

Contextual imitation in juvenile common ravens, *Corvus corax*Matthias-Claudio Loretto<sup>a, b, c, d, \*</sup>, Richard Schuster<sup>e</sup>, Ira G. Federspiel<sup>a</sup>, Bernd Heinrich<sup>f</sup>, Thomas Bugnyar<sup>a, b</sup><sup>a</sup> Department of Cognitive Biology, University of Vienna, Vienna, Austria<sup>b</sup> Konrad Lorenz Research Station, Core Facility for Behaviour and Cognition, University of Vienna, Grünau Im Almtal, Austria<sup>c</sup> Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany<sup>d</sup> Department of Biology, University of Konstanz, Konstanz, Germany<sup>e</sup> Department of Biology, Carleton University, Ottawa, Canada<sup>f</sup> PO Box 153, Weld, ME, 04285, U.S.A.

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Social learning is a powerful mechanism of information acquisition and can be found in various species. According to the type of information transmitted, animals may change their motivation to perform actions, shift their perception/attention to relevant stimuli, associate other individuals' behaviours with particular stimuli/events or learn to perform 'novel' behaviours. The latter is referred to as imitation and has been considered a cognitively demanding mechanism necessary for high-fidelity copying, which may or may not occur in nonhuman animals. We tested the ability of 20 juvenile ravens to imitate an action demonstrated by a human experimenter. Birds of two test groups could observe a familiar human executing one of two opening techniques at an artificial fruit apparatus (horizontal or vertical hand movements directed towards the same location), whereas birds of a control group observed the human touching but not opening the apparatus. Ravens of both test groups tended to use the same direction of movements as observed, when they opened the apparatus themselves with their beak. Comparison with the control group revealed that ravens had a predisposition to manipulate the apparatus by pecking. Hence, observers of vertical hand movements most likely strengthened their initial preference for executing peck movements towards an item enclosing food, whereas observers of horizontal hand movements started to apply beak/head movements that hardly occur during foraging and are 'novel' to this context. Juvenile ravens are thus capable of imitating simple motor actions, even though they may use a different body part to execute the behaviours than human demonstrators.

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One of the main advantages of social life is that individuals can make use of information provided by others, typically to improve foraging efficiency and/or predator detection (Giraldeau & Caraco, 2000). Social information use can take different forms: information may be transmitted by staying in contact with a knowledgeable individual, like elephants, *Loxodonta africana*, following their matriarch to foraging grounds and water holes (McComb, Moss, Sayialel, & Baker, 2000); it may also be transmitted through (repeated) exposure to the performance of a skilled individual, like young chimpanzees, *Pan troglodytes*, watching older ones manufacturing and using tools (Lonsdorf, Eberly, & Pusey, 2004; Matsuzawa, Tomonaga, & Tanaka, 2006), and through direct

interaction between individuals, as when affiliated animals establish communicative conventions (McGrew, 2004; Perry et al., 2003; Whitehead & Rendell, 2015).

Several of these cases fall into the definition of social learning sensu Box (1984, p. 213) as 'changes in the behaviour of one individual that result partly from paying attention to the behaviour of another' (see also Heyes, 1994, 2012 for a more refined definition); yet, the above-mentioned examples may differ with respect to (1) which type of information is transmitted, (2) under which conditions social information is used, and (3) how robust the information transmission is over time, referring to the areas of social learning mechanisms (Zentall & Galef, 1988) social learning strategies (Laland, 2004; Rendell et al., 2011) and behavioural traditions and culture (Whiten, Hinde, Laland, & Christopher, 2011), respectively.

Various social learning mechanisms have been described (Heyes, 2012; Hoppitt & Laland, 2008; Zentall & Galef, 1988), most

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of which can be well explained by learning theory (Heyes, 1994, 2012) and broadly categorized according to the type of information processed (Zentall, 2004). While surprisingly few studies have been designed to explicitly test for mechanisms at the motivational level (e.g. social facilitation), perceptual level (e.g. enhancement) and associative level (e.g. observational conditioning; Zentall, 2004), mechanisms at the 'cognitive level' have received much attention, from both a conceptual and a methodological point of view (Heyes, 1994; Hoppitt & Laland, 2008; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Specifically, action imitation, the copying of others' behaviour, has been the focus of interest. On the one hand, the translation of a visual input into a matching motor output features a 'correspondence problem' (an action looks different from an observer's perspective than when it is performed oneself) and thus may involve a special, and possibly more complex, processing than other mechanisms of social learning (Byrne & Whiten, 1988; Byrne, 1995; but see ; Ferrari, Bonini, & Fogassi, 2009; Huber et al., 2009). On the other hand, a faithful matching of observed behaviour has been considered critical for the reliable transmission of information and thus essential for cultural evolution (Boyd & Richerson, 1985, 1996; Tomasello, Kruger, & Ratner, 1993; but see Heyes, 2012).

