Journal of Comparative Psychology
2013, Vol. 127, No. 3, 272–281

0735-7036/13/$12.00 DOI: 10.1037/a0031641

Reasoning by Inference: Further Studies on Exclusion in Grey Parrots (*Psittacus erithacus*)

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Grey parrot (*Psittacus erithacus*) abilities for visual inferential reasoning by exclusion were tested in two experiments. The first replicated the Grey parrot study of Mikolasch, Kotrschal, and Schloegl (2011, African Grey Parrots (*Psittacus erithacus*) use inference by exclusion to find hidden food. *Biology Letters, 7,* 875–877), which in turn replicated that of Premack and Premck (1994, Levels of causal understanding in chimpanzees and children. *Cognition, 50,* 347–362) with apes, to learn if our subjects could succeed on this task. Here parrots watched an experimenter hide two equally desirable foods under two separate opaque cups, surreptitiously remove and then, in view of the birds, pocket/eat one of the foods, leaving birds to find the still baited cup. The experiment contained controls for various alternative explanations for the birds' behavior, but birds might still have avoided a cup from which something had been removed rather than specifically tracking the eaten food. Thus, in the second experiment, some trials were run with one food slightly more preferred than the other, during which *two* items of each type were hidden and only one of the items were removed from one cup. Sessions also included Experiment 1-type trials to see if birds tracked when and when not to use exclusion. Thus, birds would be rewarded for attending closely to all the experimental aspects needed to infer how to receive their preferred treat. Three of four birds succeeded fully.

Keywords: Grey parrots, inference by exclusion, avian cognition, avian intelligence, avian attention

Several recent studies of comparative avian cognitive competence have focused on reasoning by exclusion; that is, the ability to base a decision on the exclusion of potential alternatives. To what extent exclusion is a fair test of avian—or any nonhuman—abilities has, however, not conclusively been determined. As is the case for most cognitive abilities, exclusion is not likely a unitary phenomenon, but rather involves several levels of competence, and many experiments conflate the different levels (see review in Hill, Collier-Baker, & Suddendorf, 2011a). For example, at the simplest level, exclusion merely involves avoidance. A subject, given A and B, with significant experience or training in picking A when told "take a" but for whom B is novel, is asked to "take b." The subject generally picks B, not necessarily because of any inferential reasoning that "b" is related to B, but because it does know not to choose A in the absence of "a"; that is, to avoid choosing A in the absence of the appropriate cue. Young children at the earliest stages of language acquisition, disabled children, and several nonhuman species perform quite well on this task (Carey & Bartlett,

This article was published Online First February 18, 2013.

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This study was supported in part by NSF Grants BCS-0920878 and BCS-1026256 (to Ken Nakayama) and by donors to The Alex Foundation (particularly Alex and Michael Shuman and the Marc Haas Foundation, the Anders Sterner family, Anita Keefe, Janice Boyd, Pat Hill, Nancy Chambers, Kathryn and Walter McAdams, Nancy Sondow, Joseph Golden, Megumi Oka and the Makioka Foundation, The Platinum Parrot—Lisa and George Bono, Elva and Bob Mathiesen, Bird Paradise, Jan and Jeff Strong, Bill Broach and Nancy Clark, Ellen Paul, Deborah Rivel Goodale/Wildtones, Patti DeMar Hauver, Roni Duke, Sean Lennon, Jean Berko Gleason, Charlene Bebko, Don and Grace Wheeler, and the Raleigh-Durham Caged Bird Society). We thank Adrienne Karlovsky for assistance in carrying out trials (interobserver reliability), and Harrison's Bird Food and Fowl Play for foods and treats, Avian Adventures and Bird Paradise for Griffin's and Arthur's cages, and Carol D'Arezzo for Griffin's stand. We also thank unknown reviewers for their assistance. The study procedures comply with the current laws of the country under which they were performed (U.S.A.).

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1978; Dixon, 1977; Kaminski, Call, & Fischer, 2004; Pepperberg & Wilcox, 2000; Pilley & Reid, 2011; Schusterman & Krieger, 1984; Schusterman, Gisiner, Grimm, & Hanggi, 1993; see discussion in Aust, Range, Steurer, & Huber, 2008). However, in all these studies, full understanding of the relationship between "b" and B—strong inference by exclusion—is slower to develop. In most cases, if the subject, soon after choosing B, is then given B, C, and D, where C and D are novel, and is again asked to "take b," the level of correct response is not always above chance (Dixon, 1977; Kastak & Schusterman, 1994; again, see Aust et al., 2008), and a correct response could be a consequence of choosing the least novel item. Likewise, if B and C—both novel—have recently both been chosen by exclusion in separate trials, and are then pitted against each other in additional trials, subjects also respond mostly at chance (note Griebel & Oller, 2012; Wilkinson, Ross, & Diamond, 2003). Furthermore, extension of the targeted term "b" to anything other than the exact novel object B (i.e., to other B-like items)—that is, generalization—usually takes considerably longer to develop (e.g., Schusterman et al., 1993; Schusterman & Krieger, 1984).

