Negative emotional contagion and cognitive bias in common ravens (*Corvus corax*)

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Emotional contagion is described as an emotional state matching between subjects, and has been suggested to facilitate communication and coordination in complex social groups. Empirical studies typically focus on the measurement of behavioral contagion and emotional arousal, yet, while highly important, such an approach often disregards an additional evaluation of the underlying emotional valence. Here, we studied emotional contagion in ravens by applying a judgment bias paradigm to assess emotional valence. We experimentally manipulated positive and negative affective states in demonstrator ravens, to which they responded with increased attention and interest in the positive condition, as well as increased redirected behavior and a left-eye lateralization in the negative condition. During this emotion manipulation, another raven observed the demonstrator's behavior, and we used a bias paradigm to assess the emotional valence of the observer to determine whether emotional contagion had occurred. Observers showed a pessimism bias toward the presented ambiguous stimuli after perceiving demonstrators in a negative state, indicating emotional state matching based on the demonstrators' behavioral cues and confirming our prediction of negative emotional contagion. We did not find any judgment bias in the positive condition. This result critically expands upon observational studies of contagious play in ravens, providing experimental evidence that emotional contagion is present not only in mammalian but also in avian species. Importantly, this finding also acts as a stepping stone toward understanding the evolution of empathy, as this essential social skill may have emerged across these taxa in response to similar socioecological challenges.

emotional contagion | avian empathy | animal emotion | cognitive bias paradigm

Emotions are functionally adaptive states consisting of coordinated sets of physiological, cognitive, and behavioral changes. These changes occur in response to fitness-relevant stimuli to facilitate decision making and resource allocation (1–3). Although research in humans often focuses on subjective states, emotions are multicomponential phenomena that manifest through various observable aspects of the phenotype. This facilitates comparative research on the biology of emotions in nonhuman animals (4, 5). Emotional contagion in particular, which refers to emotional state matching between individuals (6), is a powerful mechanism for information sharing (7) and, as a consequence, an increased defense against predation (8) and the facilitation of group living (9). It has been proposed as one of the core elements of empathy (6, 10), and has been demonstrated in a variety of species (11–14). Noticeably, the majority of emotional contagion (and empathy) research focuses on distress and negative emotions (15), which is most likely due to a taxonomically widespread attention bias for negative information (16). Another limitation is that reports on emotional contagion are frequently linked to and inferred from behavioral mimicry (i.e., behavioral contagion) (17). Empirically, however, there is no conclusive support for this relationship or its directionality (18), as mimicry of a specific behavior does not necessarily imply

contagion of a corresponding emotion (19). Likewise, while behavioral and physiological measures form meaningful indicators of an animal's emotional state, and thus potential contagion, these components largely assess emotional arousal (20). However, an emotion is defined by both its arousal level and positive or negative valence (21). So, in contrast to measurements of arousal, the quantification of emotional valence often remains unexplored (4, 22, 23). For this reason, arousal changes, such as fluctuations in heart rate (24), may not necessarily be accompanied by a consistent change in valence, and thus may not be fully informative about the specific quality or even mere presence of an emotional response.

Changes in emotional states correlate with changes in behavioral, physiological, and cognitive components (2, 25). Human emotions often entail an additional subjective “feeling” component, which is currently considered challenging or even impossible to directly measure in nonhuman animals (26). Accordingly, the majority of animal research has focused on objectively measurable components to establish the presence and type of an emotional state (27). Locomotor activity, for instance, is one of the most direct, noninvasive behavioral measures for emotional expressions (25), that is, whether animals approach or avoid a stimulus may inform us on the rewarding or nonrewarding qualities of that stimulus, therefore assuming its positive or negative characteristics. However, animals tend to show consistent variation in how they respond to environmental manipulations (i.e.,

Significance

To successfully and efficiently live in social groups, we need information about each other's emotions. Emotional contagion has been suggested to facilitate such information transmission, yet it remains difficult to measure this in animals. Previous research has often focused on overt behavior but lacked additional methods for investigating emotional valence. This study provides a solution by integrating data on behavior and responses to a cognitive bias test, which is designed to infer a subject's underlying emotional state. We demonstrate that after witnessing a conspecific in a negative state, ravens perform in a negatively biased manner on a judgment task. Our findings thus suggest negative emotional contagion in ravens, and in turn advance our understanding of the evolution of empathy.

