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Mind the gap: means–end discrimination by pigeons

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Four experiments examined the discrimination performance of four pigeons in two means–end tasks. The pigeons were required to discriminate between two ribbon/food dish assemblies in a simultaneous discrimination. In the connected condition, the ribbon was attached to an out-of-reach food dish, allowing it to be retrieved by the pigeon pulling it with its beak. In the unconnected condition, the ribbon was unattached to the dish, preventing it from being used to retrieve the food. In experiment 1, the pigeons learned this means–end task in fewer than 160 trials. Experiment 2 established that this discrimination was controlled by the gap between the ribbon and dish, and, to a limited extent, by the ribbon's colour. Experiment 3 showed no transfer of this prior means–end training to a second means–end task using a different physical arrangement of 'connectedness'. Experiment 4 revealed that control of this second task was also related to the perceptual features of the gap between the ribbons. The results indicate that the pigeons did not comprehend the conceptual nature of connectedness across these means–end tasks, but did successfully learn each discrimination based on its relevant perceptual features.

Human and nonhuman animals regularly encounter problems requiring goal-directed behaviour. Some of these require completing various subgoals before the final goal can be reached. The ability to have a generalized understanding of the means to such ends would be valuable for any organism. With the development of fire maintenance and tool use, for example, understanding such means–end relations was certainly an important step in hominid evolution. The conceptual capacity to use and understand tools as a general class dramatically altered hominid behaviour and the subsequent trajectory of its biological and cultural evolution.

Piaget (1954) was among the first to appreciate these issues in the understanding of human development. More recently, to understand the evolution, biological distribution, and mechanisms of this capacity, increased attention has been paid to examining how nonhuman primates may perceive and conceptualize various kinds of means–end relations (e.g. Anderson 1993; Visalberghi & Limongelli 1994; Hauser et al. 1999; Povinelli 2000; Kralik & Hauser 2002; Fujita et al. 2003). These analyses have focused on a variety of tasks ranging from using tools to obtain food (Anderson 1993; Visalberghi & Limongelli 1994; Povinelli 2000; Fujita et al. 2003; Nakamichi 2004) to problems involving the physics of 'connectedness' and 'support' (in nonhumans: Hauser et al. 1999; Povinelli 2000; Kralik & Hauser 2002; in humans: Willats 1999).

In the domain of 'connectedness', Hauser and his colleagues tested cottontop tamarins, *Saguinus oedipus*, in a series of choice tasks in which the monkeys had to learn various means–end relations (Hauser et al. 1999, 2002; Kralik & Hauser 2002). These choice discriminations typically required the animals to recognize how out-of-reach food could be obtained correctly within the limits of various physical situations. In simultaneous discriminations involving the idea of support, food was placed directly on a cloth that the animal could pull in and retrieve or placed off to the side, in which case pulling on the cloth would not retrieve the food. In a second simultaneous discrimination testing the idea of 'connectedness', one cloth was again continuous in nature, allowing the animal to retrieve the food, while the adjacent cloth was cut in two, creating a physical gap that prevented the cloth from functioning as a means to retrieve the food (Hauser et al. 1999). In each case, the food was out of reach, so the tamarins needed to recognize which of these physical arrangements would yield reward. After learning the discrimination, the tamarins were then tested with a variety of altered arrangements of the situations (i.e. changes in colour, shape of cloth, gap size, cloth length). For the

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most part, the animals transferred quickly to these altered conditions, with changes in features relevant to the discrimination affecting behaviour more than changes in irrelevant features. Hauser concluded that the tamarins solved these tasks by understanding the abstract means–end relations (i.e. support, connectedness) mediated by the functionally relevant properties of their physical arrangement.

Povinelli (2000) questioned this claim, suggesting instead that primates only learn about the perceptual features of these types of discriminations rather than about any deeper causal understanding of mean–ends relations. That is, the animals were learning only how to retrieve the food, based on the perceptually salient features of the task (continuous nature of the cloth; gap size or placement). As such, the observed transfer across conditions in Hauser et al.'s (1999) study reflects the direct generalization of what was learned about these perceptual features rather than any reasoning about means–end relations. Accompanying experiments testing chimpanzees, *Pan troglodytes*, in various support and connection problems supported Povinelli's (2000) perceptual interpretation.

The purpose of the present study was to extend the comparative study of means–end discriminations to a nonprimate. Birds are interesting to compare with mammals because of their status as the other major class of highly active, diurnal and intelligent occupants of this planet (Cook 2001). In addition, a number of species of birds have shown the potential for using tools as a means to obtain food both in the wild and in captivity (Millikan & Bowman 1967; Aumann 1990; Hunt 1996; Tebbich et al. 2001; Chappell & Kacelnik 2002; Rutledge & Hunt 2004). Identifying the necessary conditions and mechanisms that support the formation of such means–end behaviour across different taxa and species is clearly an important question.