Despite a wealth of studies, evidence for imitation in nonhuman animals is still debatable. Depending on the criteria used, imitation can be found in a variety of species (Heyes, 2012; Hoppitt & Laland, 2008) or specifically in humans (Tomasello, Savage-Rumbaugh, & Kruger, 1993) and, possibly, some great apes (Whiten et al., 2004; but see ; Tennie, Call, & Tomasello, 2009). One of the criteria in question is how precisely behaviours are copied. Many studies on nonhuman primates report only low levels of precision in copying or even no copying at all (Clay & Tennie, 2018; Tennie, Call, & Tomasello, 2012; Tomasello, Savage-Rumbaugh, et al., 1993; Visalberghi & Fragaszy, 2002; Zuberbühler, Gyax, Harley, & Kummer, 1996), whereas some studies on birds report relatively high levels of copying precision (review in Zentall, 2004). These apparent taxonomic differences in copying precision are most likely affected by the type of experimental task: single movements such as pecking or stepping on a platform, as used in many bird studies, are easier to match than a combination or sequence of behaviours, as used in many primate studies on artificial fruits (Whiten, Custance, Gomez, Teixidor, & Bard, 1996; but see ; Voelkl & Huber, 2000). The level of precision in response topography has also been used as an argument to distinguish between 'blindly mimicking' and 'intentionally copying', as the latter is assumed to require more degrees of freedom with respect to matching than the former (Huber et al., 2009). However, empirical studies testing for intentional aspects of imitation are still scarce and the outcomes are debatable (Huber, Range, & Virányi, 2012; Kaminski, Neumann, Bräuer, Call, & Tomasello, 2011; see discussion on selective or 'rational' imitation: Range, Virányi, & Huber, 2007).

Corvids are renowned for their large brains and sophisticated sociocognitive skills, which are in many aspects comparable to those of primates (Emery & Clayton, 2004; Güntürkün & Bugnyar, 2016). Despite the importance of social information use in these birds (e.g. Bugnyar, 2013; Emery, Clayton, & Frith, 2007; Massen, Pašukonis, Schmidt, & Bugnyar, 2014), relatively few studies have focused on social learning mechanisms. Social facilitation has been reported for ravens and carrion crows, *Corvus corone*, in investigating objects (Miller, Schiestl, Whiten, Schwab, & Bugnyar, 2014; Stöwe et al., 2006a, 2006b), for rooks, *Corvus frugilegus*, in accepting new food (Dally, Clayton, & Emery, 2008) and, as a plausible mechanism for American crows, *Corvus brachyrhynchos*, forming traditions about artificially introduced predator types (Cornell, Marzluff, & Pecoraro, 2011; Marzluff, Walls, Cornell, Withey, & Craig, 2010). Local or stimulus enhancement towards feeding locations, parts of feeding

apparatuses and/or specific objects have been reported for ravens (Fritz & Kotrschal, 1999; Schwab, Bugnyar, Schloegl, & Kotrschal, 2008), jackdaws, *Corvus monedula* (Schwab et al., 2008) and New Caledonian crows, *Corvus moneduloides* (Kenward, Rutz, Weir, & Kacelnik, 2006). To our knowledge, there is no evidence for action imitation, possibly because the above-mentioned mechanisms at the motivational and perceptual levels are powerful enough to transmit the relevant information during foraging (Federspiel, Clayton, & Emery, 2009). Still, the apparent lack of action imitation is surprising: on the one hand, imitative abilities have been reported for other large-brained birds such as parrots (Dawson & Foss, 1965; Moore, 1992) that resemble corvids with respect to their social life with long-term monogamous pairs (Emery et al., 2007); on the other hand, simple forms of action imitation have been demonstrated in species such as pigeons, *Columba livia*, and quails, *Coturnix japonica* (Akins, Klein, & Zentall, 2002) that hardly face a more diverse foraging ecology than corvids, rendering a socioecological explanation for a lack of imitation in corvids unlikely.

