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“Insight” in Pigeons: Absence of Means-End Processing in Displacement Tests

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Abstract

The understanding of functional relations between action and consequence is a critical component of intelligence. To examine this linkage in pigeons, we investigated their understanding of the relations of the elements tested in an extension of Köhler's box-stacking task to this species (Epstein et al. 1984). In the experiments, the pigeons had to move a spatially displaced box under an out-of-reach target. Experiment 1 successfully replicated and extended the previous finding showing that when separately trained to move a box and stand on it to peck the target, pigeons can synthesize these behaviors to solve the single-box displacement problem quickly on their first attempt. Experiment 2 tested whether pigeons, when given a simultaneous choice among two boxes with identical reinforcement histories, would selectively choose the box with the correct functional affordance (i.e., permitting standing) to solve the problem rather than a nonfunctional one. Their extensive, equivalent, and undirected behavior in moving both boxes during these tests suggests the pigeons did not possess a means-end understanding of the functional properties of the boxes. Instead, their results were consistent with an analysis of their earlier synthetic behavior as being due to the temporal and spatial relations of the physical elements in the task and their prior learned behaviors.

In the modern comparative study of intelligent and adaptive behavior, the analysis of if and how animals generate and understand means-end relations continues to be a major focal point in the study of animal cognition and thought (e.g. Schmidt and Cook 2006; Bluff et al. 2007; Heinrich and Bugnyar 2005; Bird and Emery 2009; Kirsch et al. 2008; Auersperg et al. 2009). How animals solve problems that require physical manipulations of the environment are particularly salient because of their possible relations to the evolution and development of tool use. In birds, for example, there have been a number of recent impressive findings involving apparently goal-directed solutions to different physical problems. These include string-pulling in ravens and keas (Heinrich and Bugnyar 2005; Werdenich and Huber 2006) solving trap-tube problems in rooks (Seed et al. 2006) and the use and manufacture of tools in New Caledonian crows (Weir et al. 2002; von Bayern et al. 2009). When animals solve such problems, the pivotal issue remains: to what degree do states of cognition characterized by terms like “insight”, “reasoning” “problem solving” and “understanding” contribute to an animal's behaviors as opposed to simpler mechanisms based on experience, learning, and reward (Shettleworth 2010; Sternberg and Davidson 1995; Bluff et al. 2007; Lind et al. 2009; Mendes et al. 2007). In the following experiments, we examine this general class of questions by testing pigeons in a situation where physically relatable elements need to be combined to solve a novel problem. The task involved was an avian simulation of one of Köhler's famous experiments with chimpanzees (Epstein et al. 1984)

Köhler's (1925) general approach to testing "intelligence" and the role of insight was characterized by tests where the chimpanzees were faced with problems where circumstances blocked an obvious course of action, leaving more roundabout paths as solutions. One of the most prominent of these tasks involved hanging a banana out of reach of the chimpanzees in their enclosure. After initially frustrated attempts to directly reach the banana, several of his chimpanzees could stack boxes, available from around the enclosure, to eventually reach the food. In his explanation of their solution, Köhler emphasized the insightful nature of the behavior, with his chimpanzees arriving at the solution or the means to reach their goal by an immediate and rapid reasoning-like process that reorganizes their experience (cf. Thorpe 1956). One constraint on Köhler's observations is that little was known about his chimpanzees' prior experience with the boxes or the possible contribution of experience and maturation to their solution of the problem (Birch 1945; Schiller 1952).

One widely-cited experiment investigating the potential role of experience in such a means-end tasks involved testing pigeons in an operant reproduction of Köhler's original task (Epstein et al. 1984). Here the pigeons were trained to perform two separate behaviors using reward. The first behavior involved learning to push a box towards a target location on the floor of the testing arena. The second behavior involved learning to stand on the box and peck directly at an out-of-reach target (a banana facsimile) hung over the box. During a subsequent novel test, the pigeons were presented a situation where the box was spatially displaced some distance away from the banana target. In this *single-box displacement test*, Epstein et al. observed that the pigeons would, after an initial period of banana-directed orientation, push the box towards the banana, and once underneath it, proceed to climb up and peck the banana. This novel solution to the displacement problem reliably occurred in less than two minutes for the three pigeons that they tested. The remarkable nature of this behavior looks superficially as if the pigeons understood the means-end relations between the displaced box and reaching the target banana.

Epstein argued that the pigeons' successful solution to the problem was generated by the synthesis of the trained behaviors (Epstein et al. 1984; Epstein 1991, 1987). His generativity account suggested that different reinforced behaviors probabilistically competed with one another for control of action of a function of the elements in view. After the initial orientation to the banana extinguishes, the previously reinforced targeted-directed box pushing comes to control behavior. This results in a reduction in the difference between the box's displaced location and the banana target, leading to the increased probability of the trained standing behavior emerging, and eventually target-directed pecking. Thus by this account, the synthesis of behaviors required in the displacement test is due to the combination of the established situational behaviors in conjunction with associative principles related to reinforcement, extinction, generalization, chaining and resurgence.

Despite the widely-cited and significant nature of Epstein's et al. observations, surprisingly little research has followed up on these challenging observations (Luciano 1991; Foerder et al. 2011; Epstein 1987). For example, Luciano (1991) successfully replicated a portion of Epstein's original observations with an additional pigeon. While the interpretation of the results is complicated by repeated testing and the sequencing of training the separate behaviors, a second follow-up experiment demonstrated that specific experiences with the different elements was likely critical to the successful emergence of synthesis during a displacement test. Two pigeons trained to directionally move the box away from a goal failed their displacement test (although the control animals also did not show successful synthesis of the behaviors). Luciano's observations nonetheless support the conclusion that the nature of training is potentially critical.