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personality), such that individuals may differ in their vigilance toward threatening stimuli (28), motivation to explore novel contexts, or activity levels more generally (29). Hence, by measuring merely one (behavioral) component instead of a larger set, we narrow and potentially confound our interpretations of the particular emotional state (26). For this reason, it is valuable to expand efforts to investigate a collection of multiple components (30, 31), ranging from behaviors such as redirected behavior (32), visual orientation (33), activity level (34), or body posture (30), to vocalizations (35) and, if possible, measurements of physiological parameters (36).

Recent studies have also focused on the cognitive component of emotions through means of the cognitive bias paradigm (37). Human psychology research has shown that, for example, more anxious people make more pessimistic judgments when appraising ambiguous stimuli (26, 38), while humans in a positive mood make more optimistic judgments (39, 40). Correspondingly, the rationale of the cognitive bias paradigm is that biases found in an animal's cognitive performance serve as an objective proxy to measure the positive or negative valence of its affective states (37). The most popular application of this paradigm is the judgment bias task (41, 42). Here, animals are first trained on a discrimination task with distinct positive and negative stimuli, followed by the introduction of a novel, ambiguous stimulus. The bias hypothesis predicts that animals in a negative affective state should judge the new ambiguous stimulus more similar to a negative stimulus (i.e., display a pessimism bias suggestive of expecting punishment or no reward), while animals in a positive state should judge the ambiguous stimulus as more similar to a positive one (i.e., display optimism bias suggesting the expectation of a reward) (37). This paradigm has been repeatedly confirmed as a promising and noninvasive solution to assess emotional valence in animals (26, 37). For example, rats living in unpredictable housing showed a pessimism bias (43), while pigs housed in enriched environments demonstrated an optimism bias (44), and the manipulation of both anxiety- and depression-like states in chicks resulted in an enhanced pessimism bias and reduced optimism bias, respectively (45). Moreover, the bias paradigm has been successfully employed in a variety of species (41), including invertebrates (31, 46, 47). Finally, this paradigm has the potential for identifying less overtly expressed states, and thus phenomena that are not easily detectable by means of behavioral measures. The latter might be of particular importance for animals using bystander information, for example in the form of emotional contagion. To our knowledge, the bias paradigm has so far been used for assessing the emotional state of animals that experience a particular treatment, but not for assessing the emotional state of bystanders that merely observe the others' response to that treatment.

Here we apply a judgment bias paradigm together with behavioral measures to identify emotional contagion in common ravens. These birds are renowned for using social information (48–51) and displaying emotional sensitivity through behaviors such as consolation (52); furthermore, some of the best evidence for emotional contagion comes from birds (12, 20), including observations of physiological resonance in zebra finches (36) and play contagion in common ravens (53) and kea parrots (54). Experimentally disentangling the effects of behavioral contagion and arousal changes from the concept of emotional contagion is an important next step in our understanding of this phenomenon in birds, which will decisively extend our knowledge of the evolution of this core building block of empathy.

Results and Discussion

Emotional Expressions in Demonstrators. Ravens participated in dyads, with one subject being a demonstrator and one an observer. We experimentally manipulated the affective state of demonstrator birds by presenting two food items of different quality (phase 1), then taking one item away (phase 2), followed by handling the remaining item (phase 3) (*Methods* and Fig. 1).

In the positive condition, the unappealing food item was removed and the appealing item remained visible to the demonstrator, suggesting the induction of reward anticipation. In the negative condition, the appealing food item was taken away and the unappealing item remained visible, suggesting potential “frustration” in the demonstrator instead of reward anticipation. In the positive condition, we expected animals to look more toward the food item and locate themselves more in front of the food presentation, whereas in the negative condition, we expected the animals to lose interest in the stimulus presentation and show more redirected behavior toward the environment, such as digging in the sand. For exploratory purposes, we also coded for either left- or right-eye use when inspecting the food items (*SI Appendix, Table S1*).