In the present study we tested common ravens, highly adaptable food generalists that prefer feeding on carcasses (Haffer & Kirchner, 1993; Ratcliffe, 1997) and occupying a wide range of different habitats with a great variety of potential food items (Heinrich, 1995), often of anthropogenic origin (Loretto et al., 2017; Loretto, Schuster, & Bugnyar, 2016). Ravens are known to be sensitive to various types of social information during foraging (Bugnyar, 2013; Scheid, Pasteur, Range, & Bugnyar, 2007; Schwab, Bugnyar, Schloegl, et al., 2008), including a conspecific's demonstration of opening an apparatus containing food (Fritz & Kotrschal, 1999). We based our study on the latter findings but adapted the methods to explicitly test the ravens' capacity to copy the other individual's motor action and to distinguish imitation from other social learning mechanisms. We tested young hand-raised birds on the same apparatus as Fritz and Kotrschal (1999) but instead of a conspecific demonstrating a given opening technique, we used a human experimenter demonstrating one of two alternative opening techniques (vertical or horizontal hand movements) executed at exactly the same location of the apparatus. We were therefore able to control the motivational and perceptual information given by the demonstrator and rule out possible effects of conspecific social relationships between demonstrator and test subject. However, using a human experimenter as demonstrator put the 'correspondence problem' to its extreme as it required ravens to relate the observed hand movements to their own head/beak movements. We compared the behaviour of the two test groups (vertical pushing and horizontal pushing) to that of a control group, where the individuals did not receive any demonstration of either opening technique. However, the control birds' attention towards the apparatus was increased in a similar way as in the two test groups, by the human experimenter touching the opening location. We predicted that ravens of the two test groups would need fewer trials to solve the task than ravens of the control group and, notably, that individuals in the test groups would match their opening technique to the respective technique demonstrated by the experimenter, i.e. show vertical or horizontal movements. Individuals of the control group should show no preference for either opening technique or, if one movement for manipulating the apparatus comes more naturally to them, we predicted a predisposition to engage in vertical 'pecking-like' movements.

## METHODS

### Subjects

We used 20 juvenile ravens, originating from two groups. One group (13 birds) was hand-raised in 2004 at the Konrad Lorenz

Research Station (KLF), Austria, and another group (seven individuals) was hand-raised in 2006 at Bernd Heinrich's laboratory in Vermont (VT), U.S.A. All birds were taken into human care at an early age (10–28 days, i.e. when they had hardly any feathers and slept most of the day); they were kept in cardboard boxes in groups of two to four birds until fledging (6–7 weeks posthatch) and then housed in one social group per site (KLF, VT). During hand raising, all birds developed a strong attachment to their human caretakers. We used this attachment to familiar persons to test the ravens' responses to the demonstration by a human experimenter. We took special care that the human experimenter was treating the birds as similarly as possible, for example by hand feeding every bird each day. Ravens of the KLF group were tested 11–15 weeks post-hatching and those of the VT group 16–19 weeks posthatching. At the time of testing, all birds were group housed in large naturalistically designed outdoor enclosures (KLF: 230 m<sup>2</sup>; VT: 2x 50 m<sup>2</sup>) containing perches, vegetation cover and natural soil. The aviaries were built so that individuals could be visually but not acoustically separated. The ravens were marked with coloured leg rings for individual identification. All individuals were fully habituated to close contact with humans including the experimenter and to short separations from the group during the experiments.