The current project had two goals. The first consisted of reproducing and extending the original observations to examine its robustness to nominal changes in training procedures (Experiment 1). Establishing the original phenomenon laid the foundation for the more critical second goal. Here we wanted to experimentally investigate the pigeons' "understanding" of how the box served as a functional means towards reaching the banana target (Experiment 2). While Epstein's generativity account provides an alternative account of the pigeons' synthetic behavior, his empirical observations do not rule out an "insight" or "reasoning" account where the pigeons do understand the means-end relations of the displacement problem.

To test these different explanations in Experiment 2, we tested a new *two-box displacement procedure*. The pigeons were trained to directionally move two different boxes towards a goal within the arena. The first box was *functional* in nature, as its design permitted standing in order to reach the banana target. The second box was *nonfunctional* in design as it could not be stood upon. Thus, it could be moved but was not appropriate for solving the problem of reaching the banana. When subsequently faced with the displacement problem for the first time with both boxes, what would the pigeons do? If the pigeons possessed an understanding of the means-end relation between the elements of the problem, then they should select and move only the functional box towards the banana during the displacement test. If, on the other hand, the synthesis of behaviors is a result of the probabilistic chaining of established behaviors, the pigeons should show no such selection or preference among the boxes, as both would have an equivalent history of reinforcement for being moved in that context.

Experiment 1 - Single-Box Displacement Testing

The first experiment was a conceptual replication of Epstein's procedure. Successfully obtaining the combinatorial synthesis of the trained behaviors was a first step and an important baseline for the subsequent experimental testing of means-end understanding in Experiment 2. Training consisted of building a repertoire of two separately-trained behaviors. The first involved teaching the pigeons to push an unpainted wooden box to a small black dot target randomly located in an arena for food reward. The second involved teaching the pigeons to step up and stand on the box in a fixed location and peck at an overhead, out-of-reach, banana target. Upon successfully completing this training, a single-box displacement tests were conducted where the movable box was displaced for the first time relative to the banana target. "Successful" synthesis of the two behaviors would be judged to have occurred if the birds engaged in pushing the box towards the banana and then stepping up and pecking it. Given the numerous differences between our training procedures and those of Epstein et al. (1984) and Luciano (1991), such an outcome would suggest that such synthesis behavior is relatively robust.

A second test was conducted to examine further the pigeons' understanding of the problem. In this test, a novel red box was displaced relative to the banana. Prior to this test, the pigeons received standing and target-pecking training with the red box, but were not trained to move the red box around the arena towards a goal. The question was whether the birds would generalize their learned pushing behavior from the unpainted wooden box to the red one to solve the displacement problem.

Method

Animals—Two adult male White Carneaux pigeons (*Columba livia*) were tested. They had prior experience with visual discriminations in a touchscreen operant chamber, but no experience with physical problem-solving tasks in an open arena. They were maintained at

80–85% of their free feeding weight and individually caged in a colony room (12 hour LD cycle) with free access to water and grit. *Apparatus*

All training sessions and tests were conducted in a hexagonal arena. Each side was made of 40 cm wide x 61 cm tall gray plastic walls with a fine-grain plywood floor. A clear Plexiglas covered the top of the arena. An experimenter-controlled food hopper (Coulbourn Instruments, Whitehall, PA) was located behind a 4 cm x 4 cm opening in one wall of the arena at floor level. The hopper was internally illuminated and made an audible noise when raised.

Procedure—Training sessions had the objective of establishing a repertoire of two separate behaviors: “targeted directional pushing of the box” and “directed pecking at the banana while standing on the box.” The pigeons learned these behaviors through a series of successive approximations. The pushing behavior was trained over a period of three to four weeks. Training began with learning to peck at a 5-cm white Styrofoam® ball studded with mixed grain and proceeded to reward the pigeons for any movement of an unseeded ball. This was then replaced by any movement of a Styrofoam box (first unweighted and gradually increased in weight). This portion of the training was conducted until approximately 20 to 30 reinforcements were collected during a daily training session. At this point a 76-g unpainted wooden box (10 cm x 10 cm x 6 cm high made from basswood) replaced the weighted Styrofoam box. This wooden box was used for the remaining of training and testing.

The pigeons were then introduced to having a 20-cm diameter black paper dot placed in the center of the arena. They were then rewarded for moving the box from a random point on the edge of the arena to the central black dot. Over several sessions, the size of the dot was gradually reduced to 4 cm in diameter. When the pigeons could accurately push the box onto the smaller dot, the location of the dot was randomly varied about the arena between rewarded completions of the task. The behavior was considered to have been acquired when a pigeon could push the wooden box onto the randomly located small dot in less than 40 seconds.

Training of standing behavior occurred during the last ten minutes of each training session. The pigeons were introduced to a Styrofoam ball (5-cm diameter) suspended in the middle of the arena about 2 cm off the floor. Pigeons were rewarded for any pecking at the ball (likely facilitated by the training with the seeded ball). Over sessions, the ball was gradually raised to a height of 30 cm above the floor. This was high enough to make the pigeons stretch to reach the ball from the floor. The ball was then replaced by a 7-cm long & 2-cm wide yellow facsimile of a banana. When the pigeons reliably reached for the head-high banana, a short 2-cm wooden platform was placed underneath the banana. After the pigeons stood on the short platform, the wooden box used in training the pushing behavior was introduced and the height of the banana raised to 40 cm. During this portion of training the box was firmly fastened to the floor so that it was impossible for the pigeons to move it. These training sessions then lasted until approximately 20 reinforcements were collected with the target being randomly located above the arena. At the completion of training both behaviors, the first displacement test session was conducted.