Recently, the concept of exclusion has been extensively tested in the nonlinguistic arena in birds, involving tasks such as searching for food under one of two hiding sites after being shown that the other is empty. A number of different avian species (Grey parrots, *Psittacus erithacus*; jackdaws, *Corvus monedula*; keas, *Nestor notabilis*; ravens, *Corvus corax*; carrion crows, *Corvus corone corone*) and an assortment of related tasks have been used with varying outcomes (e.g., Mikolasch, Kotrschal, & Schloegl, 2011, 2012; Schloegl, 2011; Schloegl et al., 2009; Schloegl, Schmidt, Boeckle, Weiss, & Kotrschal, 2012). In many cases, the results were exquisitely dependent upon the details of the experimental design and possibly upon the history of the subjects. For example, Grey parrots could respond to auditory clues as to whether a closed container was full or empty, but only when the container was shaken horizontally, not vertically (Schloegl et al., 2012). In all instances, however, exclusion requires at the least a concept of object permanence (OP)—an understanding that hidden objects do not cease to exist (Piaget, 1952)—yet transferring human-based tests of even such basic concepts as OP to nonhumans require considerable care. For example, in an early study of OP, the Grey parrot Alex was incapable of succeeding on one standard task given to children until he had had experience simply interacting with multiple objects simultaneously (Pepperberg & Kozak, 1986). Notably, some subjects in exclusion studies seemed to have initial difficulties in tracking hidden objects (e.g., somewhat surprisingly, jackdaws in Schloegl, 2011; carrion crows distracted by local enhancement in Mikolasch et al., 2012) and, in other cases, tasks involved the subjects responding in a manner that did not necessitate a full understanding of exclusion (i.e., using avoidance rather than inference; see discussions in Schloegl, 2011 and Mikolasch et al., 2011).

Despite these issues, differing results for different avian species have often been used to support not only discussions of differing levels of intelligence, but also various evolutionary theories (e.g., "adaptive specialization hypotheses" concerning caching vs. noncaching, or other aspects of feeding ecology; again, see Schloegl, 2011 and Mikolasch et al., 2011, 2012). Quite likely, however, differing results may occur because of individual differences in the subjects involved (usually a small number), somewhat different experiences in living/rearing conditions for the various species, or somewhat different task constraints. We propose to examine some of these possibilities. Notably, exclusion may be a basic phenomenon underlying various cognitive abilities, and different tasks may delineate different aspects of exclusion. Such a stance argues that similar evolutionary pressures, working on different species, may have resulted in similar forms of intelligence that can be adapted for different tasks (e.g., Bolhuis & Macphail, 2001; Pepperberg, 1999).

Given that Grey parrots seem to have some sensitivity to exclusion in the linguistic sense (Pepperberg & Wilcox, 2000) and that at least one Grey parrot exhibited an understanding of physical exclusion in a study that tightly controlled for issues such as avoidance and simple associational learning (Mikolasch et al., 2011), we decided to repeat the latter study with Greys in our laboratory, who have had considerable experience with OP (Pepperberg, Willner, & Gravitz, 1997) and/or hidden objects (Péron, John, Sapowicz, Bovet, & Pepperberg, 2012) and symbolic representation (e.g., Pepperberg & Wilkes, 2004) to see if they would also pass the tests (Experiment 1), and, if so, then expand the testing to determine more about what they do or do not understand about the concept of exclusion (Experiment 2). We also tested two Greys who were "pet" birds, but who lived with humans who had formerly been trainers in our laboratory and who could be relied upon to carry out trials the same way as in the laboratory. The pet birds had never been formally tested for OP, but were given daily foraging tasks, involving the discovery of treats hidden in various ways. Given that these four birds were reared in, and now live in completely different conditions from Mikolasch, Kotrschal, and Schloegl's (2011) zoo-based Greys, that two are pets and two live in a laboratory, our findings in Experiment 1 would examine the extent to which some degree of reasoning by exclusion is widespread among Greys. Experiment 2 was designed to test exactly what Grey parrots remembered and understood about the conditions of the task.

Experiment 1

Here we repeated the study of Mikolasch et al. (2011), which required Greys to exhibit a fairly advanced level of inferential reasoning by exclusion; we also repeated part of the study of Mikolasch, Kotrschal, and Schloegl (2012) to test for local enhancement. We adapted the procedures as described below. As in the original Premack and Premack study (1994) with apes, we hid two equally desirable items under two opaque cups; subsequently the parrots were allowed to witness an experimenter eat one of the items, which had been removed secretly (invisible condition) or in full view (visible condition), or watched an experimenter simply handle an object identical to one that was hidden (association control), and were then allowed to choose one cup. Our predictions were that, like one of the Greys in Mikolasch et al. (2011), our birds would successfully reason by exclusion.