In the present study, we studied how the widely investigated pigeon, *Columba livia*, behaves in one type of means–end test. We tested four pigeons in a modified analogue of Hauser et al.'s (1999) connected/unconnected food retrieval task. The pigeons were faced with two dishes full of grain placed out of direct reach (Figs 1, 2). Selecting and pulling on the ribbon connected to the food dish could then be used to retrieve one of the dishes, but pulling on the unconnected ribbon would fail to retrieve its associated food cup. Using this task, our experiments had three aims. First, to determine whether pigeons could even learn this type of means–end discrimination (experiment 1). Second, if they did, would this learning transfer to another task with a similar means–end relation but a different physical arrangement of the components (experiment 3)? Finally, we wanted to identify the features of the task controlling any established discriminative behaviour (experiments 2, 4). Taken together, these experiments can reveal whether any learned discrimination was mediated by a conceptual understanding of the physical relations or guided by a perceptual analysis of the task's relevant features. We found that pigeons can indeed learn to perform different types of means–end tasks, similar to primates, but they do so based on the specific perceptual features of each task.

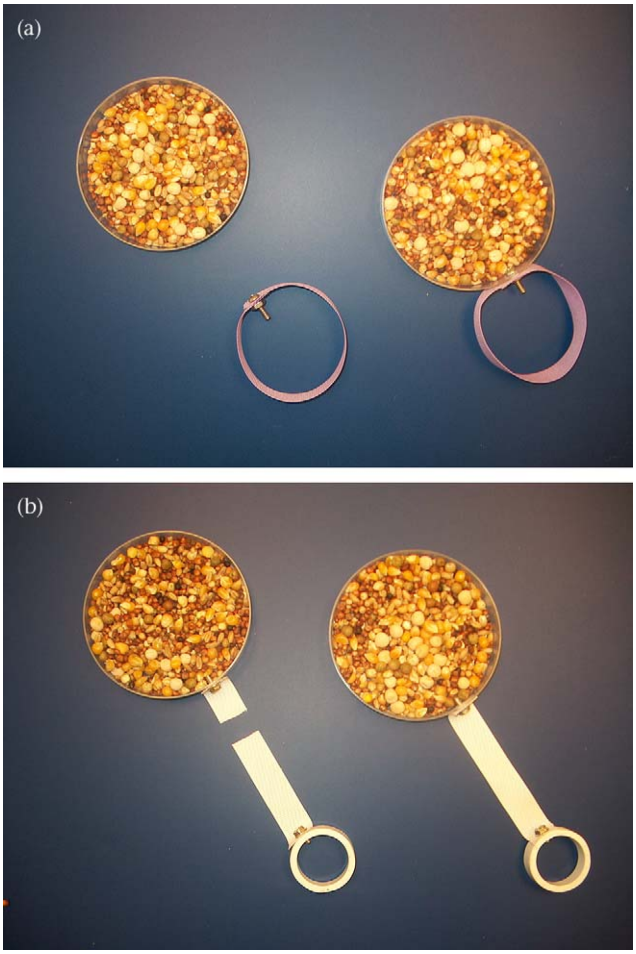

Figure 1. Examples of the means–end tasks used in (a) experiments 1 and 2 and (b) experiments 3 and 4.

EXPERIMENT 1: ACQUISITION

Methods

Subjects

Four male White Carneaux pigeons were tested. Each had prior testing experience in computerized operant chambers testing visual discriminations unrelated to the current task. They were maintained at 80–85% of their free-feeding weight and had free access to water and grit.

Apparatus

The plywood test chamber was 32 × 40 × 42 cm (l × w × h) and painted matte black. A transparent Plexiglas screen formed the front wall of the chamber. Two square openings (9 × 9 cm) in this panel allowed the pigeons access to a presentation platform (40 × 48 cm) attached to the front of the chamber. All test conditions were presented on this platform. A vertical piece of thin Plexiglas was positioned down the centre of the platform to physically divide the space into two sides. Attached to the sides of platform were pieces of matte black plywood (32 cm high) to block out any lateral distractions. A camera (Panasonic CCTV Camera, model no. BL200) was

Figure 2. Pigeon performing a trial in these experiments.

placed at the end of the testing platform to record the pigeons' choices. A small desk lamp (60-W bulb) was positioned on top of the chamber to illuminate the testing area.

The stimuli in the experiment consisted of an assembly combined from a ribbon and food dish (petri dish, 8.9 cm diameter). The ribbons in the experiment were 1.27 cm wide and purple. They were wrapped in a large loop that the pigeon could easily pull. This loop was 6.5 cm in diameter and was either attached with a small screw to the petri dish or not (Fig. 1a). In the latter unconnected condition, a 3-cm gap separated the ribbon from the dish (Fig. 1a). Both food dishes were completely filled with mixed grain.

Procedure

Initial training. Pigeons were first taught to the pull on the looped ribbon to retrieve food. Only the connected condition was used. Initial training first involved placing mixed grain within the loop itself to promote pecking and pulling. This was done until the pigeon was regularly pulling in the dish to retrieve the food. A small plastic track was used to help guide the dish in the first few sessions. Following this training, the pigeons were taught to distinguish between two connected cups, one containing food and the other empty. Sessions with 20 trials per day of this type of food/no food discrimination were conducted until the pigeons reliably chose (>90% accuracy) the food cup for three sessions. This training took about 7–10 sessions.

