emotion *19*, 665–681. https://doi.org/10.1037/emo0000476.

50. Taylor, D., Hartmann, D., Dezecache, G., Te Wong, S., and Davila-Ross, M. (2019). Facial Complexity in Sun Bears: Exact Facial Mimicry and Social Sensitivity. Sci. Rep. *9*, 4961. https://doi.org/10.1038/s41598-019-39932-6.

51. Kuczaj, S.A., Makecha, R., Trone, M., Paulos, R.D., and Ramos, J.A.A. (2006). Role of Peers in Cultural Innovation and Cultural Transmission: Evidence from the Play of Dolphin Calves. Int. J. Comp. Psychol. *19*, 223–240. https://doi.org/10.46867/IJCP.2006.19.02.02.

52. Balsby, T.J.S., and Bradbury, J.W. (2009). Vocal matching by orange-fronted conures (Aratinga canicularis). Behav. Process. *82*, 133–139. https://doi.org/10.1016/j.beproc.2009.05.005.

53. Scarl, J.C., and Bradbury, J.W. (2009). Rapid vocal convergence in an Australian cockatoo, the galah Eolophus roseicapillus. Anim. Behav. *77*, 1019–1026. https://doi.org/10.1016/j.anbehav.2008.11.024.

54. Balsby, T.J.S., Momberg, J.V., and Dabelsteen, T. (2012). Vocal Imitation in Parrots Allows Addressing of Specific Individuals in a Dynamic Communication Network. PLoS One *7*, e49747. https://doi.org/10.1371/journal.pone.0049747.

55. Balsby, T.J.S., and Scarl, J.C. (2008). Sex-specific responses to vocal convergence and divergence of contact calls in orange-fronted conures (*Aratinga canicularis*). Proc. Biol. Sci. *275*, 2147–2154. https://doi.org/10.1098/rspb.2008.0517.

56. Hesse, A.J., and Duffield, G.E. (2000). The status and conservation of the Blue-Throated Macaw Ara glaucogularis. Bird. Conserv. Int. *10*, 255–275. https://doi.org/10.1017/S0959270900000216.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	https://doi.org/10.6084/m9.figshare.26400400
Exemplary Video	This paper	Video S1
Exemplary Video	This paper	Video S2
Experimental models: Organisms/strains		
Blue-throated macaws	Loro Parque, Tenerife, Spain	
Software and algorithms		
Solomon Coder	Peter Andras	https://solomon.andraspeter.com/webhelp/cnt.htm
RStudio version R.4.1.2	Posit PBC	https://posit.co/products/opensource/rstudio/

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Macaw subjects

The subjects were seven hand-raised *Ara glaucogularis* individuals kept at the Max Planck Comparative Cognition Research Station facility at Loro Parque Fundacion, Tenerife, Spain. Table 1 shows the age, sex, and the groups of the subjects. The subjects were randomly assigned to a compatible group of three and an incompatible group of four individuals. The age of the subjects ranged from 3 to 15 years old. The subjects also acted as demonstrators (in addition to the four pre-assigned demonstrators) in few sessions only after they had completed their own experimental sessions and had reached the learning criterion (see Tables S1 and S2 for details on demonstrators). As Blue-throated macaws are a critically endangered species, their availability in captivity is limited.

Macaw demonstrators

We used four conspecific demonstrators that had been already well trained to perform the two actions 'lift leg' and 'flap wings' with gestural commands. These individuals did not participate as experimental subjects in the current study (because of their training history in previous experiments) and only participated as trained demonstrators. The demonstrators were assigned randomly to the subjects for each session and performed both the actions. Details (age/sex) of the demonstrators are furnished in Table S1.

Housing conditions

All subjects were group-housed in 3 adjacent semi-outdoor aviaries contiguous with the lab facility. The aviaries measured approximately 1.80 × 3.40 × 3 m (width × length × height) with interconnected windows (1 m × 1 m) which remained closed throughout the experiment to avoid social conflicts between certain individuals. All aviaries were equipped with UV-light lamps namely Arcadia Zoo Bars (Arcadia 54W Freshwater Pro and Arcadia 54W D3 Reptile lamp) to ensure sufficient exposure to UV light. All birds had 24-h access to the outside aviary, allowing them to follow a natural light cycle. Outdoor temperatures during the research period fluctuated between 20 and 26°C during the day and 15 to 21°C during the night with interspersed periods of light raining. All birds had *ad libitum* access to water and mineral blocks. They were fed with fresh fruits, vegetables twice a day along with a seed mix (Ara LP mix) only in the afternoon. To transport the subjects to the testing rooms, the aviaries were connected with mobile feeding cages, which the birds entered voluntarily for participating in the tests and which could be wheeled with ease with the birds inside.

Ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Under the German Animal Welfare Act of 25th May 1998, Section V, Article 7 and the Spanish Animal Welfare Act 32/2007 of 7th November 2007, Preliminary Title, Article 3, the study was classified as a non-animal experiment and did not require any approval from a relevant body. This article does not contain any studies with human participants performed by any of the authors.

METHOD DETAILS

Experimental setup

Testing took place in an indoor chamber (3.0 m × 1.5 m × 1.5 m, height × width × length) equipped with flicker free lamps covering the birds' full range of visible light (Arcadia 39 W Freshwater Pro and Arcadia 39 W D3 Reptile lamp). During the training phase, the subjects were in the testing room with one experimenter. During the tests, the subject was placed next to a conspecific model, facing

an experimenter each. The subject and the conspecific demonstrator were placed on two adjacent standing perches (height 1.13m) and could clearly see each other in the testing room. An opaque curtain passed between the experimenters so that experimenter 1, who was facing the subject, was hidden from the view of the model and experimenter 2. The experimenters and the birds could hear each other distinctly. An illustration of the experimental set-up is shown in Figure 1. A sound-buffered one-way glass system permitted zoo visitors to see the experimental sessions but did not allow the birds and the experimenters to see out. Each corner of the room was equipped with a cctv camera which recorded soundless videos of the testing sessions from different angles. Additionally, a Sony HDR-CX240E video camera was used to record all the testing sessions. Testing took place from May 2023 till October 2023 for 2 h almost regularly with occasional breaks.

Actions and commands

During the first training phase of the experiment, the subjects were trained to perform two intransitive actions reliably on specific hand commands: lifting one of the legs up while perching, hereafter named, 'lift leg', and spreading their wings while perching, hereafter named 'flap wings'. The hand command for 'lift leg' was holding the right index finger up and the command for 'flap wings' was to flutter the palm of the right hand in front of the subject (Figure 2A). Another hand command, the 'do it now' signal, was given to the subjects in the non-cued response test, which only denoted to the subjects to execute the action now, without specifying which one. Here, the experimenter struck the right fist on the left open palm (Figure 2B). Since there was no indication of the correct action, the subjects had to figure out for themselves whether they had to perform 'the same action' as the demonstrator (compatible group) or 'the opposite action' as the demonstrator (incompatible group) in order to receive a reward. For one subject Long John, which was an amputee, we replaced 'lift leg' with another intransitive action 'fluff'. For more details on the actions and the corresponding hand signals refer to Table S3.

General procedure

The study was divided into a training phase followed by two tests, the cue-response test and the non-cued response test. The training phase consisted of five sessions of 30 trials for every subject. The subsequently conducted cued-response test sessions comprised 20 trials each (counterbalanced and varying pseudo randomly between the two actions). Occasionally it was necessary to perform 1–3 extra motivational trials in order to end the sessions with a positive experience for the subjects, in case they performed poorly. The compatible group reached the learning criterion in two sessions while the incompatible group took six sessions to reach the criterion. For the non-cued response test, we followed the same procedure as in the cued-response test conduction sessions of 20 trials plus 1–3 extra trials where necessary to keep up the motivation of the subject. The compatible group took a maximum of five sessions while the incompatible group took a maximum of 14 sessions in this test to reach the criterion. For further details on the test sessions (trials, demonstrators in each session), see Table S2.

Acquisition training phase

At the first stage of the experiment, the subjects were trained to learn and discriminate between the two actions 'lift leg' and 'flap wings' in response to the specific hand commands. The subjects were trained to respond appropriately to the hand commands until they reached the discrimination criterion of 80% correct responses in two consecutive sessions. Each session consisted of a maximum of 30 trials with the two actions counterbalanced and randomly listed.

Test 1: Cued response

In this SRC test the experimenter gave a hand command to the subject parallel to the conspecific demonstration, which cued the rewarded responses in that trial to the subjects of each group (see details in Video S1). The compatible group received the command for the action that matched the demonstration, while the incompatible group received the command for the action that did not match the demonstration.