Method

Subjects

One set of Grey parrots (*Psittacus erithacus*) to be studied, Griffin and Arthur, was tested in a laboratory at Brandeis University. Both birds have served as subjects of continuing studies on comparative cognition and interspecies communication (e.g., Pepperberg & Wilcox, 2000; Pepperberg & Wilkes, 2004). Griffin was 16 years old at the time of the experiment and had demonstrated full OP as a juvenile (Pepperberg et al., 1997); he had been in the lab since he was 7.5 weeks old. Arthur was 13 years old and had been in the lab since he was 1 year old. Arthur had not been formally tested on OP, but, like Griffin, had been the subject of a study requiring both birds to choose one of four cups, each of which had different reward consequences (Péron et al., 2012). Thus, both birds understood that the vocal phrase "Go pick up cup" was a request to make a choice and that items that had been hidden under the cups should still be available (depending on cup color; in Péron et al., one cup color also indicated "empty"). Housing and general feeding conditions are described in Pepperberg and Wilkes (2004). Birds were not food or water deprived at any time. For Griffin, testing occurred on a T-stand outside his cage; for Arthur, testing occurred atop or at the entrance to his cage.

Another set of Greys, Pepper and Franco, lived in a suburban household (Hartsfield) with two adult humans who had previously been trainers in the Brandeis lab. Humans and birds had visited Brandeis where humans had observed an exclusion session with Griffin and Arthur. During the visit, Pepper and Franco engaged in preliminary trials demonstrating that they would indeed choose cups on demand. Pepper, a female, was 15 years old and had lived with the Hartsfields since she was about 3 months old; Franco, a male, was 10 years old and had joined the household when he was 7 years old, having lived with another family previously. Pepper had received considerable training on referential communication (e.g., Pepperberg, 1981), but had not been formally tested on her production or comprehension; Franco had entered the Hartsfield household with the capacity to produce some human speech, but his referential knowledge was unknown. He subsequently had about 3 years of referential training, but no formal testing. Again, neither bird was food nor water deprived. Trials occurred on a parrot stand near their cage (Franco) or atop their cage (Pepper).

Materials

The Brandeis apparatus consisted of two same-sized plastic cups of differing colors (First Years Stack N Count Cups™) placed on a felt-covered tray equidistant from each other and from the parrot's beak (see Figure 1). The specific cups and the tray had been used in various ways in previous experiments (e.g., Pepperberg et al., 1997; Péron et al., 2012) and were thus familiar. A similar tray and equally familiar cups were used for the Hartsfield birds. A preliminary trial showed that two differently colored cups assisted birds in tracking what was under each cup, possibly as a consequence of previous experience (Péron et al., 2012). Moreover, distinguishing identical cups, as in the Schloegl et al. (2009), Schloegl (2011), and Mikolasch et al. (2011) studies, relies on spatial memory (i.e., for left vs. right position), which was not what the experiment was intended to test (note Hill et al., 2011a). Rewards consisted of equally desirable small treats (bits of differently colored jelly beans) not available outside of sessions; birds had shown no preference for particular colors or flavors of the beans used in previous experiments (e.g., L. A. Hartsfield, personal communication, November 2011; Péron et al., 2012). The colors of the cups and the beans could not be the same, because in training in a concurrent study, Griffin was cued to choose a particular cup via a particular corresponding color cue. Cup colors (yellow and green) were thus chosen to be distinct from the jelly beans used (orange and purple). So that the experimenter could, when appropriate, cover the rewards simultaneously with the cups and demonstrate the various manipulations, in the Brandeis lab the tray was initially placed on a wooden stool in front of the bird; the stool was a fixture in the laboratory and on which the tray was often placed during other studies (Péron, Thornberg, Gray, & Pepperberg, in preparation). For invisible manipulations, the tray was placed on a second stool out of sight of the bird, so that a treat could be removed without the bird seeing which cup was being manipulated. Hartsfield used comparable methodology (i.e., slightly larger cups that were as familiar to her birds as the cups in the Brandeis laboratory were to the Brandeis birds).

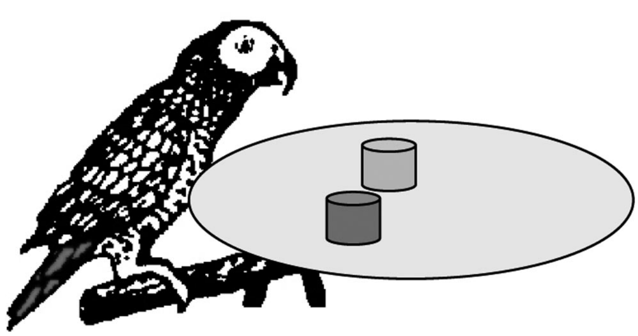

Figure 1. Schematic of parrot and tray, with two differently colored cups.