Discrimination training. While the experimenter was arranging the stimuli, an opaque black cover was placed over the front of the chamber. This prevented the pigeon from seeing the presentation platform. The dishes for the connected and unconnected conditions were then placed on the platform. The front loop of each condition was approximately 5 cm from the choice openings and angled at approximately 45° relative to the front of the chamber. This presentation angle for the two conditions provided the pigeons with a better view of the features relevant to the discrimination. The rightward and leftward presentation angles of the conditions were counterbalanced within each session.

Each trial began with the removal of the opaque cover. The pigeon then reached out its head and neck through the small openings in the transparent front panel to retrieve the food (Fig. 2). The accuracy of each choice was scored based on the animal's first contact with either ribbon. If it correctly pulled in the connected condition, the pigeon had approximately 3–5 s to eat some of the food, at which point the experimenter removed the dish. If it incorrectly pulled the unconnected condition, the opaque cover was replaced back in front of the pigeon. Intertrial intervals were about 30 s. Training sessions consisted of 20 discrimination trials, with each condition presented equally often on the right and left in a randomized order. Four to five sessions were conducted per week. At least 15 sessions of training were conducted with each pigeon.

Results and Discussion

Pigeons took a mean of eight sessions to reach their second session with at least 80% accuracy, and over the last three sessions of training, mean accuracy for all four birds was 93.5% (single mean t test: $t_3 = 68.6$, $P < 0.05$; Fig. 3). There was a significant main effect across sessions (repeated measures ANOVA: $F_{14,42} = 11.2$, $P < 0.001$). The pigeons usually made their choices within 10 s of the black plastic sheet being lifted. The experimenter's subjective impression was that the pigeons looked at both options more often than not.

These results indicate that the pigeons readily learned this means–end task. The rapid improvement across sessions and high accuracy suggest that this was a relatively easy task for the birds, despite having two large piles of food directly in front of them. Hungry animals sometimes have a hard time learning discriminations where food is directly visible (Boysen & Berntson 1995), but that was

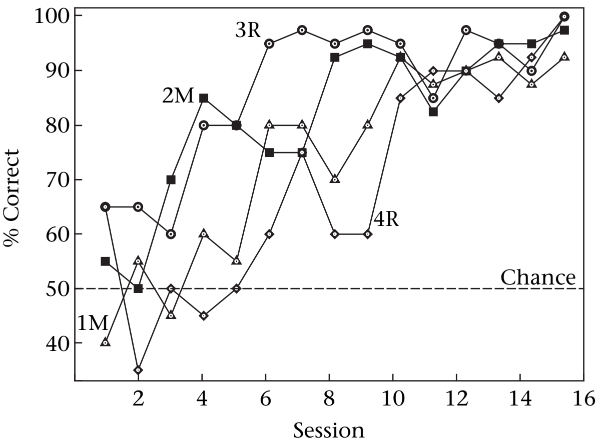

Figure 3. Mean percentage correct for four birds (labelled 1M, 2M, 3R, 4R) in the first 15 sessions of experiment 1. The dotted line represents chance performance.

not the case here. What pigeons understood about the means–end problem, however, was unclear. They may have understood the concept of the 'connection'. Likewise, they might have quickly shifted their visual attention from the food, the relevant feature during their initial training, to the visual differences (e.g. the gap) that distinguished the connected and unconnected conditions. The visual differences would have allowed them to solve the task without a deeper understanding of the means–end problem.

EXPERIMENT 2: VARIATION OF RELEVANT AND IRRELEVANT FEATURES

Hauser et al. (1999) argued that distinguishing between relevant and irrelevant features is an essential element of any means–end discrimination. Relevant features are those components of the means (e.g. connectedness) that allow the end to be obtained. Irrelevant features are those that are not related to this goal (e.g. the colour of the connection). In experiment 2, we manipulated three features of the task to see how they influenced performance. One manipulation focused on the distance or size of the gap between ribbon and cup. If the pigeons attended to the connection between the ribbon and cup, then this feature of the task might influence discrimination. If 'connectedness' was the sole factor involved in mediating the discrimination, then the size of the gap should not affect performance as long as the size could be detected. The second manipulation focused on the relative proximity of the food dish and ribbon in determining choice. The presence of the gap in ribbon caused the food dish of the unconnected condition to be slightly further away. We considered it important to test conditions in which this distance was equalized to ensure that the pigeons did not choose the connected condition because of its food's proximity. The third manipulation was the colour of the ribbon. Changes in this irrelevant property of the arrangement should have little influence on performance if 'connectedness' controlled behaviour.

Methods

Subjects and apparatus

The same pigeons and apparatus were used as in experiment 1.

Procedure

Variation in ribbon/dish distance. Each session, the pigeons were tested on 20 trials arranged in the same manner as experiment 1. The first four trials were conducted with a 3-cm gap size and were not scored. The subsequent 16 trials tested three different-sized gaps between the ribbons and dish in the unconnected condition: 3 cm (eight trials), 5 cm (four trials), 1 cm (four trials). The order of these 16 test trials was randomized with all left and right positions counterbalanced. Five test sessions were conducted.