#### *Ethical Note*

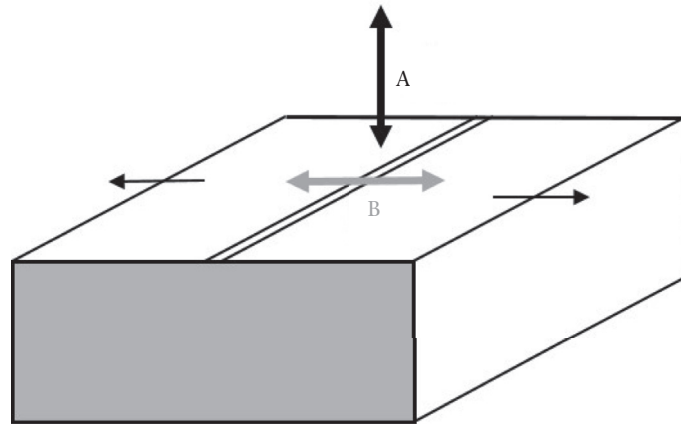
All 20 individuals were hand-raised under similar conditions (see above) and participated in experiments voluntarily. The birds were never deprived of food, and water was available ad libitum for drinking and bathing. This study adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, the Austrian and local government guidelines, the US law on animal research and treatment, the institutional guidelines of the Konrad Lorenz Research Station, University of Vienna and the University of Vermont. Some of the raven nestlings were provided by zoos (four from Munich, three from Wuppertal); the others were taken from the wild in Germany (six) with permission from the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg on 25 February 2004 and in Vermont (seven) with permits from the US Federal Fish and Wildlife Permit Number MB689376-0, State of Maine Department of Inland Fisheries and Wildlife Permit 22077, and Vermont Fish and Wildlife Department Scientific Collecting Permit. The study subjects in Austria remained in captivity at the Cumberland Wildpark after the completion of this study for further research, while subjects in Vermont were released from the aviary in the year after the study.

#### *Procedure and Analysis*

We used the same test apparatus as [Fritz and Kotrschal \(1999\)](#), which was a box that consisted of a wooden frame (30 x 30 cm and 10 cm high) with a cover and bottom of white polystyrene ([Fig. 1](#)). The cover was movable and consisted of two lids which could slide in opposite directions, either by directing force at the gap between the lids on the top of the apparatus or by pulling on one side from a lateral position next to the box. Unlike in the original study by [Fritz and Kotrschal \(1999\)](#), we did not provide lashes on the lids to facilitate pulling from the side and we demonstrated both opening techniques at the top of the apparatus exclusively (i.e. at the gap between the lids). In [Fritz and Kotrschal's \(1999\)](#) study, pecks directed towards the lids were vertical head/beak movements performed by the ravens when sitting on top of the apparatus. We thus modelled this pecking behaviour with vertical hand movements performed by the experimenter. The alternative horizontal movements demonstrated by the experimenter resembled the horizontal head movements ravens perform for cleaning their

beak; this behaviour may occur during foraging but, to our knowledge, is not used for extracting food; we thus considered it to be 'novel' in the context of food acquisition. Before starting the experiment, we presented the apparatus to the birds in the aviary without lids for habituation. After 1–2 weeks, all birds were used to taking small pieces of reward out of the opened box.

The 13 individuals kept at KLF were randomly assigned to one of two test groups (six birds in group A, seven in group B). One bird of group A had to be excluded from the tests due to severe illness during the study period and was replaced by one raven raised in VT. The other six ravens in VT were assigned to the control group C, whereas again one bird could not be tested as it showed much higher levels of neophobia. Note that the study was conducted stepwise because we were initially not sure of getting a second group of hand-raised ravens in VT; we therefore did not randomly allocate birds to all three conditions (group A, B and control C) across the two sites, but focused on the two test conditions in Austria first. However, we took special care that the ravens at both sites were raised and kept as similarly as possible. The same person (M.L.) acted as experimenter for all birds. For an experimental session, he visually separated one of the birds from the others, presented the opened box and filled it with a small but highly preferred food reward (dry dog food). After closing the box with the lids, he performed one of three behaviours: (1) with birds from group A, he performed vertical hand movements into the small gap between the lids, making the lids slide open; (2) with birds from group B, he performed horizontal hand movements by moving the hand from the small gap between the lids towards the edge of the lids, making them slide open; (3) with birds from control group C, he put his hands on top of the lids, but did not perform any hand movements to open them. Note that all three behaviours were directed towards the same location at the apparatus and the two opening techniques were executed at the same starting point (where the two lids met; [Fig. 1](#)). We thus provided information about the relevant part of the box (local enhancement) and about the fact that it was safe to manipulate the apparatus (social facilitation) in all three conditions. The only difference between the conditions was what the hands of the experimenter were doing, that is, resting on the lids (control) or pushing the lids via vertical or horizontal movements. The demonstrations were conducted only when the birds showed no signs of arousal (feather/body position, vocalization) and their head and eyes were oriented towards the experimenter (which could take up to 10 min). The demonstrations of vertical and horizontal movements were repeated three times in a row; the touching of the lids in the control group lasted approximately as long as these movement demonstrations (3 s). Before the birds got access to the test apparatus themselves for 5 min, it was turned 90° to control for any orientation on environmental cues in the test compartment (e.g. left or right wall). We videotaped the ravens during the trials (examples are available in the video in the [Supplementary Material](#)), and we categorized and scored every contact of the birds with the box, until they could obtain the food by opening the lids. We considered trials as 'unsuccessful' when the birds did not approach the apparatus in 5 min and/or disturbances like background noise caused the birds to panic in the experimental room. These trials were excluded from the analysis. For each bird, we thus analysed the first three trials in which it touched the box and eventually opened the box successfully. The contacts with the box were classified as follows: (1) vertical push: the individual showed a pecking-like action by moving the head in a vertical direction, often inserting the beak at the gap between the two lids of the box, which led to a partial opening without any horizontal movement of the head; (2) horizontal push: after inserting the beak in the gap between the lids, the individual moved its head horizontally and thus pushed one of