Single-box displacement testing: A test session was comprised of warm-up “trials” that included pushing the box to the dot three times as located within two diagonal quadrants of the arena. The pigeon then received three warm-up “trials” of standing on the fastened box with it located in the same two quadrants. Reward was presented during these warm-up trials. At this point, the box and banana target were removed from the arena. On the subsequent test trial, the banana was hung back into the arena in one of the two quadrants

not used for warm-up trials and the box placed approximately 30 cm away in the remaining quadrant. A successful test was determined to have occurred when the pigeon maneuvered the box underneath the banana, climbed onto it, and pecked the banana. A test trial was terminated after 20 minutes if no synthesis of the behaviors had occurred by that point. No food reward was delivered during the tests.

Behavioral Scoring: Data from the displacement tests were analyzed by having two observers score each test session as to the number and timing of four events related to the birds' behavior (box pushing, standing on the box, orienting or pecking towards the banana target while on the ground, orienting or pecking towards the banana target while on the box). Agreement about the time of overt actions like box pushing and standing was high (Pearson $r(15)=.99$ across the two raters using 10-s bins). More subjectively judged events involving target orienting were slightly lower (mean among Pearson $r_s(15)=.95$). Videos were scored for the spatial position of the boxes relative to the camera's location by digitizing their position from every fifth frame. The angular displacement of the camera resulted in a slight, but consistent, distortion of these values within a video.

Novel box displacement testing: This test occurred approximately ten days after the prior tests. To prepare for this test, regular training sessions continued, except that during the box-standing portion of training the pigeons were introduced to standing on a novel box of the same dimensions and weight, but painted red, to peck at the banana. This box was also firmly fastened in place during this training. After three training sessions with the red box, another displacement test session was conducted with each bird using this novel box.

Results

Single-box displacement testing—Pigeon #2B was tested twice for synthesis behavior. This bird failed the first test and succeeded in the second one. The pigeon's behavior during the first test was nonetheless instructive regarding the organization of our behavioral training and the bird's interpretation of its contingencies. The first test lasted 20 minutes. During this time, the pigeon constantly pushed the box around the arena, covering virtually its entire spatial extent. Despite the box's frequent location near the banana during this time, the pigeon continued to push the box in favor of stepping up and pecking at the banana. He oriented towards the banana several times during the session, suggesting he was alert to its presence, but never synthesized the established behaviors into a "successful" solution.

During the first test, the pigeon's extensive and "directionless" box-directed pushing behavior was the obvious problem. A rereading of Epstein et al. (1984) noted that extinguishing pushing behavior in the absence of the dot was included in their training, something we had not done. Instead, during training, #2B had received immediate reward upon pushing the box onto the dot. Although this increased the frequency of getting the box to the target dot, it did not require the pigeon to adjust or stop the box onto the dot as a "goal". Thus, the pigeon may have learned to just push the box until reward was delivered. As a result, we made two modifications to daily training to encourage goal-directed action. First, two five-minute periods of extinction within a training session were added, where the dot was removed and no reward was given for any box-directed behaviors. Second, a 2-s delay between pushing the box onto the dot and reward was added. After six modified training sessions, #2B no longer pushed the box in the absence of the dot and reliably pushed the box to the dot and stopped, appearing to wait and check for the upcoming food reward.

At this point, a second displacement test session was conducted. During this test, pushing behavior was more directed and the bird successfully completed the task by moving the

displaced box towards the banana and contacting it after 128 seconds. After an initial period of orienting towards the banana, the pigeon began to push the box in its direction. At three separate times it alternated this pushing behavior with brief periods of standing on the box and orienting towards the target banana. The pigeon was quite close to reaching the banana target as early as 94 seconds into the test. The lower left diagram in Figure 1 shows the path of the box during the session and the three points (open circles in left diagram) where the bird stood on the box prior to the solution. Digitally reconstructing the location of the box over time revealed that the pigeon moved the box a distance of 27 cm during the session. Each contact with the box moved it on average about 3.4 cm in distance. Consistent with a form of goal directed behavior, this analysis revealed that 100% of the bird's pushing behaviors reduced the distance between the box's starting location and that of the banana. The upper right graph depicts the frequency of the scored behaviors over time during the test session.

Prior to its first displacement test, pigeon #1A's training was modified to include extinction periods and delayed reinforcement to similarly encourage goal-directed box pushing. Perhaps as a result, pigeon #1A successfully displayed synthesis behavior on the first test. This pigeon succeeded in pushing the box underneath the banana and stepping up and making contact with the banana at 166 seconds into the session. Like bird #2B, he made initial orientations and pecks towards the banana target from the ground before beginning to push the box. Again box pushing was in the direction of the banana target once it had begun. As the box moved closer to the banana, target-directed behavior from the box also increased. The pigeon moved the box a total of 136 cm, with 86% of its pushing behaviors reducing the distance between the box's original location and that of the banana (average of 3.5 cm per movement). The lower two panels of Figure 1 provide the same summaries of #1A's behavior during its test as for the prior bird.