Procedure

Human cuing controls. We conducted controls to see if humans might be cuing the birds to choose the appropriate cup via head, eye, or body position, although we did not expect such cuing to be an issue. Earlier studies had already demonstrated that Greys do not use human cues in choice experiments unless the cues are deliberate and obvious. Specifically, parrots did not previously respond to human gaze direction when objects on a tray were closely spaced ($<$5 cm) and the human head was about 30 cm away from the tray (Pepperberg, 1990, 1999), which was also the case here. In the Giret, Miklósi, and Kreutzer (2009) study in which Grey parrots did respond to human gaze, the two objects of interest were 1.6 m apart and the human face was deliberately turned in the direction of one of the objects; thus, the bird could easily distinguish the line of sight, unlike the situation in the current study.

Given that the jelly bean treats are not a healthy food for parrots in large quantities, and such controls required a massing of trials, we initially performed these controls with pieces of raw cashew or other healthier treats. Out of sight from the bird, a treat was placed under one cup on the tray; the tray with both cups was then presented to the bird with the experimenter looking directly between the two cups; the bird was then allowed to choose. Placement of the treat and cup color was randomized from trial to trial, using www.random.org. Because birds had not demonstrated any preferences in an earlier study (Péron et al., 2012), we performed only two sessions/bird of 10 trials each, and tested the Hartsfield birds in only one session. Fewer nut trials were given to the Hartsfield birds because they were losing interest or beginning to use a side preference. Both touching the cup with the beak and overturning the cup were considered choices. (Sometimes birds grabbed the cup from an angle that made overturning difficult; we labeled such actions "touching.")

Olfactory cues. Similar controls were conducted for olfactory cues with jelly beans, which were slightly more scented than nuts. Because of health reasons as noted above, only 10 trials were administered for each bird. Again, placement of the bean was randomized from trial-to-trial.

Visible/invisible tests. Tests consisted of two conditions, a visible and an invisible one. Although we performed statistics on the tasks independently, trials were intermixed so that birds never knew what type of session they would receive. The order of conditions was randomized. Both sessions began with the placement of a bird in his or her respective position. Out of sight from the bird, the experimenter placed a bean in front of each of the two cups. She then turned to the bird and placed the tray on the stool. Right-left placement of the differently colored cups and beans were randomized among the trials, again using random.org. In both conditions, the experimenter initially called the bird by name, telling the bird to "Look" or "Pay attention" as she covered both beans simultaneously. Sometimes, if the bird's attention seemed to be wandering, she simultaneously uncovered and then recovered the beans. Sessions of two or three trials for each bird, sometimes separated by several days, were conducted per condition until 30 trials total were completed for each condition for each bird.

In the visible condition, in full view of the subjects, the experimenter lifted one cup, manipulated the bean, returned the cup, lifted the other cup, manipulated the bean, returned the cup. The control manipulation consisted of taking the bean, showing it to the bird, putting it back on the tray, covering it, and showing an empty hand after returning the cup. The test manipulation consisted of taking the bean, showing it to the bird and eating it or putting it in her pocket before returning the cup. The right-left order of manipulations was randomized as was placement of the beans, and no bean type was removed more than three times in a row (random.org). Afterward the bird was allowed to make a choice. The bird received the reward for a correct choice, and was shown the empty space under the cup if an error was made.

The invisible condition was identical to the visible condition with the exception that after covering the beans with the cups, the experimenter turned away with the tray, removed a bean out of sight of the bird, turned back, and, in obvious sight of the bird, then either put the bean in her pocket and showed the bird an empty hand or ate the bean.

Association trials. Intermixed with formal testing trials, association control trials were performed with the birds to test if the birds had developed an association rule, "Always choose the cup with the food type not having been shown." Here the experimenter visibly placed the two different beans on the tray, covered them with the cups and then took—in full view of the subject—one jelly bean (of the same type as one of the beans being hidden) out of her pocket, showed it to the bird and put it back in her pocket or ate it. Afterward the bird was allowed to choose. Thirty trials were intermixed with visible and invisible trials.

Local enhancement. Invisible trials effectively controlled for local enhancement—that is, picking, in error, the cup that had been handled—in that the cups and tray were out of sight while the treat was removed, but we decided to run separate tests on the Brandeis birds as an additional control. For Griffin and Arthur, we thus intermixed 30 visible trials in which we did not handle both cups equally, but rather only handled the cup from which the bean was removed. Had Griffin and/or Arthur shown an effect of local enhancement, we would also have tested Pepper and Franco (see below).