**Figure 1.** ‘Artificial fruit’ used in experiments: black arrow (A) and grey arrow (B) indicate hand movement of the demonstrator for group A and group B, respectively. Thin black arrows show direction of opening of the two sliding lids.

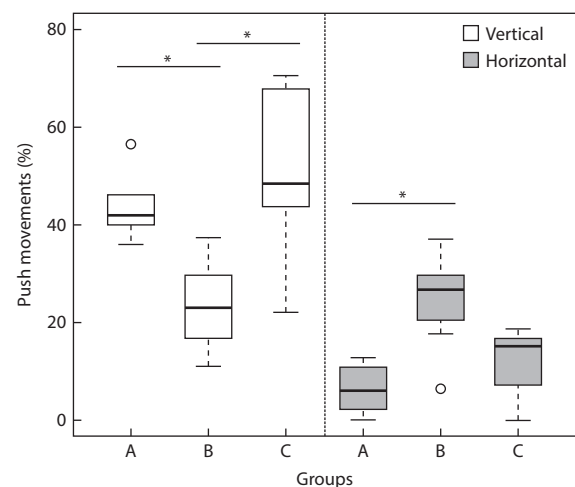
the lids to the side, or it took one lid with the beak and pushed it to the side; (3) every other beak contact with the cover or parts of the box was categorized as ‘other box contacts’. A typical example was pecking at the wooden frame or poking with the beak underneath the apparatus. Importantly, none of these ‘other box contacts’ caused any movement of the lids.

Recordings were independently coded by two observers (M.L. and T.B.) with very high interobserver agreement (Cohen’s kappa = 0.852,  $P < 0.001$ , 95% confidence interval = 0.714, 0.989; Landis & Koch, 1977). The coding of T.B. was mostly blind to the test condition, as we tried to avoid filming the hand movements of the experimenter. Since some individuals were much more active than others (see also Stöwe et al., 2006a, 2006b), we calculated the proportion of each category (vertical push, horizontal push and other box contacts) over the first three successful trials together and compared these values between test groups A and B and the control group C. We used nonparametric tests, i.e. Kruskal–Wallis rank sum tests for differences between all groups and the Mann–Whitney test for pairwise comparisons between groups and adjusted the  $P$  value following the Benjamini and Hochberg (1995) correction. Since nonparametric tests are not very powerful, especially with a relatively low sample size, we additionally followed a generalized linear model (beta distribution) approach employing a Markov chain Monte Carlo algorithm to investigate the posterior distribution of the treatment effects. This allowed us to directly draw inference about the difference between treatments based on the calculated credible intervals (Baldwin & Fellingham, 2013). The advantage of this Bayesian approach is that the analysis does not suffer the dependencies in the researcher’s intentions like classical hypothesis testing using  $P$  values does (Kruschke, 2010). Instead it allowed us to calculate the believability of candidate values given the data we observed and thus yielded a natural way to assess the credibility of null values and the probability of achieving research goals (Kruschke, 2010). All analyses were conducted with the statistical software R, version 3.5.3 (R Development Core Team, 2019) and connected to OpenBUGS v.3.2.3 (Lunn, Spiegelhalter, Thomas, & Best, 2009) via package R2OpenBUGS v.3.2–2.2 (Sturtz, Ligges, & Gelman, 2005).