Variation in food dish distance. The pigeons were tested on 20 trials each session. The first four trials were conducted with a 3-cm gap size and were not scored. The subsequent 16 trials tested three conditions. Eight of these trials were the same as those used during training in experiment 1 (baseline). The other eight trials tested two arrangements of the ribbon and food dish distances. Four trials tested an equalized dishes condition, in which the front edge of the food cup in the unconnected and connected conditions was placed equidistant from the pigeons. This meant that the ribbon loop was now closer to the pigeons in the unconnected condition. Four trials tested an equalized all condition, in which the gap size was reduced to 1 cm and the front edge of the ribbon and the food dish was equalized as best as possible, given the geometric constraints, by splitting the difference between the front and back edges (3 mm for each edge). The testing order of these 16 trials was randomized with all left and right positions counterbalanced. Six test sessions were conducted.

Variation in ribbon colour. The first four trials were conducted with a 3-cm gap size and were not scored. Of the subsequent 16 test trials, eight trials were conducted using the training (purple) ribbon for both the connected and unconnected conditions (baseline) and eight trials were conducted using a novel green ribbon of the same dimensions for both conditions (colour change). The order of these 16 test trials was randomized, with all left and right positions counterbalanced. The gap for the unconnected condition was 5 cm for all trials. Five test sessions were conducted.

Results and Discussion

Variation in ribbon/dish distance

Overall, there was a slight decline in accuracy as the distance between the ribbon and cup was decreased in the unconnected condition. There were significant main effects for distance (two-way repeated measures ANOVA: $F_{2,24} = 6.9$, $P = 0.028$) and session ($F_{4,24} = 5.7$, $P = 0.008$; Fig. 4). There was, however, no significant interaction

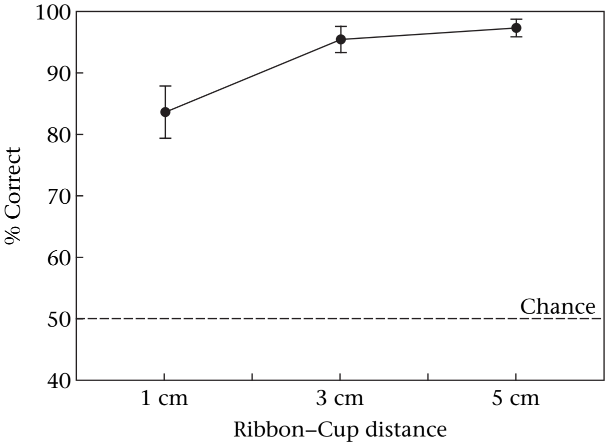

Figure 4. Mean ± SE percentage correct for the four pigeons as a function of ribbon–cup distance in experiment 2. The dotted line represents chance performance.

between these factors ($F_{8,24} = 1.9$, $P = 0.11$). All three distances supported above-chance discrimination by the pigeons (Student's t tests: 1 cm: $t_3 = 7.9$; 3 cm: $t_3 = 21.4$; 5 cm: $t_3 = 32.9$, all $P\text{s} < 0.01$).

These results indicate that as gap size varied, the pigeons' accuracy varied. As the distance between the ribbon and cup became smaller, accuracy declined. The significant effect of varying distance suggests that the pigeons were attending to one of the most relevant features of the task, the gap between the ribbon and the cup in the unconnected condition. Nevertheless, the pigeons were still quite good at the task even with the smallest gap tested. These results indicate that the pigeons did not exclusively process just the continuous nature of the ribbon in the connected condition, but also attended to the gap in the unconnected condition as well.

Variation in food dish distance

For the baseline and the two equalized distance conditions, a repeated measures ANOVA showed no significant effect of condition or its interaction with sessions (Fig. 5a). These results suggest that the closer proximity of food in the baseline condition or the ribbon in the equalized dishes conditions had very little effect on choice behaviour. The nonsignificant reduction in accuracy in the equalized all condition was comparable to the levels seen in the 1-cm condition of the prior test (Fig. 5a). These results suggest that these geometric features that related to ribbon and dish placement were not important to the discrimination.

Variation in ribbon colour

For the two different colour conditions, overall, changing the colour of the ribbon reduced accuracy in comparison to the baseline condition, but pigeons still maintained the basic discrimination at well above chance levels. A two-way repeated measures ANOVA revealed a significant main effect of colour ($F_{1,15} = 25.3$, $P < 0.01$) but no main effect ($F_{5,15} = 0.1$, $P = 0.984$) or significant interaction with session ($F_{5,15} = 0.7$, $P = 0.62$). Choice behaviour was significantly above chance in both the purple baseline condition ($t_3 = 13.9$, $P < 0.001$) and green transfer condition ($t_3 = 11.2$, $P < 0.01$).