Interobserver reliability. In the lab, a second individual independently viewed all trials and noted the birds' choices. Observations were compared for interobserver reliability. A small percentage of trials (10%) were videotaped for additional reliability checks in the absence of data sheets by someone (I.M.P.) who had not watched the trials. In the Hartsfield home, where an independent observer was not always available, 24 trials (12 for each bird for each experiment) were videotaped, digitized, and sent to the lab for identical interobserver reliability tests.

Results

Data for each bird was processed individually, because Arthur and Griffin had previously demonstrated strikingly different results for nonverbal tasks (Pepperberg, 2004, 2007; note also Péron et al., 2012), and Pepper and Franco might have similarly differed.

Visible Tests

All four birds succeeded on the visible task (see Figure 2). Statistics were binomial tests, chance of 1/2. Griffin's score was 24/30 ($p < .01$), Arthur's was 21/30 ($p = 0.02$), Pepper's was 23/30 ($p < .01$), and Franco's was 21/30 ($p = 0.02$). We checked to see if any of the birds made more mistakes on the first versus the last half of the tests (i.e., if learning was involved). Using Fisher's exact test, two-tailed, for Griffin, $p = 1.0$, for Arthur, $p = 1.0$, for Pepper, $p = 1.0$, and for Franco, $p = .43$. All birds were correct on their very first trials. Griffin was correct on all his first five trials, Pepper and Franco on four of first five trials, and Arthur on three of his first five trials.

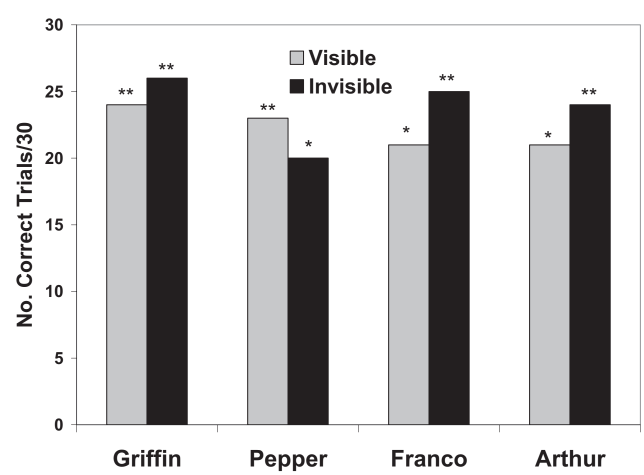

Figure 2. Results for visible and invisible tests involving only jelly beans (* means statistical significance at $p \leq 0.05$; ** at <0.01).

Invisible Tests

All four birds also succeeded on the invisible tasks (see Figure 2). We again used binomial tests, chance of 1/2. Griffin's score was 26/30 ($p < .01$), Arthur's was 24/30 ($p < .01$), Pepper's was 20/30 ($p = .05$), and Franco's was 25/30 ($p < .01$). Arthur and Franco were correct on all five of their first five trials; Griffin and Pepper were correct on four of their first five trials, Griffin missing only the first trial, Pepper the fourth. Pepper was also correct on the very first trial, but because she made 10 errors, we checked to see if her performance differed between the first and last 15 trials (i.e., if learning was involved), but found no difference: 10/15 correct for each half.

Association Tests

On the association tests, birds demonstrated that seeing a trainer simply handle a particular treat did not cause them to choose that treat. All birds chose at chance, that is, chose, for example, orange at the about same rate when either orange or purple were displayed, and vice versa (Fisher's exact test, two-tailed), Griffin at $p = 1.0$ (nine choices of orange when purple was handled, six choices of orange when purple was handled, six choices of purple when purple was handled, and nine choices of orange when orange was handled), Arthur at $p = .71$ (eight choices of orange when purple was handled, five choices of purple when orange was handled, seven choices of purple when purple was handled, and 10 choices of orange when orange was handled), Pepper at $p = .71$ (eight choices of orange when purple was handled, 10 choices of purple when orange was handled, seven choices of purple when purple was handled, and five choices of orange when orange was handled), and Franco at $p = 1.0$ (seven choices of orange when purple was handled, seven choices of purple when orange was handled, eight choices of purple when purple was handled, and eight choices of orange when orange was handled).

Local Enhancement

On these tests, Griffin was slightly less accurate, with a correct score of 21/30, but still statistically significant ($p = .02$, binomial test, chance of 1/2); Arthur was slightly more accurate, with a score of 23/30 ($p < .01$, binomial, chance 1/2). Griffin made essentially the same number of errors in the first half as the second (5 vs. 4), but did err on his first three trials. Arthur also divided his errors essentially equally (3 vs. 4), but was correct on his first trial and four of his first five trials. Given that, in contrast to previous findings (e.g., Pepperberg, 2004), the Brandeis birds performed quite similarly here, as well as the similarity of data among all parrots on all other tasks in Experiment 1, we felt justified in not testing the Hartsfield birds on this particular task.