A trial was initiated by experimenter 1, who provided a vocal cue to experimenter 2 by saying the word 'Now'. Out of view of the subject, Experimenter 2 then requested the demonstrator to perform one of the two actions. Immediately followed by the correct demonstration and a clicker sound, experimenter 1 gave the corresponding command to the subject (i.e., the command for the same action to the compatible group and the command for another action to the subject in the incompatible group, namely, leg command for wing and vice versa). The demonstrator received no food following its performance whereas the subject was rewarded for a correct response (matching response in the compatible group and opposite response in the incompatible group). After 3–4 completed trials, the opaque curtain was completely drawn between subject and demonstrator and experimenter 2 fed the demonstrator to keep its motivation up and ensure it continued to perform in the following trials. If the demonstrator performed a wrong action, experimenter 2 clearly said 'NO', which alerted experimenter 1 to annul the trial. The sequence of actions was counterbalanced and pseudorandomized for all subjects, with no action being repeated more than twice consecutively throughout the 20–23 trial session. Subjects proceeded to the subsequent non-cued test only after meeting the 80% correct response criterion in two consecutive sessions.

Test 2: Non-cued response

The testing procedure for non-cued response test consisted of a stimulus-response task, with a neutral 'do it now' command (see Video S2). Each trial started with experimenter 1 saying 'Now', upon which experimenter 2 instructed the model to perform

the respective action. Immediately afterward, experimenter 1 signaled 'do it now' to the subject. The subjects were rewarded for performing the matching action in the compatible group and the non-matching action in the incompatible group. If a subject did not respond to the 'do it now' command within 5 s, with any action, the demonstration and subsequent 'do it now' command was repeated. If the subject did not respond in two consecutive trials or if the subject performed two errors in a row for the same action, the experimenter 'helped' the subject by giving the respective hand command associated with that action in a 'correction trial,' in order to entice the subject to respond appropriately to the demonstrated action (i.e., either performing the same or the opposite action). Such 'correction trials' were not considered in the analysis. If the subjects executed both actions simultaneously (e.g., opened two wings and simultaneously performed a 'lift leg'), we considered the trial as invalid and repeated it. However, when the birds inhibited their automatic responses by showing a slight implied response (e.g., a twitch of the forelimbs, or a slight movement of the feet) followed by the execution of the other action, we considered the fully executed action as the response. If both actions were executed consecutively, the trial was also counted invalid and repeated as action sequences were not reinforced. The demonstrators were rewarded every 3–4 trials obscured from the view of the subject as described for cued-response test. We conducted a maximum of 14 sessions per subject. If a subject performed 80% correct out of 20–23 trials in two consecutive sessions, we considered it to have reached the correct response criterion and stopped testing.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data scoring

All the videos were coded by two experimenters using Solomon Coder (version Beta 19.08.02, 2019 by András Péter). Imitative responses in each trial were coded as correct responses for the compatible group and incorrect responses for the incompatible group. Conversely, counter-imitative responses were coded as incorrect trials for the compatible group and correct responses for the incompatible group. The response rate in each session was calculated as the number of correct responses divided by the total number of trials. The mean response rate was calculated as the sum of response rates divided by total number of sessions for each bird. The mean of correction trials in the non-cued test was calculated as total correction trials divided by total number of trials each subject faced during the test. The total number of sessions required to reach criterion for learning to perform the actions with specific commands was taken as the 'learning speed'. We compared the imitative responses for the two actions to determine contagiousness like effect for the two actions. Contagiousness in the behaviors, for example, 'pecking' in budgerigars, may influence the result of the experiment as the subjects may commit more errors in the incompatible group against the contagious action. We also calculated the response time (RT) or latency of response as the time difference between end of 'do it now' command and initiation of the action response. For our analysis, the mean latency of correct responses for each session was only calculated as the sum of latencies divided by the number of correct trials in a session.

Statistical analysis

All statistical analyses were performed in RStudio (R Core Team 2019, RStudio version R.4.1.2). The central tendency and dispersion of the data are measured by Mean ± S.E. We conducted Shapiro-Wilk test to check for normality of the distribution. We conducted one way ANOVA to compare independent sample means of two groups without any repeated measures for the normally distributed datasets. For the nonnormal distribution, we used Wilcoxon rank-sum test to compare the means of two independent groups. For examining the effect of action type on imitative responses of the two groups in the non-cued test, we conducted a two-way ANOVA with action type and groups as independent variables. For examining the effect of groups and sessions on latency, we conducted a generalised linear model with groups and sessions predicting mean latency. Threshold for statistical significance used was $p < 0.05$. Exact values of 'p' are denoted in the results, figure and figure legends. Sample size is indicated in figure legends as N.