As predicted, the demonstrator's behavioral expressions differed significantly between the two conditions (Fig. 2). Moreover, we were able to capture a change in the demonstrator's behavior across two phases, namely between the first 30 s of presenting the two items (i.e., phase 1) and the final 30 s of handling the remaining preferred or unpreferred food item (i.e., phase 3) (*Methods*). Across phase 1 and phase 3 of the positive condition, ravens showed less locomotion (difference within condition: $\beta = -1.31$, $z = -4.37$, $P = 0.01$; difference in phase 3 between condition: $\beta = -0.79$, $z = -2.48$, $P = 0.01$), spent more time looking at and being in front of the preferable food item (within condition: $\beta = 3.17$, $z = 5.16$, $P = 0.01$; between condition: $\beta = 2.27$, $z = 3.69$, $P = 0.01$), while also displaying more arousal (i.e., increase in body and head movements in front of the food item) (within condition: $\beta = 0.24$, $z = 2.26$, $P = 0.03$; between condition: $\beta = 0.66$, $z = 5.27$, $P = 0.01$). This implies heightened attention, and suggests that the ravens indeed anticipated receiving this food item (34, 55). In the negative condition, ravens showed less locomotion around the experimental room (within condition: $\beta = -0.50$, $z = -2.19$, $P = 0.03$) but remained more active than in the positive condition, while displaying an increase in redirected behavior toward the environment ($\beta = 1.76$, $z = 3.63$, $P = 0.01$). Redirected behavior may occur in situations when an expected reward is omitted or is spatially restricted and reflects frustration about unrewarded outcomes (32, 56). However, when periodically returning to inspect the remaining unappealing food item, ravens showed less body and head movements when standing in front of the food item ($\beta = -0.26$, $z = -2.04$, $P = 0.03$), as well as a significant increase in left-eye use ($\beta = 1.00$, $z = 2.50$, $P = 0.03$), implying a

Fig. 1. Experimental procedure. The procedure consists chronologically of a discrimination training before the experiment (1), a premanipulation cognitive bias test (2), a positive or negative emotion manipulation of the demonstrator (3), and a postmanipulation bias test (4).

Fig. 2. Demonstrator behavior. Predicted behavioral responses (mean $\pm$ SE) for an average demonstrator before and after the positive and negative conditions, including locomotion (A), time spent in front of the food items (B), head and body movements (C), redirected behavior (D), and left-eye use upon inspecting the food items (E). Note that A, C, and D are count frequencies, while B and E are duration proportions (s). Planned comparisons were conducted within conditions from phase 1 to phase 3 and between positive and negative conditions for phase 3 (see *SI Appendix, Table S2* for further details). * $P < 0.05$; ** $P \leq 0.01$.

negative emotional lateralization and providing support for the emotional valence hypothesis [which suggests that the right hemisphere is dominant for processing negative stimuli (57)]. We did not find a significant difference between left-eye use across the positive and negative conditions during phase 3, which is potentially a consequence of a higher baseline proportion of left-eye use in phase 1 of the positive condition (Fig. 2). Nevertheless, the significant increase in left-eye use from phase 1 to phase 3 within the negative condition suggests an important behavioral change according to that condition.

The combination of different behavioral variables in the positive condition indicated attention and interest for the manipulation. In addition, less attention and an increase in redirected behavior in only the negative condition suggested a meaningful difference in emotional expressions in demonstrators. For this distinction between conditions, the difference in saliency between the loss of preferred food and the dislike of unpreferred food was irrelevant and, moreover, none of the demonstrators' behaviors were specifically indicative of food presence or loss, respectively (58, 59). Instead, the combination of certain behaviors and the frequency of their expression seemed to reflect the predicted differences in the demonstrators' affective state. To further support this interpretation, we aimed to independently assess the valence of our manipulation by means of a judgment bias test in the demonstrator birds. However, due to unanticipated procedural constraints, the obtained data were unsuitable for interpretation (*SI Appendix, Results*).

