African grey parrots (Psittacus erithacus) use inference by exclusion to find hidden food

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Exclusion allows the detection of hidden food when confronted with the choice between an empty and a potentially baited food location. However, exclusion may be based on avoidance of the empty location without drawing inferences about the presence of the food in the baited location. So far, such inferences have been demonstrated in the great apes only: after seeing an experimenter eating one of two food types, which both had been hidden previously in two boxes, the apes were able to choose the box that still contained the other food type. African grey parrots are capable of exclusion, and we here assessed if they are capable of inference by exclusion. In our task, two different but equally preferred food items were hidden in full view of the birds under two opaque cups. Then, an experimenter secretly removed one food type from the two cups. The position that one of the two food items (the same as in the training) simultaneously on the movable platform and covered them with the two cups. Then, the experimenter could present the set-up out of their reach on the movable platform and could push it within their reach to allow them to choose.

(a) Pre-tests
(i) Choice training
This test was introduced to ensure that the birds were aware that they would have to make a choice. One piece of food (e.g. a seed or a piece of walnut, depending on known preferences of the birds) was placed on the movable platform and covered with an opaque cup. Simultaneously, the second cup was placed on the same platform at a distance of approximately 20 cm. Then, the platform was pushed forward to allow the bird to make a choice by touching a cup with its beak and retrieve a food item if correct. One session consisted of 10 trials; the training criterion to reach the next step was set to be correct on at least eight trials in two consecutive sessions.

(ii) Preference test
This test was introduced to ensure that the test performance would not be influenced by food preferences. We visibly placed two different food items (the same as in the training) simultaneously on the movable platform and covered with the two cups. Then, the bird was allowed to choose and retrieve one food item. The position of the food types was semi-randomized with the stipulation that the same food type was not placed on the same side for more than three consecutive trials. Two sessions were conducted, each consisting of 10 trials. Birds were advanced to the test if they did not show a preference for one food type, i.e. did not select one item more than 13 times over the two sessions.

(b) Tests
In the test phase, these two equally preferred food items were then placed simultaneously on the movable platform and covered with the two cups.

(i) Visible condition
Standing equidistantly between the cups and in full view of the subject, the experimenter looked straight ahead, lifted the left cup,
They are capable of true inferential reasoning. However, whereas several subjects solved the task when they could see the experimenter’s actions, only one individual was able to solve the task when it had to infer the outcome of the experimenter’s actions; still, these findings are in line with the inter-individual differences found in the great apes [2,11]. The birds were clearly motivated to obtain the reward, even though side biases occurred (see the electronic supplementary material). As they were highly attentive and never refrained from making a choice, we are confident that the success of only a single bird in the invisible condition is not owing to motivational issues; rather, it supports the assumption that these inference tasks are not trivial but cognitively demanding. Again, this result demonstrates substantial inter-individual differences in grey parrot cognitive performance [15] and that the level of performance depends on subtle differences between tasks [13,16].

Importantly, the successful bird significantly improved her performance only within the invisible condition. This improvement does not necessarily point to associative learning, as the bird performed at chance level in the association control. We suggest that the improvement is owing to the fact that the bird did not comprehend the relevance of the food presentation at the beginning of the test. This is plausible in particular because this bird

**Figure 1.** Percentage of correct choices in the visible and invisible condition. The horizontal line indicates the chance level. The box plot shows median and quartiles. The whiskers represent the 10% and 90% range, dots indicate the 5% and 95% range.

**Table 1.** Individual performances given as percentage of correct choices. Significant performances (according to a Binomial-test) are highlighted in bold (f = female; m = male).

<table>
<thead>
<tr>
<th>Individual</th>
<th>Sex</th>
<th>Visible</th>
<th>Invisible</th>
<th>Olfaction</th>
<th>Association</th>
</tr>
</thead>
<tbody>
<tr>
<td>Awisa</td>
<td>f</td>
<td>70.0</td>
<td>76.7</td>
<td>46.7</td>
<td>56.7</td>
</tr>
<tr>
<td>Cocohan</td>
<td>m</td>
<td>63.3</td>
<td>50.0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Kasi</td>
<td>f</td>
<td>63.3</td>
<td>60.0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Leo</td>
<td>m</td>
<td>60.0</td>
<td>53.3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Maja</td>
<td>f</td>
<td>76.7</td>
<td>46.7</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Moritz</td>
<td>m</td>
<td>73.3</td>
<td>63.3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Rocky</td>
<td>m</td>
<td>66.7</td>
<td>43.3</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

3. RESULTS

The parrots received 22.9 ± 4.9 (x ± s.d., range 20–30) trials of choice training. In the preference test, no bird chose one food type more than 12 times (binomial-tests: p ≥ 0.503). In the test, the birds significantly preferred the baited cup in the visible (one-sample t-test: n = 7, d.f. = 6, t = 7.772, p < 0.001), but not in the invisible condition (t = 1.430, p = 0.203; figure 1). On an individual level, all birds selected the baited cup in the majority of the trials in the visible condition and three birds were significantly above chance level (p ≤ 0.043; table 1 and the electronic supplementary material, results). In the invisible condition, one out of seven birds was significantly above chance (binomial-test: p = 0.005; all others: p ≥ 0.200; table 1). The successful bird (a female of approx. 13 years) chose at chance level in the olfaction and in the association control (binomial-test: p = 0.856 in both cases). When comparing her performance in the first and last 15 trials, we found no difference in the visible condition (McNemar-test: n = 15, p > 0.999) or in the olfaction (p = 0.625) and association control (p = 0.508), but a significant improvement in the invisible condition (p = 0.016).

4. DISCUSSION

Our study shows that African grey parrots can use partial information about the removed food item not only to choose by exclusion based on avoidance, but that
was first tested in the invisible condition. Probably, the bird needed a few trials to become acquainted with the test. Thus, we suggest that this bird’s performance was not based on learning instead of reasoning, but rather that the bird learned to reason about the experimenter’s action to solve the task.

The experiments comply with Austrian law.

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