## RESULTS

Against our expectation, there was no clear difference between groups in the number of trials individuals needed to successfully open the box (group A: 9–15 trials, mean = 12, SD = 2.683; group B: 3–39 trials, mean = 26, SD = 18.565; group C: 15–45 trials,

mean = 31.2, SD = 11.145; Kruskal–Wallis test:  $\chi^2 = 5.254$ ,  $P = 0.072$ ). Thus, we did not find that the opportunity for social learning affected the ravens’ efficiency in solving the task. However, groups differed with respect to the relative proportion of vertical push movements (Kruskal–Wallis test:  $\chi^2 = 9.353$ ,  $P = 0.009$ ) and horizontal push movements (Kruskal–Wallis test:  $\chi^2 = 8.434$ ,  $P = 0.015$ ), respectively. As expected, post hoc tests revealed a significant difference between the two test groups A and B (pairwise comparisons Mann–Whitney test: vertical pushing:  $W = 41$ ,  $N_1 = 6$ ,  $N_2 = 7$ ,  $P_{\text{adjusted}} = 0.016$ ; horizontal pushing:  $W = 3$ ,  $N_1 = 6$ ,  $N_2 = 7$ ,  $P_{\text{adjusted}} = 0.024$ ; Fig. 2). Interestingly, there was no significant difference between test group A and control group C (Mann–Whitney test: vertical pushing:  $W = 10$ ,  $N_1 = 6$ ,  $N_2 = 5$ ,  $P_{\text{adjusted}} = 0.410$ ; horizontal pushing:  $W = 30$ ,  $N_1 = 6$ ,  $N_2 = 5$ ,  $P_{\text{adjusted}} = 0.272$ ), but there was a significant difference between test group B and control group C for vertical pushing (Mann–Whitney test:  $W = 8.5$ ,  $N_1 = 7$ ,  $N_2 = 5$ ,  $P_{\text{adjusted}} = 0.045$ ) and a marginally nonsignificant difference for horizontal pushing ( $W = 30$ ,  $N_1 = 7$ ,  $N_2 = 5$ ,  $P_{\text{adjusted}} = 0.072$ ). There was no difference between the three groups regarding the



**Figure 2.** Box plots show the percentages of vertical and horizontal pushing for each of the three groups (A, B and C) with median (thick line), quartiles (box limits), 5th and 95th percentiles (error bars) and outliers (open circles). Birds in group A saw a human make vertical hand movements, birds in group B saw a human make horizontal hand movements and birds in group C were not shown any hand movements. Percentages refer to the total number of box contacts over the first three successful trials. Asterisks indicate significant differences between groups ( $P < 0.05$ ).

category of other box contacts (Kruskal–Wallis test:  $\chi^2 = 2.976$ ,  $P = 0.226$ ).

For vertical pushing the estimated means of the beta distribution back-transformed to probabilities were 0.44 for group A (95% credible interval, CI = 0.36–0.52), 0.24 for group B (CI = 0.17–0.34) and 0.50 for control group C (CI = 0.32–0.69). The posterior distributions of these estimates are shown in Fig. 3a. The mean estimated probabilities for horizontal pushing were 0.07 for group A (CI = 0.02–0.24), 0.25 for group B (CI = 0.16–0.36) and 0.12 for control group C (CI = 0.04–0.37). The posterior distributions of these estimates are shown in Fig. 3b. For vertical and horizontal pushing the posterior distributions of the estimates are very similar for groups A and C with smaller credible intervals for group A. This indicates a predisposition for vertical pushing (group C), which was strengthened by the demonstrations for group A and it suggests that the difference between test groups is mainly driven by the modified preference of ravens in group B.