Together, these three tests suggest that the pigeons had encoded something about a relevant feature of the task (the gap), an irrelevant feature of the task (ribbon colour), but little about the task's geometric properties (food or ribbon proximity). The reduced performance in the green transfer condition suggests that the pigeons were sensitive in part to the colour change of the ribbon. However, the corresponding above-chance discrimination in this transfer condition also indicates that features critical to mediating the original learning were still present and

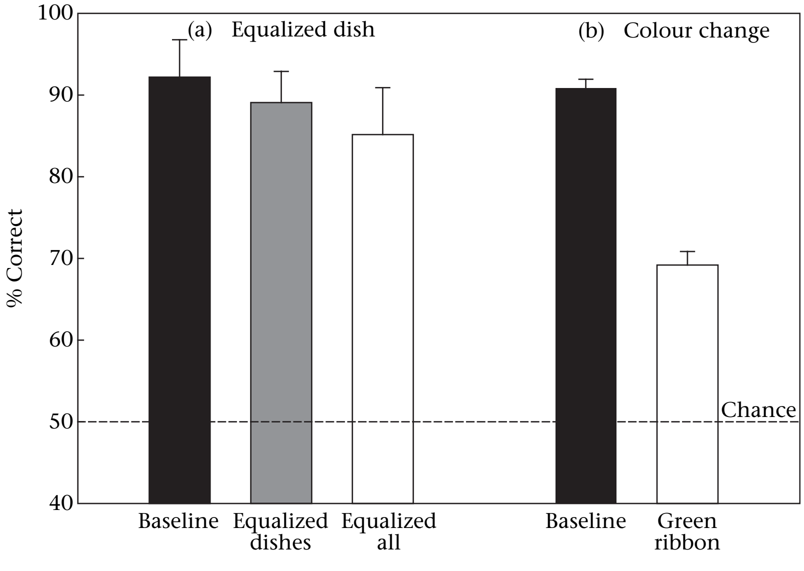

Figure 5. Mean ± SE percentage correct for the four pigeons in the test conditions of experiment 2. (a) Performance in the baseline and different test conditions when the edges of the food dishes were manipulated. (b) Performance in the baseline and colour change conditions. The dotted line represents chance performance.

recognized. Of course, if the pigeons had been attending exclusively to the concept of ‘connectedness’, this colour change should have had no effect, since this feature is functionally irrelevant to this relation. It is well established, however, that pigeons are highly prone to memorizing many features of a task (Greene 1983; Vaughan & Greene 1984; Edwards & Honig 1987; Cook et al. 2005), and that colour is a salient dimension for them. Therefore, it is not too surprising that the pigeons initial representation of the task contained the purple quality of the ribbons. Thus, the recognition of the colour change may have produced a neophobic reaction to the novel test conditions, resulting in reduced levels of choice accuracy. Another possibility is that the pigeons attended to just the perceptual features of the task. In this case, green colour against the black background may have resulted in a reduced capacity to see or recognize the gap.

EXPERIMENT 3: TRANSFER OF MEANS–END BEHAVIOUR

Experiments 1 and 2 showed that pigeons can learn a means–end task and do so in part by attending to features related to the connection between the ribbon and food dish. If the pigeons had learned this discrimination based on a more conceptual understanding of ‘connectedness’, then this behaviour should transfer to other discriminations in which the same means–end relationship of connectedness is present, even if the individual components are arranged differently. Hauser et al. (1999) explored this by testing their tamarins with many small variations in their connection task, and on which the tamarins performed quite well.

In experiment 3, we tested for the potential conceptual basis of the pigeons’ discrimination by transferring them to a new means–end task. We changed the physical arrangement of the second task in several ways to provide the most demanding task of this hypothesis (Figs 1b, 2). The ‘connectedness’ of the ribbon to be pulled and the cup remained the essential feature of the task for retrieving food, but it was now implemented such that the unconnected gap was in a different spatial position and mediated by a different-coloured ribbon that was flattened on the platform’s surface. If birds were able to transfer accurately to this new discrimination, this result would provide strong evidence that they attended to the generalized feature of ‘connectedness’. On the other hand, if they failed to show immediate transfer, or at least some savings during subsequent acquisition, this result would indicate that the key features mediating the first task were not present in the second. Such a finding would be more consistent with a more perceptually based mediation of these discriminations.

Methods

Subjects and apparatus

The same pigeons and chamber were used as in experiments 1 and 2.

Procedure

Everything remained the same as in the prior experiments, except that a different physical ribbon/dish arrangement was introduced. The connected condition consisted of a 7-cm-long white ribbon, 1.5 cm wide, attached by screw to a white plastic PVC ring (3.2 cm diameter) and petri dish (Fig. 1b). In the unconnected condition, the ribbon was cut into two segments 3 cm from the food dish, with a 1-cm gap between these two lengths of ribbon (Fig. 1b).

The testing procedure was otherwise the same as in experiments 1 and 2. Both the connected and unconnected conditions were placed on the platform so that the plastic ring was close enough (5 cm) for the pigeon to pull in and retrieve the out-of-reach food. The conditions were again angled at approximately 45 °. Sessions consisted of 20 trials. Each pigeon experienced at least 26 sessions of testing. The pigeons had trouble learning the task, so for sessions 7 and 8 only, we tested a 4-cm gap in the unconnected ribbon, and for sessions 11 and 12, we tested small white ropes because we thought that they might be easier to see. These replaced the ribbons in both connected and unconnected conditions.