Emotional Contagion. The demonstrator's behavioral expressions to the different manipulations were witnessed by an observer raven present in an adjacent room (Fig. 1). On average, observers were visually oriented toward the demonstrator for 74 to 77% (~23 to 27 s/30 s) of the time during the positive and negative manipulations, respectively, suggesting that observers were attentive to the demonstrators' behavioral expressions. Importantly, the observer was naïve about the food items presented to the demonstrator and the handling of these items by an experimenter. By means of a judgment bias paradigm, we investigated whether the observer's affective state would change according to the demonstrator's state. We first assessed the efficacy of the discrimination training (*Methods*), for which we found that, across box locations, observers showed significantly

shorter peck latencies at the positive location ($\beta = -0.67$, $z = -3.67$, $P = 0.01$) and significantly longer latencies at the negative location ($\beta = 1.23$, $z = 6.95$, $P = 0.01$). This indicates that the ravens effectively learned to discriminate between positive and negative locations and their respective reward value, and that our training was successful. Additionally, during testing, nonsignificant differences were observed before and after emotion manipulation at the trained locations, suggesting that the effect of our training and the motivation to participate were sustained throughout the duration of the experiment (positive condition: positive location: $\beta = 0.27$, $z = 1.17$, $P = 0.26$; negative location: $\beta = 0.03$, $z = 0.14$, $P = 0.90$; negative condition: positive location: $\beta = 0.18$, $z = 0.72$, $P = 0.50$; negative location: $\beta = 0.11$, $z = 0.44$, $P = 0.67$).

Essential to our central hypothesis, we predicted that, compared with a bias test taken before the experimental manipulation, the observers' responses after manipulation would become more pessimistic or optimistic depending on whether they had experienced the demonstrator in the negative or positive condition, respectively. Such pessimistic or optimistic tendencies were quantified by measuring latency to approach a box placed on an ambiguous location, in comparison with the latencies of approaching trained positive and negative locations. Our analysis shows that observers significantly increased their latency to peck the ambiguous location after witnessing the demonstrator in the negative condition (within-condition pre- and postmanipulation response: $\beta = 0.84$, $z = 3.22$, $P = 0.02$; between-condition postmanipulation response: $\beta = 0.76$, $z = 2.91$, $P = 0.01$), confirming the predicted pessimism bias (Fig. 3). In contrast, we did not observe the expected decrease in observer response latency after the positive manipulation (within condition: $\beta = 0.40$, $z = 1.53$, $P = 0.16$). Notably, in our study procedure, we opted to compare pre- and postmanipulation bias results, instead of using an additional control session or merely relying on postmanipulation results. The premanipulation results are considered as a baseline to which we compared the postmanipulation results within each condition, allowing us to exclude any general mood effect that perhaps already existed in our subjects beforehand. Both our within- and between-condition comparisons confirm our negative manipulation predictions, and demonstrated that the postmanipulation test was able to pick up the negative manipulation effect. Importantly, the finding of a nonsignificant, small difference in pecking latency across ambiguous trials ($\beta = 0.01$, $SE = 0.01$, $z = 1.11$, $P = 0.30$) suggested that the response to this location was not detectably extinguished due to lack of reinforcement (*SI Appendix, Results*). The observers' distinct responses in the cognitive bias test after the negative manipulation, compared with the positive, indicate that the observer ravens were influenced by the demonstrators' behaviors and

Fig. 3. Observer cognitive bias test. Predicted latencies to peck (mean $\pm$ SE) for an average observer raven in an average dyad at each location across the positive and negative conditions. We conducted planned comparisons of observer response latencies at each location before (full line) and after (dotted line) the emotion manipulations (see *SI Appendix, Table S3* for further details). * $P \leq 0.05$.

affective states. Observers did not perform similar behaviors themselves but showed a pessimistic judgment of an ambiguous stimulus. Hence, we find support for negative emotional contagion, whereas our results remain inconclusive about positive emotional contagion.