## DISCUSSION

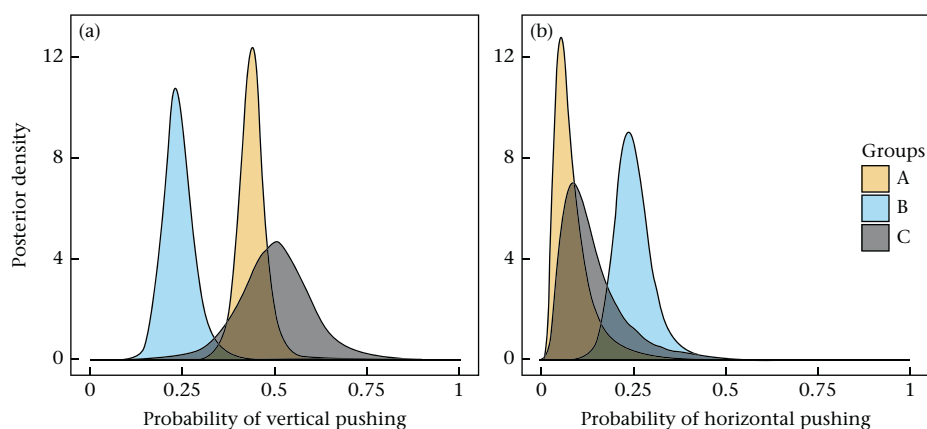
After observing a familiar human experimenter opening an artificial fruit apparatus with horizontal or vertical hand movements, juvenile ravens that witnessed horizontal hand movements increased the relative frequency of horizontal beak movements in comparison to juveniles that witnessed vertical movements. The comparison with birds of the control group, which observed the experimenter touching but not opening the apparatus, revealed that ravens have a predisposition to manipulate the lids by pecking, which resembles the demonstrated vertical movements. Hence, ravens that had observed vertical hand movements most likely strengthened their initial preference for executing peck movements towards an item enclosing food, whereas ravens that had observed horizontal hand movements did not show any preference for vertical pecking but tended to exhibit more horizontal push movements towards the apparatus. Note that ravens may show horizontal head movements during foraging, but typically for wiping/cleaning their beak and not for extracting food.

Our results indicate that young ravens are capable of simple forms of action imitation, corroborating similar findings from other birds such as pigeons (Klein & Zentall, 2003), quails (Akins & Zentall, 1996), starlings, *Sturnus vulgaris* (Campbell, Heyes, & Goldsmith, 1999), budgerigars, *Melospittacus undulatus* (Mui, Haselgrove, Pearce, & Heyes, 2008) and tits (Aplin et al., 2015). In particular the ravens' tendency to copy horizontal movements is in

line with the idea of a specific category of action imitation, that is, contextual imitation (Hoppitt & Laland, 2008), as ravens seemingly learned to execute a behaviour that is within the species' repertoire (e.g. for cleaning the beak) in a novel context, extracting food. Whether their imitative skills are based on 'blindly mimicking' other individuals' actions (as demonstrated in pigeons, McGregor, Saggerson, Pearce, & Heyes, 2006) or guided by observational learning about outcomes needs to be addressed in future studies.

Note that in contrast to most other avian imitation studies, ravens were not exposed to a trained conspecific, but had to copy the motor patterns of a human experimenter. Copying of human behaviour has so far only been reported for chimpanzees (Custance, Whiten, & Bard, 1995; Tomasello, Savage-Rumbaugh, et al., 1993), orang-utans, *Pongo pygmaeus* (Call, 2001), bottlenose dolphins, *Tursiops truncatus* (Jaakkola, Guarino, Rodriguez, & Hecksher, 2013; Tayler & Saayman, 1973), pet dogs, *Canis lupus familiaris* (Range, Huber, & Heyes, 2011; Topál, Byrne, Miklósi, & Csányi, 2006), and a grey parrot, *Psittacus erithacus* (Moore, 1992). Such an ability is striking with respect to the 'correspondence problem' (Nehaniv & Dautenhahn, 2002), as what an animal sees being executed (in this case, hand movements) is very different to the action it subsequently performs itself (in this case, head movement). However, regardless of the topography of the actions, that is, how given body parts move, the effects on the environment are similar (in this case, lids are slid open). This functional matching of observed behaviours with different body parts leads to interesting questions at the neuronal level, as these results may be difficult to explain solely on the basis of mirror neurons (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