Controls

On nut and jelly bean controls, respectively, Griffin scored 10/20 (binomial test, chance of 1/2, $p = .59$) and 5/10 ($p = .62$); Arthur scored 9/20 ($p = .41$) and 5/10 ($p = .62$). On nut and jelly bean controls, Pepper scored 3/10 ($p = .17$) for both; Franco scored 4/10 ($p = .38$) and 3/10 ($p = 0.17$), respectively. Thus, no bird was being inadvertently cued.

Interobserver Reliability

Birds never dithered and made all choices deliberately. No disagreement occurred on any trial between on-site observers as to which cup a bird had chosen in the lab. Once a trial was under way, all birds were motivated to participate and their attention did not wander. For the videotaped trials, the independent observer agreed with the original scorers on 100% of the trials.

Discussion

All birds in our study succeeded on the tasks, and demonstrated that they were not cued in any way, nor were they simply choosing the cup that represented the food type that had not been shown. They were all highly attentive and never dithered. Arthur sometimes refused to participate, but in such instances he simply failed to approach the tray, so no trial could be performed. Birds made few errors overall, and for all birds in all conditions, the number of errors in the first and last half of trials were not statistically significantly different. Thus, the birds were not learning the task over time, but seemed to understand the exclusionary concept from the beginning, with most birds choosing correctly on all of their very first trials (only Griffin missed his first invisible trial), and all but Arthur choosing correctly on their first four of five trials for all tasks (Arthur was three for five on his first visible trials, but, again, correct on his first). That is, the birds seemed capable of true inferential reasoning. Given Griffin's overall success, his error in the first invisible trial might have been a consequence of the novelty of the task.

Arthur was not strongly affected by issues of local enhancement and although Griffin did miss his first three trials when we did not control for local enhancement, he seemed to recover fairly quickly and his overall score was correct at a statistically significant level. Thus, neither bird consistently preferred the cup that had been most recently handled, unlike, for example, carrion crows (Mikolasch et al., 2012). The crows eventually did indeed learn to choose by exclusion, but local enhancement could overshadow their inferential abilities. Conceivably, of course, our parrots' prior experience (e.g., with studies on OP and on tokens representing presence and absence of treats, Péron et al., 2012) might have helped them to focus. We know that prior experience can indeed affect the outcome of various tasks for Greys (Pepperberg, 2004, 2007).

We note that the greater success of our birds compared with those of Mikolasch et al. (2011) was not likely a consequence of overall experience in an experimental laboratory, as Franco and Pepper responded as well as did Griffin and Arthur. The major difference in our study was that we used two differently colored cups so that the birds did not have to remember a spatial cue (right-left), but could use cup color instead. Color per se was not a cue, however, as it was randomized on every trial, and did not lessen the need to respond based on inferential reasoning. Possibly, given that Greys eat fruits in the wild whose color indicates ripeness (May, 2004), do not cache/recover foods, fly toward and thus approach familiar spots from different angles and are not likely trying to remember specific location markers (e.g., a rock whose proximity may denote a cache), right-left spatial knowledge might be less useful to Greys than color cues.

We note, too, that Grey parrots, like keas (Gajdon, Amann, & Huber, 2011) and large-billed crows (Izawa & Watanabe, 2011) will, after succeeding on various tasks, often later employ other, less successful or simply different methods, possibly from boredom or maybe to find other possible solutions (exploratory behavior; e.g., Pepperberg & Gordon, 2005). Such exploration could explain some subsequent failures after successes on these tasks (e.g., Arthur missing two of his first five trials after succeeding on his initial trial). In all cases in Experiment 1, however, such behavior occurred only after correct responses, showing that the subject did initially understand and succeed on the task.

We note that, like the successful bird in Mikolasch et al. (2011), our parrots were all able to reason by exclusion, as they all passed the invisible test. We, too, ruled out olfactory cues or associative learning. The birds had to view the bean that was removed invisibly, remember where it had been, and, by exclusion, deduce where the remaining treat had been hidden. We were still concerned, however, that birds might simply be avoiding the cup from which a reward had been removed.

Experiment 2

Here we wanted to determine exactly what the birds knew about what was under each cup. Although the association control trials in Experiment 1 ensured that the birds were not simply going to the cup that represented the food that had not been handled, we wanted to see if both sets of birds conceivably might have focused on the lack of removal of *an* object in these controls, not on a specific object. Thus, we wanted to determine if the bird would still be willing to return to a cup from which a favored reward was partially removed in contrast to a cup that held something to which they were indifferent. Success on these Favorite trials would show that the birds were truly focusing on what was under each cup, and, when intermixed with additional Experiment 1 trials, provide another control that their visible and invisible trials were indeed based on inference. Our main goal, however, was to test whether the birds knew when to use and when not to use inference by exclusion to solve the problem.