Results and Discussion

At the end of task 1, using the looped purple ribbon, the pigeons were performing with a mean accuracy of 99.3%, but upon the switch to task 2, using a white ribbon with a PVC loop, accuracy declined (mean of the first three sessions = 54.5%; ANOVA comparing accuracy in the last three sessions of task 1 with that from the first three sessions of task 2: task type: $F_{1,3} = 122.9$, $P = 0.002$; Fig. 6). There was no main effect ($F_{2,6} = 2.7$, $P = 0.14$) or interaction with session ($F_{2,6} = 0.4$, $P = 0.68$). Task 2 accuracy over the first three sessions also did not differ significantly from that expected by chance (Student’s t test: $t_3 = 1.1$, $P = 0.35$). With experience, the pigeons improved with task 2, reaching a mean of 80% accuracy by session 15

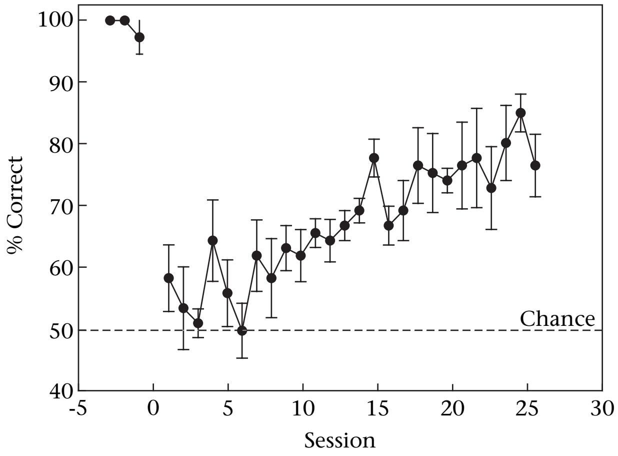

Figure 6. Mean ± SE percentage correct for the four pigeons over sessions in experiment 3. The first three data points show task 1 accuracy before transfer to task 2 (remaining points). The dotted line represents chance performance.

(repeated measures ANOVA comparing accuracy over the 26 training sessions: $F_{25,75} = 3.6$, $P < 0.001$). By the end of training, the pigeons were significantly above chance (Student's *t* test: $t_3 = 7.2$, $P < 0.01$) with a mean accuracy of 81.6% for the last three training sessions.

If a generalized concept of 'connectedness' was the basis for task 1, then we expected some type of transfer to task 2. The pattern of results suggests little transfer from task 1 to task 2. First, initial transfer to the second task was quite poor and not significantly different from chance. Second, while the pigeons showed a clear acquisition function with task 2 compared to their acquisition in experiment 1, they learned this second task more slowly. This result suggests that there was little acquisition savings between the two tasks. Rather, we observed features that looked like acquisition of a new task, which seems most consistent with the idea that the features mediating each task were perceptually different and had to be learned separately.

EXPERIMENT 4: EVALUATION OF CONTROLLING FEATURES

The purpose of experiment 4 was to better identify the features that might be controlling the discrimination of the new task introduced in experiment 3. Again, the presence of the gap in ribbon caused the food dish of the unconnected condition to be further away in this second task. As in experiment 2, we considered it important to test conditions in which this distance was equalized. Thus, in the first test of experiment 4, we again equated the distance to the food dishes.

To establish that the gap in the ribbon was the essential feature involved with the discrimination of task 2's condition, the second test of experiment 4 eliminated this feature by means of occlusion. This occlusion was accomplished by placing a small pink piece of paper over the ribbons of both the connected and unconnected conditions. This rendered them essentially identical in appearance except for food distance (test 1). If the pigeons relied on this gap feature, then any discrimination should drop to chance in the occluded condition.

Methods

Subjects and apparatus

The same pigeons and chamber were used as in experiment 3.

Procedure

Equalizing food dish distance. The pigeons were tested on 20 trials in each session. The first four trials were conducted as warm-up trials and were not scored. The subsequent 16 trials tested two conditions. Eight of these trials were the same as those used during training in experiment 3. The other eight trials tested an arrangement in which the food dish in the unconnected and connected conditions was placed equidistant from the pigeons. Thus, the PVC loop used for grasping was closer to the pigeons in the unconnected condition. The testing order of these 16 trials was randomized with all left and right positions counterbalanced. Six test sessions were conducted.

Connection occlusion. The pigeons were tested on 22 trials in each session. The first four trials were conducted as warm-up trials. The subsequent 18 trials tested two conditions. Twelve of these trials tested the baseline task. The remaining six trials tested the pigeons with a 2 × 5-cm rectangular piece of pink paper covering the 1-cm gap in the unconnected condition and placed in the same location on the connected condition. The testing order of these 18 trials was randomized with all left and right positions counterbalanced. Three test sessions were conducted. Finally, one additional session was conducted in which the pink paper was placed over part of the food dish. This partially hid some of the food but allowed the ribbons to be fully visible. This condition tested for any neophobic effect of the pink paper itself.