Novel box displacement testing—Both pigeon #1A and #2B also successfully completed the novel box test by eventually pushing the red box underneath the banana and stepping up to peck at it. The completion times were several times longer than in the first test. Bird #1A completed the task in 470 seconds, while #2B took 586 seconds. The longer completion times suggests that that the novel location of the red box relative to the banana target disrupted behavior. Again the earliest parts of the session consisted of initial orientations towards the out of reach target. Both pigeons appeared “tentative” in contacting the red box, not making their first contacts until 130 and 185 seconds into the test, respectively. Interestingly, both birds' initial contact with the red box consisted of pushing it rather than the previously reinforced standing behavior. After this initial contact, both birds began to increasingly contact and push the red box over the course of the session. With this increased pushing behavior, the behaviors exhibited involved the same basic sequence as detailed, with increasing standing behavior as the box was moved closer to the target, leading to delayed successful resolution of the task.

Discussion

Experiment 1 confirms and extends Epstein's et al. results. When tested in a single-box displacement test following training to engage in directed pushing of a box towards a dotted target and standing on the box to reaching a different target, pigeons can synthesize these behaviors into an ordered sequence that solves the problem. This consists of an initial orientation towards the banana target, followed by directed box pushing towards the banana (with occasional attempts to prematurely reach the banana), and followed by the successful resolution of the task by standing on the box and contacting the target. This synthesis of behavior emerged relatively quickly (~120 seconds). The same synthesis of behaviors was slower with the introduction of a novel red box to move, but otherwise proceeded in

essentially the same fashion. Given the numerous small to moderate differences in the training procedures employed in the different studies, the synthesis of these behaviors by the pigeons to solve a displacement problem appears to be a robust and reliable phenomenon.

Although the synthesis of the behavior is relatively quick and reliable, the shaping and training of the different behaviors was slow and took several weeks to complete. Nevertheless, the form of the training seemed critical. Pigeon #2B's first test was the most instructive here. Without the incorporation of the extinction contingency, the pigeon did not solve the task on the first pass. The effect of this change was subtle, but important. It apparently caused the bird to treat the dot as a "goal" for its pushing behavior. Without this instruction, this bird engaged in the same type of directionless pushing described for some of the pigeons in Epstein et al.'s control conditions.

The successful, yet slower, synthesis of behaviors when tested with the novel red box is also instructive. Because of the pigeons' history of reward with standing on this box, the slowness of their reactions was likely not due to neophobia. Because of this specific history, however, it is interesting that the pigeons' first action towards the box was to push it rather than to stand on it. A means-end account of this behavior would suggest that the pigeons may have indeed had a concept of "box" and its potential functional application or affordance for solving the displacement problem. A reinforcement account, on the other hand, would have to say this behavior emerged from the generalization of goal-directed behavior established with the similar wooden box and its history of appearing in different locations. Here the partially shared perceptual similarity of the boxes' shape and their shared history of reinforced standing behavior may have provided the linkage that allowed the wooden box's pushing behavior to generalize to the displaced red box.

Experiment 2 - Two-Box Displacement Testing

In Experiment 2 we tested the pigeons' understanding of the means-end relations between the standing properties or affordances of the box and its potential role in reaching the banana. For this we challenged pigeons with a new type of displacement test. After a similar training regime established from the results in Experiment 1, the pigeons were offered a simultaneous choice between two boxes to solve the displacement problem. The first box was *functional* in that it permitted standing to reaching the banana. The second box was *non-functional* in that its design prohibited standing and would not be useful in reaching the banana. In this case, several blunt protrusions from the top of the box, similar in logic to those used in many public places to prevent roosting by these birds, prevented standing or perching.

Would the pigeons correctly choose the functional box over the non-functional box to solve to displacement problem? If they did, it would suggest an understanding of the means-end relations was involved with the situation. A reinforcement-based account of Experiment 1's synthetic behavior would, in contrast, predict that both boxes should be actively moved prior to the solution, since both boxes would have an equivalent history of goal-directed reinforcement to the dot target in the arena. Thus, any failure or interference with completing the displacement task would be consistent with the theory that the synthesis of behaviors that occurs in conditions like those tested in Experiment 1 are most likely due to reinforcement and the chaining of learned behaviors rather than any means-end understanding.

Method

Animals & Apparatus—Two male pigeons were tested. Pigeon #1A had served in Experiment 1, while #3L was experimentally naïve. The same arena as in Experiment 1 was used.

Two new boxes were introduced and used during training and testing. The *functional* box was similar to that in the first experiment with identical dimensions, but painted blue. Because the top of the box was flat and smooth, it permitted standing. The *non-functional* box had identical dimensions and also was blue. It was modified to not permit or afford standing. Its upper surface was removed and within the resulting empty space an inverted 10-cm blue plastic funnel was placed. This funnel tapered to 1 cm at the top and protruded centrally 4 cm above the highest edge of this box. This box also had three blunt metal protrusions on each side that were ~ 1.25 cm above the outside perimeter of the box. These modifications functioned as intended as we observed only one instance during training and testing in which a pigeon briefly perched, in an uncomfortable-appearing posture, on this box. Finally, during the Experiment 1 we noticed times when the pigeons appeared to want to grasp and pull the box rather than push it. This suggested that allowing birds to additionally “pull” by grasping the box with their beaks might increase a bird’s ability to move and adjust the boxes. Thus, for the experimentally-naïve pigeon we added a 1.5-cm Styrofoam border around the top edge of the boxes that allowed grasping with the beak. This pigeon did use a combination of pushing and pulling to move the boxes.