For Favorite trials, we thus needed to use two foods differing somewhat in desirability. Both Brandeis and Hartsfield birds consistently choose jelly beans over their standard chow when given a choice outside of testing. Thus, beans and chow were contrasted. The number of correct trials would be the number in which the bird chose the favored food. If a bird chose but discarded beans during testing, it was offered another favorite food to encourage it to continue working.

Method

Subjects and Materials

The same four subjects, the same cups, the same tray, and the same basic setup were used as in Experiment 1. Trials commenced several weeks (Hartsfield) to 2 months (Brandeis) after the end of Experiment 1, timing dependent upon student vacation schedules at the Brandeis laboratory. Again, each bird had two or three trials per session per condition until 30 trials/condition occurred per bird.

Procedures

Favorite trials. Favorite trials, both invisible and visible, were interspersed with the same type of standard visible and invisible trials from Experiment 1, so we could test whether birds could switch between types of trials; the one exception was Arthur, whose standard trials were all invisible. The reason for this difference was that Arthur still had several invisible standard trials to perform for Experiment 1, whereas for the other birds, these trials were in addition to those of Experiment 1. Griffin and Arthur began with a visible Favorite trial, but Pepper and Franco with an invisible Favorite trial, to see if order affected behavior and if the latter pair could succeed on the most challenging problem immediately. Such a contrast was feasible, given that both sets of birds had performed at comparable levels in Experiment 1. In all Favorite trials, birds saw two beans placed under one cup and two pieces of chow under another. Here the experimenter acted as in Experiment 1, and removed either one piece of chow or a bean, invisibly or visibly, and then the birds were allowed to choose; 17 trials were visible and 13 invisible. (Note: We had intended to perform 15 trials in each condition, but the student forming the test schedule interchanged two trials. Furthermore, miscommunication led to Pepper and Franco being given additional trials; however, only the first 17 of their visible and 13 of their invisible trials were counted so that their data collection corresponded to that of Griffin and Arthur.) The question was whether the birds would attend to both the identity and the number of treats and their placement. In all cases, the birds could get at least one bean if they realized that one or both beans had been left under the cups. These trials thus were an additional control for the possibility that the birds had learned to avoid the cup containing what the experimenter had recently eaten, but only when they remembered that multiple items had been stored.

Results

As before, results were calculated for each bird independently.

On Favorite trials, Griffin succeeded on 13/17 visible trials ($p = .02$) and 12/13 invisible trials ($p < .01$). He succeeded on his first trial in each task (see Figure 3). Interestingly, he succeeded on 3/3 of his first visible tasks then missed two, but was correct on 5/5 of his first invisible tasks. On visible Favorite trials, he made more

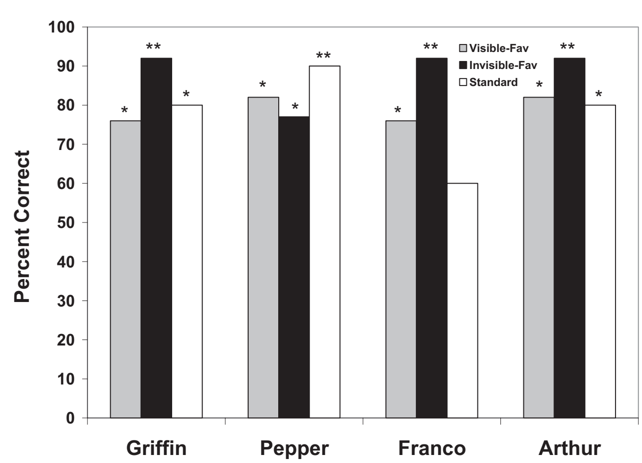

Figure 3. Results of the Favorite trials (visible and invisible) compared with standard trials (* represents statistical significance at ≤0.05, ** at <0.01).

errors on the first than on the second half of his trials, but recovered accuracy quite rapidly: The difference between halves was not statistically significant (Fisher's exact test, two-tailed, $p =$ .29 if the split is 8 and 9 and $p = .58$ if the split is 9 and 8). Errors on visible trials seemed not to involve the side on which the beans were placed (Fisher's exact test, $p = .57$, two-tailed). For intermixed Experiment 1-type trials, he was correct on 8/10 ($p = .05$).

On Favorite trials, Arthur succeeded on 14/17 visible trials ($p <$ .01) and 12/13 invisible trials ($p < .01$). He also succeeded on his first trial in each task. He also succeeded in his first four of five trials in the visible condition, and in five of five first trials in the invisible condition. Thus, learning was not an issue. On Favorite visible trials, Arthur made a few more errors when the beans were in one color cup than the other, but not statistically significantly (Fisher's exact test, two-tailed, $p = 1.0$). He also made a few more errors when beans were on right than left, but again differences were not statistically significant ($p = 1.0$, two-tailed). He made only a single error on the invisible trials. For Experiment 1 trials, he was correct on 8/10 invisible trials ($p = .05$).