Results and Discussion

Equalizing food dish distance

A repeated measures ANOVA showed no significant interactions ($F_{3,9} = 2.0$, $P = 0.17$) or main effects of condition ($F_{1,3} = 0.0009$, $P = 0.93$; Fig. 7a). This result indicates that the pigeons were unaffected by equalizing the distance to the food dishes or the closer proximity of the PVC loop in the unconnected condition. Combined with the results of experiment 2, these results indicate that these geometric features related to ribbon and dish placement were not particularly salient to the birds' choice behaviour.

Connection occlusion

The pigeons' accuracy averaged 81.3% on baseline trials and 55.4% on occlusion trials (Fig. 7b). Occluding the gap in the unconnected condition dropped accuracy to chance levels (Student's *t* test: $t_3 = 1.2$, NS). There was a significant main effect of occlusion (repeated measures ANOVA: $F_{1,3} = 15.5$, $P < 0.05$) and no main effect ($F_{2,6} = 1.9$, $P = 0.24$) or interactions with sessions ($F_{2,6} = 1.0$, $P = 0.41$). The high accuracy observed in the control session where the pink paper was on the food dish (79.2%) suggests that the prior drop in the occluded conditions was not related to a neophobic reaction to this introduced feature. The significant decrement in accuracy with occlusion strongly suggests that the perceptual features guiding the pigeons were related to the continuous length of ribbon in the connected condition, the visible break created by the ribbons in the unconnected condition or both.

GENERAL DISCUSSION

Using two different tasks, these experiments demonstrate for the first time that pigeons can solve an analogue of a means–end task previously tested with primates (experiments 1, 3). Both tasks took 100–300 trials to learn to criterion. The lack of transfer between these tasks suggests,

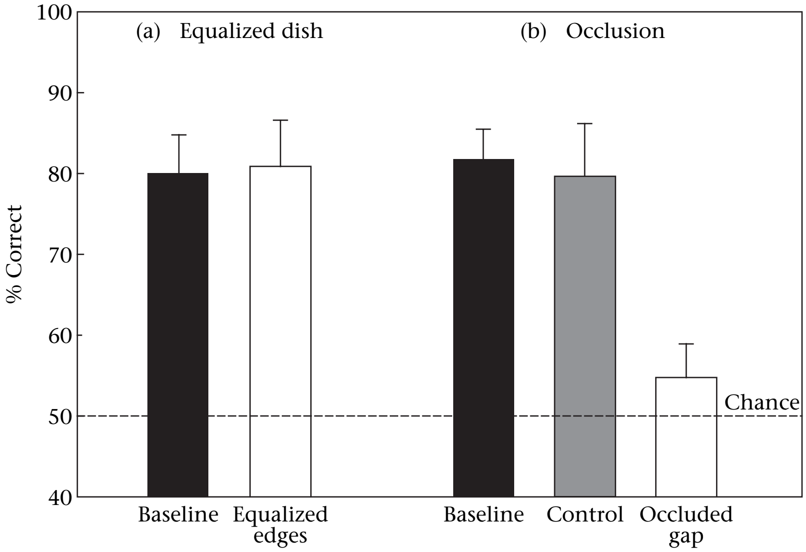

Figure 7. Mean ± SE percentage correct for the four pigeons in the test conditions of experiment 4. (a) Performance in the baseline and test conditions when the edges of the food dishes were equalized. (b) Performance in the baseline and test conditions when the gap was either covered or not. The dotted line represents chance performance.

however, that the pigeons failed to comprehend the conceptual nature of 'connectedness' in these means–end tasks (experiment 3). They did successfully learn to perform them by attending to the relevant features of both tasks (experiments 2, 4). In each case, however, the learned basis of the discrimination seems best ascribed to the simple and direct processing of the perceptual features of the connected and unconnected conditions.

These features were, after all, readily available and quite reliable indicators of the correct solution to each problem. While deriving a more conceptual or deeper understanding of the physics of the situation might be highly desirable, the costs of this capacity may be too high or impossible to implement in the pigeon brain. Given the natural or urban history of pigeons, just how often do means–end problems of this type actually occur? If they are relatively infrequent, it may be cognitively more efficient to solve such problems on an ad hoc basis by relying on trial and error learning, rather than generating or acquiring more complex generalized behaviours that cover a wide range of sporadically occurring situations. This perceptually based account also agrees with Visalberghi & Limongelli's (1994) and Povinelli's (2000) suggestions that, in certain settings, animals may rely on readily observable perceptual features to guide their understanding of the physical world.