Procedure

Pigeon #1A: Approximately two weeks after Experiment 1, the functional and non-functional boxes were now introduced to the portion of each session used to train goal-directed pushing behavior. Training was then divided equally among the three boxes (the original box and the two new boxes) with each box being training separately in randomized sequences. Because of its prior experience, this pigeon successfully and quickly learned to move both the functional and non-functional boxes to the randomly-located dot in three sessions. The standing portion of a session was conducted using only the plain wooden and red box tested in Experiment 1.

At this point, two-box displacement tests were conducted. In the test session, the functional and non-functional blue boxes were put into the arena together and displaced equidistant from the out-of-reach banana and in a triangular arrangement. This pigeon then participated in two baseline training sessions and was tested a second time three days later with the blue boxes and banana in the same arrangement, but in new locations. Both test sessions lasted approximately 10 minutes.

Pigeon #3L: Because this pigeon was experimentally naïve, it was trained from the beginning using only the functional and non-functional boxes based on the same training protocol described in Experiment 1. Training of the standing/target pecking behavior was conducted using only the red box.

Once training was completed after several weeks, this pigeon participated in a series of displacement tests. The pigeon was first tested in two different two-box displacement tests, separated by seven baseline training sessions. The pigeon was then tested in a single-box displacement test using just the functional box. Finally, the bird was tested a third time in the two-box displacement test.

After this, #3L continued to be tested for several additional training sessions. The purpose of these sessions was to establish that the functional and non-functional boxes could be visually

discriminated. In these sessions, both boxes were present during the goal-directed portion of training. Only moving of the non-functional box onto the small black target dot was reinforced, however. Any manipulation of the functional box was not reinforced. After the pigeon obtained reward for moving the non-functional box to the dot, both boxes were briefly removed from the arena and reset to new locations. These daily differential training sessions lasted until 20 rewards were obtained.

Behavioral Scoring: Data from the displacement tests were analyzed by having two observers score each session as to the number and timing of the same events as before, but expanded to include the non-functional box. Agreement was high for the different box contacts (correlation $r(25)=.99$ across the two raters using 30-s bins). Videos were again scored for the spatial position of the boxes relative to the camera's location by digitizing their position from every fifth frame.

Results

Both pigeons learned to move the two different boxes to the black target dot during training. There was no difference in their ability to move either box to the target dot. The mean time required to move the boxes to the target dot after initial contact with a box was equivalent as measured during the warm-up portions before their first displacement test (#1A – functional = 31.5 ± 4.9 , non-functional = 31.3 ± 18.5 s; #3L functional = 32.5 ± 12.5 s, non-functional = 46.2 ± 21.8 s). Both pigeons also readily learned to stand on the red box and peck the banana target and did so quickly and repeatedly during warm-up. The next sections separately describe each bird's results for the two-box displacement tests.

Pigeon #1A—When both the displaced functional and non-functional boxes were available as potential means to reach the banana, this pigeon exhibited no differential behavior directed towards the functional box during either test. This suggests little insightful or functional understanding of the means-end relations required to solve this modified form of the displacement problem.

During the first test, the functional box was contacted first at 14 s into the test. This was shortly followed by attempts to move the non-functional box at 23 s. After that, the pigeon equally distributed its behavior towards both boxes, alternating his efforts of moving the two boxes around the arena. Shown in the top left panel of Figure 2 are the mean number of times the pigeon contacted the two boxes during this test. Over the first two minutes, the pigeon alternately moved both boxes around the arena, at which point these box-directed behaviors gradually decreased as pushing behavior appeared to extinguish. Shown in the top left panel of Figure 3 are the tracks of each box around the arena during the test. Overall, the number of contacts with the non-functional box were slightly greater and this box was moved a greater total distance (138 cm) around the arena than the functional box (108 cm). Approximately 73% of the movements of the non-functional box reduced the distance to the banana target, while only 53% of the movements of the functional box did so. Thus, when presented with two competing boxes having equal experience, the directed movement and target-oriented synthetic behavior documented for this bird in Experiment 1, failed to emerge.

The second test was a repeat of the first one, with the pigeon exhibiting little differential behavior to the two boxes. The pigeon again began pushing both boxes soon after being placed in the arena. The non-functional box was contacted at 29 s into the test and the functional box at 46 s. After this, behavior once again alternated between moving the two boxes around the arena with no strong preference for either one. The top right panels of Figures 2 and 3 again show the mean number of contacts with the functional and non-

functional boxes and their varied tracks around the arena during the second test. The functional box was moved a total of 335 cm, with approximately 48% of these movements reducing the distance to the target at some point. The non-functional box was moved a total of 237 cm, with approximately 69% of these movements reducing the distance to the target. Thus in both tests, this bird showed no evidence of the directed synthetic behavior it exhibited in Experiment 1. Further, no differential behavior among the boxes emerged that could be attributed to the recognition of their different functional properties towards resolving the displacement test.

Pigeon #3L—The behavior of this pigeon contrasted somewhat from that of the first bird. It did exhibit differential behavior to the boxes within test sessions, although not consistently across the sessions. It solved the task in each test by eventually standing on the functional box, but the pattern of behavior and movement of the boxes across the sessions suggests that this bird did not have a strong understanding of the different functional properties of the boxes.