Several of the above-mentioned imitation studies involved animals that had been raised and/or kept in close contact with humans and thus may be regarded as 'enculturated' (Tomasello, Savage-Rumbaugh, et al., 1993). In great apes, for example, extensive human training and human contact has been identified as a critical driver of imitation (Call, 2001); consequently, it has been suggested that the performance of these 'enculturated' subjects is not representative of great apes in general (Henrich & Tennie, 2017; but see Byrne & Russon, 1998 for studies under naturalistic conditions). The same argument may apply to species of other taxonomic groups, whereby different individuals and/or species may experience different degrees of 'enculturation' and its effects. Our ravens received intensive human care as chicks which certainly affected their behaviour towards humans later in life. Yet, we suggest that their upbringing concerned mainly their behaviour



**Figure 3.** Posterior distributions based on 90 000 draws from the joint posterior distribution of each model's parameters are shown for (a) vertical and (b) horizontal push movements over the three trials combined. Birds in group A saw a human make vertical hand movements, birds in group B saw a human make horizontal hand movements and birds in group C were not shown any hand movements.

towards humans (e.g. the amount of attention they paid to humans) rather than their cognitive abilities. The fact that budgerigars and pigeons kept under laboratory conditions can discriminate natural movements of humans and dogs (walking forwards versus backwards) indicates that enculturation is not necessary for animals to discriminate between human dynamic cues (Mui et al., 2007).

Could any social learning mechanism other than imitation account for the behavioural biases towards the method demonstrated by the human model? In the study by Fritz and Kotrschal (1999), it was difficult to distinguish between stimulus enhancement and action imitation because the two actions were executed at two different locations of the apparatus. Here, we controlled for this possibility by directing all demonstrated actions towards the same location at the apparatus. Furthermore, we controlled for the possibility that birds associate the direction of lid movements with particular features in the environment by turning the box by 90° before testing (compare Heyes, 1994). It might be possible that ravens tried to emulate the end or outcome of an action sequence (Whiten et al., 2004), but in this case birds of the two test groups should not have differed in their directions of head movements. Because a human model was used, motivational factors in terms of biases towards a certain model should also be more comparable between the groups than if there had been two or more conspecific models used with different social relationships to the observers (Coussi-Korbel & Frigaszy, 1995; Laland, 2004). We therefore conclude that the current results can be best explained by a form of action imitation. Note that this interpretation refers solely to the capacity of copying other individuals' behaviour (Box, 1984; Heyes, 1994) and does not make any assumptions about the ravens' intentionality of copying.

Against our expectation, individuals from the two test groups did not always open the box more quickly or successfully than birds from the control group. This finding indicates that although imitation alters the ravens' propensity to perform particular behaviours, it does not necessarily affect their efficiency in solving the task, at least not in our set-up. Future studies should thus address not only whether imitation can be used but also under which conditions it pays off, relative to other social learning mechanisms. We propose that ravens, and possibly other corvids, employ imitation in situations when it is crucial to learn about using certain types of behaviour. Young ravens might apply this skill during extractive foraging, when they are confronted with novel problems (as in our current study); older birds that already have ample experience with foraging techniques might employ it in other domains, such as in self-aggrandizing or joint displays in the context of pair formation and during play. Another interesting question for future studies concerns the ravens' capacity to selectively imitate (Buttelmann, Zmyj, Daum, & Carpenter, 2013; Range et al., 2007). So far, we only know that ravens are highly selective in choosing whom to learn from, both in dyadic and in group settings (Kulahci et al., 2016; Schwab, Bugnyar, Schloegl, et al., 2008). Future studies need to test whether they 'blindly' mimic every behaviour demonstrated or selectively copy only those components that 'make sense' in a given situation (Gergely, Bekkering, & Király, 2002). Using a human experimenter as demonstrator seems to be a promising way to proceed along these lines.

Taken together, with the present study we have shown an information transfer via social learning between a human demonstrator and observing ravens. Our controlled set-up and specificities of the results (i.e. the matching of movement directions) allows us to conclude that action imitation is the underlying social learning mechanism. As the actions in question were probably already in the species' repertoire, we argue that the imitation is contextual, that is, the ravens have learned to perform a given behaviour in a novel context. Birds in the imitation groups were not quicker in solving

the task than birds in the control group, raising the question under which conditions imitation pays off.

## Data Availability

Data and R code for the Bayesian analysis are available at <https://osf.io/wqrze/>.

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## Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2020.03.007>.

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