Our study experimentally disentangles effects of behavioral contagion and arousal changes from the concept of emotional contagion, by taking the valence element of an emotional state into account. Behavioral contagion and arousal are frequently used as evidence for emotional contagion. However, though they may mechanistically underpin emotional contagion, they are distinct phenomena (20). For instance, examples of behavioral contagion such as yawn or play contagion do not necessarily disclose information on the underlying affective state (19, 60). Similarly, different emotions may show similar physiological profiles (26), and thus variations in arousal levels such as a decrease in body temperature may be observed in both positively and negatively valenced contexts (61). Therefore, to exclude these alternative explanations and overcome the limitations of previous studies, researchers need to employ methodologies focusing on the measurement of different modalities instead of a single measure of emotion (25, 31). The cognitive bias test is a favorable approach to tap into the multi-componential nature of emotions, as it not only allows us to investigate an additional cognitive element but also provides the opportunity to differentiate between changes in valence. Here we used two different components to assess potential state matching and found an alignment between the expressions of these two components; in the negative condition, the avoidance behavior shown by the demonstrator was matched with a pessimistic judgment in the observer. These results are consistent with the interpretation that an underlying negative affective state was transferred to the observer, subsequently biasing their response in the judgment test. We consider this convergence to suggest emotional contagion between the demonstrator and the observer.

The observers' pessimistic response to seeing others in a negative state indicates that the cognitive bias paradigm is a useful method to detect changes in the affective states of ravens. Our study design meets two imperative bias paradigm requirements, which are relevant in supporting our conclusions about the pessimism bias and excluding alternative explanations (42). First, we found the expected training effect, suggesting that the ravens successfully learned the positive and negative discrimination, and their performance before and after manipulations remained consistent. This finding is important to exclude potential effects of "boredom": Observer ravens could have become disinterested in the demonstrator's situation, which could carry over to the bias task, resulting in a drop in performance and, potentially, a "pessimism" bias because of boredom rather than emotional contagion. However, we see a consistent pattern of motivation for both conditions and both the negative and positive trials, which allows us to rule out this explanation. Second, our data show the absence of a clear learning effect across unreinforced ambiguous trials, indicating that the ravens' responses did not decrease due to the lack of reward in these trials. This suggests that ravens treated these trials as truly ambiguous throughout the whole study, and that their responses were thus based on an evaluation of the anticipated reward value. When trials remain unreinforced, animals may become less motivated to perform, which could result in the observation of an apparent pessimism bias. The absence of a learning effect is thus relevant to our interpretation, as it provides evidence that such learning is not the underlying reason for the observed pessimism bias. The observers' response to ambiguous stimuli in the negative condition, and the significant differences for both within- and between-condition comparisons, emphasizes that the negative manipulation effect on the demonstrator was in turn picked up by the bias test for the observer. This verifies that the cognitive bias paradigm is sensitive not only to long-term manipulations of affective states (i.e., moods), for example due to housing conditions (44), but also to short-term manipulations (e.g., 30 s in ref. 62). Furthermore, our study

demonstrates that subjects do not have to be involved in a social interaction themselves but that merely witnessing a conspecific's response to a mild negative manipulation is sufficient to elicit an effect. Notably, the demonstrators showed numerous behavioral expressions, but they did not give any food-specific signals such as food-associated calls or cues toward food caching. Although parts of the redirected behavior observed in the demonstrators consisted of digging in gravel substrate, these sweep-like beak motions clearly differ from caching (whereby an item is inserted in the substrate by means of vertical head movements). Hence, it seems unlikely that observers detected the cause of the demonstrators' negative state, namely change in food availability, and more likely that they responded to the "negativity" of the situation experienced by the demonstrator. Our interpretation of negative emotional contagion is therefore supported by the found pessimism bias in the observer, which is confirmed by both between- and within-condition comparisons, the presence of a consistent discrimination training effect, and the absence of a learning effect for the unrewarded stimuli.

While our results confirm contagion of a relatively mild negative affective state, our unclear findings for potential positive contagion might be explained by the following factors. Negative emotions may be easier to experimentally induce than positive emotions, and they may be more salient in their expression than positive emotions (11, 15, 62). Moreover, animals (as well as humans) attend more to negative than positive information in their environment (16, 33). Accordingly, the demonstrators' reduction in locomotion and shift in visual attention in the positive condition could have been less informative for observers than the demonstrators' redirected behavior and increased locomotion displayed in the negative condition. Alternatively, the affective states of both birds may not have matched in the positive condition. Upon seeing demonstrators in a positive state, observers might have experienced negativity due to being unable to access the source of excitement themselves. Although we cannot exclude this possibility, we aimed to reduce such an effect by testing birds in highly affiliated dyads only, so that observers might have anticipated getting (bits of) the reward shared by their affiliate after the experiment. In the same vein, demonstrators may have initially experienced an anticipation of reward, but the positive effect was short and partially masked by our aforementioned procedural constraints. Note that demonstrators never received the presented food item for consumption before the postmanipulation bias test was performed (*SI Appendix, Results*). This procedure might have elicited additional frustration in the demonstrators for not receiving their preferred item and consequently eliminated any potentially present positive state. If observers picked up on this change in the demonstrators' state, this would explain the observers' "neutral" responses in the cognitive bias test following the positive condition. In the negative condition, the affective state of the demonstrators likely remained negative throughout the procedure, facilitating the detected effect in the observers.