In the first test, #3L showed some elements of behavior expected of a means-end analysis of the situation. This bird spent the first 30 s of the session initially orienting towards the banana target and attempting to reach it directly by standing beneath it. The pigeon first contacted the functional box at 32 s into the test. The bird then proceeded to move this box around the arena, but did so along a trajectory that did not greatly reduce the distance to the target. While moving the functional box, the bird also made first contact with the non-functional box at 53 s. This contact resulted in moving this box towards the outside of the arena. The pigeon then spent most of the remainder of the test moving the now generally more central functional box, with brief breaks to orient towards the banana. Bird #3L did successfully reach the banana, however, on his second climbing attempt at 214 s into the session. Thus, after about 3.5 minutes after the start of the test, this bird exhibited behavior which by our pre-experimental criteria would have suggested a means-end analysis of the situation, as the bird selectively and exclusively directed behavior towards only the functional box and solving the problem.

Shown in the bottom left panel of Figure 2 are the mean number of times the pigeon was scored as making contact with the two boxes over the test. It is clear that #3L behaved differentially towards the two boxes by this measure. Shown in the bottom left panel of Figure 3 are the tracks of the two boxes around the arena during the test. Similar to the first bird in the two-box tests, but unlike the results of Experiment 1, the track of the functional box is spatially widely distributed and often undirected towards the banana goal. A number of times the box was in proximity to the overhead banana, but the bird failed to stop moving it to stand on it. The bird moved the functional box a total of 597 cm around the arena, with 53% of its movement resulting in reducing the distance to the banana target. Thus, the total length and variability of the functional box's movement relative to the target was far less directed than observed during any of the prior single-box tests. Thus, it is possible that the pigeon had fallen into its solution by virtue of its exclusive movement of the functional box around the arena rather than the more directed solutions we had previously observed in the single-box case. An additional concern was that the initial contact with the non-functional box had resulted in it being displaced to the outside of the arena, which might have contributed to the focused behavior on the functional box.

The results of the second test were clearly inconsistent with a mean-end analysis. Here the first contact to the non-functional box was made at 20 s into the test, while the first contact with the functional box occurred at 73 s. The bird then spent most of the first two minutes moving the non-functional box around the region of the banana (see middle bottom panel of Figure 3). After this, both boxes were then alternately moved around the arena with the bird

directing behavior back and forth towards both boxes because of their proximity to each other. The trajectories of the boxes are shown in Figure 3. The bird moved the functional box a total of 183 cm around the arena, with approximately 75% of these movements resulting in reducing the distance to the banana target. The bird moved the non-functional box a total of 302 cm around the arena, with approximately 55% of these movements reducing the distance to the target. Eventually after this alternating focus on both boxes, the functional box arrived at a location that permitted reaching the banana and #3L climbed on the functional box and pecked the banana at 262 s into the test. While successful, the considerably greater time and effort spent devoted to moving the non-functional box and the variable and undirected paths of both boxes around the arena again suggested that the eventual solution was not the product of functionally-directed behavior.

The purpose of the third test was to compare how this bird behaved in a single-box displacement test. When tested with only the functional box present, pigeon #3L successfully completed the test in just 24 s. Although performed more quickly, this bird's behavior was highly similar to the two birds tested in Experiment 1. This bird directed its initial behavior towards the banana target and then proceeded to move the single box directly to the vicinity of the banana, stand upon it, and peck the banana. Figure 4 shows the track of the box and behaviors exhibited by this bird displayed as in Figure 1. The bird moved the functional box a total of 45 cm around the arena, with 92% of these movements resulting in reducing the distance to the banana target.

Although this pigeon had now been tested in three displacement tests without reward, we tried a third two-box displacement test. The bird's behavior in this test was similar to the second test, although its solution occurred sooner. The pigeon made contact with both boxes early in the test (functional-3.4 s; non-functional-5.4 s) and moved them about the arena by alternately moving each. Shown in the bottom right panels of Figures 2 and 3 are the mean number of times the pigeon made contact with the two boxes and the separate tracks during the third test. The bird moved the functional box a total of 103 cm around the arena, with 55% of these movements resulting in reducing the distance to the banana target, while the non-functional box was moved a total of 64 cm around the arena with 69% of these movements reducing the distance to the banana target. With both boxes moved quickly into proximity to the banana, this bird then stood on the functional box and pecked the banana at 57 seconds into the test.

Finally, #3L was tested to see if the bird could visually discriminate among the two boxes. This discrimination was quickly learned, with the bird moving only the nonfunctional box to the target dot by the end of the first session and continuing to do this in the next session. Pigeon #3L's success at this discrimination indicates that the visual appearances of the two boxes were distinctive.

We did train and test a third pigeon. In two different two-box displacement tests, this bird failed to exhibit differential behavior to the two boxes and never "solved" the task. However, this bird also exhibited very low levels of behavior to the two boxes during the test. We also never had the opportunity to confirm that this bird could solve the single-box displacement problem. While the latter consideration limits the interpretation of this bird's failure to perform in the two-box tests, its implied non-differential behavior towards the two boxes was in keeping with that observed with the two birds detailed above.

Discussion

Overall, the results of Experiment 2 were not consistent with a means-end analysis of the pigeons' synthetic behavior. Both birds demonstrated a capacity to solve the single box problem (#1A in Experiment 1, #3L in Experiment 2) in manner analogous to that described

by Epstein et al. (1984). When confronted with choosing between two boxes with functionally different characteristics, but equivalent reinforcement histories, the birds engaged in actions suggesting they were not performing any functional analysis of the situation. Pigeon #1A repeatedly failed to show selective or differential behavior towards the functional and non-functional boxes, interacting with and moving both boxes about the arena equally over the course of the test sessions. Unlike the directed pushing behavior demonstrated in the single-box case, this bird's goal-directed behavior was highly disrupted during the two-box tests, as both were moved extensively about the arena in an aimless manner.