One way to test this perceptual account for the pigeons would be in a setting where the normal physical structure of the natural world was violated. If the perceptual features of the task are all that matter, then the pigeons should have no problems solving an identical task where they must learn to pull on the 'unconnected' condition to retrieve the food. Pigeons might be just as adept at learning this inverted and 'unnatural' contingency using magnets, very fine wires or other appropriate mechanical deceptions as they were at learning to pull the connected ribbon in the above experiments. Despite the fact that pigeons surely do not understand the concept of invisible forces, we suspect that they would have little trouble adapting to such a contingency provided that the visual features were the same as in the above experiments. Given our laboratory's past experience in testing pigeons in computerized operant tasks (Cook 1980, 1992, 2000; Wright et al. 1988; Cook et al. 1990, 1995, 1997a, b, 2001, 2005), if pigeons were presented with such natural and inverted task contingencies using an operant technique similar to that used in Kralik & Hauser's (2002) experiments examining connectedness in tamarins, we are reasonably confident that the pigeons would have learned the two tasks equally quickly. Nevertheless, pigeons have a long history of interacting with causality that involves object contact, and, as a result, this inverted contingency condition might be more difficult to learn even if the current results are mediated by perceptual factors. The effects of this inversion also might be more evident in a more 'ecologically valid' setting involving real objects.

One key question is whether our results represent a species difference between animals or a class difference between birds and primates. Given the over 8000 species of birds in the world, one should not generalize too far about this class based on the current results. Although pigeons retrieve and manipulate items to construct nests, for example, one can question the naturalness of the present task for this species (of course, much the same criticism holds for primates, too). Even after several months of practise, the pigeons still occasionally had trouble efficiently pulling in a dish. Perhaps a species that relies on tool use or 'general intelligence' to survive might do better at conceptualizing the means–end demands of the current task. For instance, New Caledonian crows, *Corvus moneduloides*, modify wire and select sticks that are appropriate for food retrieval (Chappell & Kacelnik 2002; Weir et al. 2002), and common ravens, *Corvus corax*, show some degree of immediate flexibility in pulling up a string to retrieve distal food (Heinrich 1995). Thus, these potentially generalized problem-solving abilities would make these species interesting animals to test in a task similar to the current one to evaluate the relative contribution of perceptual and means–end factors in controlling discrimination. Species that hunt among the leaf litter, such as towhees, would also be good candidate species, because they often have a partially disconnected view of objects hidden among the litter, and therefore, might understand ‘connectedness’ in a different way than do pigeons. We suspect, however, that most birds probably rely on direct physical features to solve most problems.

Among the animals tested in various means–end tasks involving connectedness, it is not clear exactly how large the species differences might be. Although the tasks that have been used to test pigeons, tamarins and chimpanzees are analogous, they are far from identical. The differing degrees of success reported for each species may be related to the different arrangement of the task components. The tamarins, for example, were presented with many examples of connectedness from the start, whereas the pigeons experienced only two contrasting examples. Furthermore, because of the placement of the conditions, the tamarins may have had improved opportunity to see both options than did the pigeons. Unlike the tamarins, the pigeons first learned to pull in the food cup in a setting that did not require a discrimination, and the transfer tests conducted in each case also differed in difficulty. For instance, in comparison to most of the transfer tests conducted with tamarins, the difference between our first and second tasks was considerable. The location, colour, orientation and nature of the connection (ribbon to cup; ribbon cut in two) were all changed to provide the best test of the conceptual hypothesis. In contrast, most of Hauser et al.’s (1999) transfer tests involved smaller changes in the configuration of the gap, all of which the tamarins passed with ease. Often overlooked are the several reported conditions (G2, G3, K), involving larger featural changes, which did give the tamarins more problems; supporting both poor transfer and requiring several sessions or trials to reach criterion. Our transfer test may be more like the latter. The above considerations all suggest that appropriate caution is needed in drawing conclusions about the relations between current results and those previously collected with primates. An evaluation of the importance of different perceptual or physical differences between the testing situations is clearly needed, and tests involving more directly comparable tasks and transfer tests are required to better assess whether any true comparative difference exists. With appropriate modifications, animals that fail one kind of transfer test, as is the case here, may under more favourable conditions yield a more positive result.

Although the pigeons did not seem to grasp the concept behind the means–end tasks presented here, they did eventually solve them. Even the simplest means–end tasks have perceptual elements that provide their solution, so learning to attend to and to use these relevant perceptual elements is the first step towards eventually understanding deeper mean–ends relations. The first animals to succeed at means–end tasks almost certainly did so perceptually. The crucial evolutionary step is when these perceptual origins begin to support a more conceptual representation of the problem. The next crucial step would be when these closely linked perceptual/conceptual representations begin to mentally separate, and conceptual reasoning about means and ends can be done without the aid of any obvious perceptual linkage between events. The final step might be when an animal can imagine these conceptual relations for extended periods. Farming could not develop, for instance, until humans could both understand that seeds and maintenance lead to food, but could also tolerate and reason about the long delays involved, as well. Within this transformational framework, the present results suggest that pigeons can only process perceptual relations leading to an end. Given recent reports about crow tool use it seems that this species, or corvids in general, may potentially have cognitively evolved to the point where they have a rudimentary concept of means–end relations that are not directly reliant on perceptual features. Given the likely perceptual origins of learning about means–end relations, researchers in general should be cautious in interpreting how animals solve such problems, especially when the visual characteristics of the task are salient.

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