Overall, by combining an emotional contagion setup with a cognitive bias paradigm, our study contributes to the investigation of different emotion components. So far, animal emotional contagion studies have depended solely on behavioral parameters (33, 53, 54) or a combination of behavioral and physiological measures (11, 12). Future research should therefore consider using a cognitive bias test as an additional tool to behavioral and physiological methods for measuring the valence underlying emotional contagion. This will allow us to construct a full picture of an animal's emotional state in an empathy setting; moreover, it enables us to measure emotional contagion in situations that are characterized by low or no direct behavioral matching, such as when using bystander vocalizations (i.e., observing others or eavesdropping on others' communicative interactions) (33, 63). Unfortunately, we were unable to interpret the cognitive bias results of demonstrators due to our design decisions. Future work should address these limitations to further explore the application

of the bias paradigm in assessing emotional state matching and strengthening interpretations of behavioral findings. Current research on (avian) emotions is still in its early developmental stages, and thus, although we may classify the demonstrator's situation as negative or frustrating, we do not have direct indicators of a specific emotional state. Some major contemporary discussions in comparative affective science concern what we label in animals as emotions, whether animals truly feel and experience such emotions, and what the best objective measures are to assess these questions (46, 64). This may be seen as a limitation when concluding emotional contagion of a specific emotion, in any species for that matter. However, the apparent disadvantage of having no verbal report, or direct measures of subjective feelings, prompts us to systematically and rigorously evaluate our observations in animals with the prevailing methods available. For this reason, given the current state of the art and theoretical consensus in animal emotion research, the componential approach proposed here offers the opportunity to accumulate information derived from various modalities. This accumulation may provide evidence of the convergence of congruent emotional components, such as the congruency found in our data between the demonstrators' behavior and the observers' pessimism bias, which supports our interpretation of converging emotional states. Future studies need to address whether the birds would react similarly to different negative situations (within and outside of a food context), and thus to valence in general compared with specific details of the context. Correspondingly, future studies should incorporate nonfood contexts for testing positive emotions. Note that early studies on social learning, for example observational conditioning in blackbirds, hint at an emotional transfer between individuals (65); yet such an explanation was nonexistent at the time, and it is unclear whether the observed learning implied an emotional response. Nonetheless, matching the other's emotional state is indeed a plausible mechanism for facilitating adaptive responses to various social situations requiring rapid information sharing, such as predator mobbing (65), foraging under risk (66), or conflict management (67). We are convinced that these topics would be highly relevant for future emotional contagion research.

Taken together, our study shows differences in the behavioral expression of demonstrator ravens that have been informed about the quality of hidden food items and, critically, a pessimistic response of naïve ravens in a cognitive bias test after they witnessed the informed conspecific in the negative condition. This finding provides experimental support for emotional contagion in ravens, which is in line with previous observations on corvid and parrot play (53, 54) and the claim that this fundamental component of empathy is present not only in mammalian but also in avian taxa (6). Previous research demonstrates that similarities in cognitive complexity between distantly related taxonomic groups, such as primates and corvids, are typically the result of convergent evolution (68, 69). Similar socioecological challenges may have therefore led to independent selection for emotional contagion in ravens and various mammalian species. Alternatively, given that primary emotions are localized in phylogenetically ancient brain structures (70), the underlying neural mechanisms of emotional contagion might be homologous in both mammals and birds. While answering this question is beyond the scope of our study, the present findings may act as a crucial stepping stone toward a better comparative understanding of complex social skills, such as empathy, and their evolution.