The actions of pigeon #3L were perhaps more suggestive of a means-end analysis in that this bird was more selective towards the boxes within a session and did eventually "solve" the problem in all three two-box tests. When compared to its performance in the single box condition, however, #3L's overall behavior in multiple two-box tests lacked the selective and directed action indicative of a functional understanding of the problem at hand. This is revealed in several facts. While this bird did initially select the functional box in the first test, when combined over all three tests, however, this bird showed little selectivity by making extensive contact with both boxes. In the second test, for example, most of the behavior was selectively directed to the non-functional box. In addition, for the majority of time during the second and third tests, this bird was focused on alternately moving both boxes around the arena in tandem. Spatially as well, this bird's movements of the boxes seemed undirected and highly variable in comparison to its single box behavior, often moving the boxes away from the target as well as towards it. Finally, the solution times for the two-box cases were consistently slower than its single box case and those observed in Experiment 1 with the two other birds. While the aggregate of this bird's behavior to both boxes eventually resulted in a "solution", there was little convincing evidence suggestive of it exclusively moving the functional box towards the banana as a goal-directed action in the same way as in the single box case. If the birds had been acting in a manner consistent with a means-end analysis, the non-functional box should have been ignored. This kind of selectivity is often taken as evidence of planned actions and mean-ends analysis in tool use, for example (Chappell and Kacelnik 2002, 2004; Visalberghi et al. 2009). The consistent "error" by both birds in selecting, contacting, and moving the non-functional box about the arena, the undirected movement of both boxes, and the considerably slowing or nonexistent solution in the two-box cases are inconsistent with any means-end analysis of this form of the displacement problem.

General Discussion

The results of the current experiments suggest that pigeons may not possess a strong appreciation of the means-end relations of the elements involved with solving box displacement problems. We were able to replicate the kind of directed action and solution outlined in the original report for the single-box case. When confronted with a two-box situation in which functional information (i.e., a flat solid standing surface) derived from the elements would have provided the best solution, the pigeons exhibited no behavior reflecting the use of such information. Instead of selecting the appropriate box and quickly directing it towards the banana target, the pigeons engaged in moving both functional and non-functional boxes extensively around the arena. Their manner of doing so contrasted sharply with the more directed behavior exhibited in the single box case. The behavior of both birds suggests the addition of the non-functional second box disrupted the smooth integration of behaviors that emerges in the single box case. What was the source of this interference?

One possibility is that the origin of the problem involves the history of reinforcement from learning to move both boxes towards the target dot goal. Summarized in Figure 5 is a

potential analysis of this situation. The upper part of the diagram reflects Epstein's chaining analysis of the single box task (Epstein 1991). The major argument is that birds successfully show synthetic behavior in the single box case because they can smoothly link transitions between established behaviors. The pigeons initially engage in orientation behaviors towards the target banana due to its history of direct reinforcement during the training of standing behavior. Because the target is not directly obtainable, this behavior diminishes and is then replaced by the only other behavior that has been reinforced in the situation, box pushing. This results in the box moving closer to the target banana, which in turn causes box standing to begin to emerge as its proximity to the banana target decreases. This sequencing or chaining of established behavior results in the apparently seamless solution to the single box case.

The lower panel of Figure 5 shows why this chaining breaks down in the two-box case. Without the higher-order information of any means-end analysis tied to the functional characteristics of the boxes to disambiguate the situation, when challenged with a situation in which two equally reinforced possible elements or paths for future action are available, the pigeons seemingly engage in both with approximately equal frequency and thus interferes with the sequencing of behaviors need to solve the problem. A second possibility is that with two rewarded items present in the arena for the first time, their combination creates an added salience that causes behavior to be strongly directed to the boxes and overshadows or prevents selective action or the emergence of standing behavior. Either way, this competition from the presence of two boxes results in the interference with the seamless synthetic behavior observed in the single box case. If this is the case, it suggests that the prior synthetic behavior from a single box case might also a product of the combination of learned simpler behaviors rather than a more sophisticated analysis of means-end relations (Shettleworth 2010).

Perhaps the functional properties of the different boxes could have been acquired with more experience. The pigeons certainly had considerable exposure to the two boxes during their training to move the two boxes. Thus, simple exposure seemed to be insufficient for them to learn their functional characteristics, at least as related to standing. Could the pigeons have been taught to attend to the functional characteristics of the different boxes? The answer is surely, yes. Perhaps if we had done the box standing training on the functional box rather than one of a different color, then this direct experience might have more easily generalized and been visually recognized in the two-box test situation. That such explicit experience is needed is partly the point. Without some form of direct experience, the pigeons did not seem to naturally recognize or perform any means-end analysis of the functional properties of the elements involved, at least in the present case.

One possibility to consider is that the displacement task tested here is a highly artificial and contrived one for pigeons. Perhaps a problem using characteristics more naturally attuned to the pigeons' typical behavior might serve to reveal this animal's ability to detect, extract, and use functional information (Call 2006). For instance, what if the artificial "banana" and its secondary relationship to food were replaced with real food hanging from the ceiling? Such direct arrangements have been successful with some birds in string pulling tests for example (Pepperberg 2004; Werdenich and Huber 2006; Heinrich and Bugnyar 2005). However such arrangements with food can also have their own separate motivational problems that can interfere with the successful solution of a task (Boysen et al. 1996). This is certainly something to explore, however.