Methods

Study Animals and Housing. Eight common ravens (5 M, 3 F) participated in the study. All birds were individually marked and socially housed in a nonbreeder group at the Haidlhof Research Station (see *SI Appendix, Methods* for further details).

Ethical Note. The study followed Austrian law and local government guidelines, and the design was approved by the ethical board of the Behavioral Research Group at the Faculty of Life Sciences, University of Vienna (2018-004).

After the study, the ravens remained at the Haidlhof Research Station for further research projects.

Pilot and Habituation. Before the experiment, two pilot studies were conducted and a habituation period of 3 mo took place.

Cognitive Bias Paradigm: Discrimination Training. A wooden box was presented consecutively either on the left or right side of the animal. Only one side contained a reward (positive location), while the other side remained unrewarded (negative location). The criterion to pass was a minimum of 95% correct pecking on the positive location and 70% correct no pecking on the negative location, calculated over 3 consecutive days with 12 trials per session per d (*SI Appendix, Table S4*).

Cognitive Bias Paradigm: Testing. After successful training, the ravens were assessed on a bias test immediately before and after the emotion manipulation of the demonstrator. During this test, the box was consecutively presented on the trained positive and negative location, as well as on one new, ambiguous location. The maximum latency to peck was 3.5 s, and trial order presentation was semirandom.

Experimental Procedure. The study had a within-subject design. On each testing day, a dyad was called into the experimental compartment and given a cognitive bias test. Afterward, the demonstrator went into another compartment for either the positive or negative manipulation. The manipulation included a baseline of 30 s followed by a presentation of two different food items. The food items were out of view of the observer. After this presentation (phase 1, duration 30 s), one food item was taken away and the other remained visible (phase 2, duration 30 s). This was followed by an experimenter handling the remaining item (phase 3, duration 30 s). The experimenter held and moved the food item in the palm of the hand, between two fingers, broke the food into pieces, and lifted the pieces in the direction of the demonstrator. After the food handling, the demonstrator went back into the initial compartment and both birds underwent a postmanipulation cognitive bias test. At the end of the test, both birds were free to join their social group and the demonstrator was given the food item according to the emotion condition.

Video Coding. The experiment was recorded by four video cameras. All coding was done by the main author and a second, trained observer blind to the experimental hypotheses independently video-coded for 15% of the behavior and cognitive bias sessions. Interobserver reliability was found to be high across all parameters, intra-class correlation coefficient (3,1) range: 0.95–1.00.

Quantification and Statistical Analysis. We utilized generalized linear mixed models (GLMMs) for all analyses to account for repeated measurements within subjects and dyads, enhance statistical power, and avoid artificially reducing the variability in our dataset through aggregation (71). GLMMs were fit with the lme4 package (72) for the R 3.4.4 statistical environment (73). To ensure the robustness of the *P* values returned from these models, we implemented a parametric bootstrapping procedure.

Demonstrator Behavior Analysis. To assess the validity of our demonstrator emotion manipulations, we estimated behavioral variation in demonstrators both between and within the positive and negative conditions. We analyzed a subset of behaviors hypothesized to reflect components of arousal and valence, which are further described in our ethogram (*SI Appendix, Table S1*). In particular, we analyzed differences across phases 1 and 3 of the manipulation, as the latter phase was expected to elicit the strongest emotional response in the demonstrators.

Cognitive Bias Test Analysis. Considering that pecking occurred frequently across all conditions and latencies to peck exhibited more consistent differences, we utilized latencies to peck rather than peck/no peck responses for our primary analyses. To assess potential differences in subjects' reaction times across experimental conditions, GLMMs were specified with Gamma error distributions and log link functions appropriate for modeling proportional change in response latencies (74). We first assessed whether latency to peck at the ambiguous location increased across sessions due to the absence of reinforcement (75), and we determined the efficacy of our discrimination training. We then compared before and after manipulation latencies across all locations in each condition to test our main hypothesis. A likelihood ratio testing comparing this full model to a reduced model without the interactions among location and condition fixed effects for observers supported further consideration of the specific pairwise comparisons of interest, $\chi^2(6) = 22.84$, $P < 0.001$.

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