A number of extensions of the current task should be examined in the future to better understand how context and experience influences the emergence of synthetic behavior in displacement tasks. One of the more compelling questions, especially for any experiential-

based analysis, regards how and why the pigeon in the single box case directs the box towards the banana target in the first place. While pushing might be expected given its previously reinforced nature, this experience had only been to the variably-located dot target. In the single box test situation, this stimulus/goal is absent and the pigeon instead directs the box towards the location of the banana. Short of a means-end analysis, this new “goal” must be derived by determining that this location is the best place in the arena for obtaining reward. This is presumably determined by the history of reinforcement at locations proximal to the banana. If so, an interesting future test would be to have a situation in which two potential spatial locations in the arena have similar histories of reinforcement - one functional (under the banana) and one that is not. If the current analysis is correct, much like in the two-box case, the pigeon should find it difficult to figure out which of these two locations it should direct its actions towards, when faced with the single-box displacement problem.

Further tests that varied the spatial arrangement of the multiple boxes would also be of value. We doubt, for example, that a pigeon could walk by a previously rewarded non-functional box to obtain a more distant functional one (even one also used for standing training) in pursuit of a solution to the displacement problem. In such a context, we would guess the dominance of sign-tracking behavior would override any potential functionally-motivated analysis (Hearst and Jenkins 1974). Looking at contextual factors would also be valuable. For instance, if box-standing and box-pushing were trained in different looking contexts could the pigeons show the same degree of integration as when these two behaviors are trained in the same context as done here? A mean-end analysis would predict that this type of integration should not be a challenge, whereas an experiential analysis would suggest that this situation would limit the pigeons’ ability to link these separate behaviors.

The current results are consistent with other observations from our lab that pigeons do not have a strongly developed sense of means-end relations in physical tasks. Schmidt and Cook (2006) found that pigeons likely did not comprehend the functional nature of connectedness across different versions of a “string-pulling” support task. Instead, they likely learn to perform such discriminations based on the perceptual features present in the task. Although pigeons are excellent learners of various kinds of complex visual and auditory relations in operant settings (Cook and Wasserman 2006, 2007; Cook 2002; Cook and Brooks 2009), it appears their understanding of mean-ends relations in physical settings may be more poorly developed, especially in comparison to other species of birds. One challenge for the future is the integration of these approaches and their opposing assessments of the cognitive capacities of this species.

There is a growing literature documenting the capacity of various psittacid and corvid species’ to solve a number of physical tasks seemingly involving mean-ends analyses and solutions (Heinrich 1995; Funk 2002; Pepperberg 2004; Dürcker and Rensch 1977; Liedtke et al. 2011). The reasons why certain species can perform well in these different kinds of physical means-end tasks, while others apparently cannot, is still not well established (e.g. Emery 2006; Lea et al. 2006; Werdenich and Huber 2006; Kirsch et al. 2008), but may be related to their natural history. For instance, it is worth noting that pigeons are a species that is not adept at using their beak or feet for manipulating or processing objects, unlike parrots, keas, and corvids (Bluff et al. 2007). Whether there is a relation between such embodied physical and motor manipulation and corresponding cognitive characteristics is an open question for future investigation (Wilson 2002). Of course, this “limitation” might not be such a big obstacle for pigeons. Their niche just may not make much call on means-end analysis or its associated behavioral flexibility. Instead, relying on their learned experience with specific situations may be sufficient to successfully mediate the vast majority of their daily interactions with environment. This certainly hasn’t greatly limited their geographic

distribution or their transition to and recent success in urban settings. Because the exact origins of the different behaviors involved can be monitored and assessed, it would be F and valuable to see how other avian species with potentially better developed capacities for physical cognition perform in the kinds of displacement tasks developed here. Such results will help us understand the relations between reasoning, experience, action, and consequence in the distribution and evolution of intelligent and adaptive behaviors across animals.

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Figure 1. Behavior exhibited by the two pigeons tested in Experiment 1. The two pictures to the left show the path of the box and the locations (open circles) and times (in seconds) where the pigeons stood on the box during the test session. The graphs to the right show the behaviors exhibited by the pigeons over the test in 10-s bins (filled circle=box contact/push; open squares=target directed behavior from the ground; filled circles=target directed behavior from box).

Figure 2.

Behaviors to the two boxes exhibit by the two pigeons during the two-box displacement tests of Experiment 2. The top two panels show the mean number of functional and non-functional box contacts for pigeon #1A during its two tests in 30-s bins. The bottom panels show the mean number of functional and nonfunctional box contacts for pigeon #3L during its three tests in 30-s bins.

Figure 3.

The spatial position of the functional and non-functional boxes for each pigeon during the two-box displacement tests of Experiment 2. The top two panels show these data for the two tests with pigeon #1A. The bottom three panels show these data for the three tests with pigeon #3L.

Figure 4. Behaviors exhibited by pigeon #3L in the single-box displacement test of Experiment 2. The left panel shows the path of the box and where the pigeon stood on the box during the test session. The graph to the right shows the behaviors exhibited by the pigeon over the test in 10-s bins (filled circle=box contact/push; open squares=target directed behavior from the ground; filled circles=target directed behavior from box).

Analysis of Single Box Task

Analysis of Two Box Task

Figure 5.

The hypothesized sequence of behaviors in the different tests conducted in these experiments. The top panel shows the behaviors involved with the synthetic solution observed in a single-box displacement test. The bottom panel shows the behaviors generated during a two-box displacement test and why it results in interfering with the pigeons' abilities to effectively solve this form of the displacement problem.