On Favorite trials, Franco similarly succeeded on 13/17 visible trials ($p = 0.02$) and 12/13 invisible trials ($p < .01$). In each task, he failed on his first trial but succeeded on his next four of five trials. On visible Favorite trials, he made a few more errors when the beans were in one color cup than the other, but not statistically significantly (Fisher's exact test, two-tailed, $p = .1$). He also made a few more errors when beans were on right than left, but again differences were not statistically significant ($p = .29$, two-tailed). He made a few more mistakes in his first than in his second half of trials, but, as with Griffin, differences were not statistically significant (for a 8–9 split, $p = 0.29$; for a 9–8 split, $p = .58$, two-tailed). Thus, he also recovered quickly. Again, like Griffin, he made only a single error on invisible trials. For intermixed Experiment 1-type trials, he was correct on only 6/10 ($p = .38$), erring on two visible and two invisible trials.

On Favorite trials, Pepper succeeded in 14/17 visible trials ($p <$ .01) and 10/13 invisible trials ($p = 0.05$). She made only one more error on the second half than on the first, so no difference existed. Interestingly, on the invisible Favorite trials, two of her three errors were in her first five trials, but she was correct on her very first invisible trial and on 5/5 of her first visible trials; there were no statistically significant differences between her error on whether beans were in green or yellow cups ($p = .07$) or left versus right cups ($p = .56$). For intermixed Experiment 1-type trials, she was correct on 9/10 ($p = .01$), erring on one visible trial.

Discussion

All four birds succeeded on the Favorite trials, visible or invisible, demonstrating that they did not simply avoid a cup from which something had been removed. Three birds (Griffin, Arthur, and Pepper) also appeared to be able to switch between experimental conditions, that is, to understand something about when to use or to ignore exclusion. Even if we choose to eliminate Arthur because all his standard trials were invisible (a task on which he was slightly more accurate than visible trials, though not at a statistically significant level, $p = .55$, Fisher's exact test, two-tailed), two of three birds understood when to ignore versus use exclusion. Some succeeded in their very first trial in both conditions. Franco's failures on his very first trials might have been a consequence of the novelty of the trials; remember, his first trial in this experiment was the more challenging, invisible condition. By looking at the individual data for each bird, we see how they came to understand the task.

Griffin did seem to understand the task, immediately and fully. By chance, his first four trials were visible, the first involving removal of a bean and then chow and bean alternating; he initially tracked the number of treats appropriately. After the first four successful trials, exploratory behavior might have emerged, only to be eliminated later in favor of achieving the reward. He was also correct on his first two invisible trials in which chow was removed; however, he could have solved the problem by using knowledge from Experiment 1—that is, avoiding the cup from which food had been removed. He was nevertheless also correct on all invisible trials in which beans were removed, again suggesting that he actually was tracking the number of beans. He could switch back and forth between visible/invisible trials and standard trials, as he was marginally statistically significantly correct on the standard trials as well.

Arthur also seemed to understand the task, immediately and fully. His data are strikingly similar to those of Griffin, with even slightly greater accuracy on the visible Favorite trials. He also was correct on all the jelly bean removal trials. He also seemed able to switch back and forth between the Experiment 1 and Favorite trials, even though all his Experiment 1 trials were invisible. Although he was somewhat more accurate on invisible than visible trials, local enhancement seemed not likely to play much of a role in his errors: Errors in both cases were very few and never on first trials; rather, he may have erred more from exploratory behavior, because errors usually occurred only after correct responses.

Franco's data are intriguing. In the invisible condition, he succeeded on all but the first invisible trial. Interestingly, on this trial, chow had been removed, suggesting that he was indeed confused by the overall situation: Had he followed what he had learned in Experiment 1, he would have known to go for the bean side. He was correct on all the other invisible trials, suggesting that he figured out the task rather quickly. Notably, he also erred on his first visible trial in which a bean was removed, again suggesting he was confused by the presence of multiple beans. He was, however, correct on the next four of his first five visible trials, in which either a bean or chow was removed, suggesting that he learned not to be distracted by removal of a single item, whether it be a bean or not. Given his accuracy in Experiment 1, his lack of accuracy on the intermixed standard trials is somewhat surprising and suggested some difficulty in switching between the standard and Favorite tasks; he was, however, correct on his first visible and invisible standard trials, so possibly his later failures involved exploratory behavior. Remember, these trials were in addition to the 60 previous trials, so that exploratory behavior or boredom would not be completely unexpected, given our experience with Greys (e.g., Pepperberg & Gordon, 2005).

Pepper's data are also interesting. She succeeded on her first invisible trial, which was the same as that given Franco; she, too, could have solved it by using information from Experiment 1. She erred in the second and third invisible trials, in which beans had been removed, suggesting she was still functioning with respect to Experiment 1. However, she apparently quickly realized that she had to track the beans, that is, to reason about the task, and had no problem tracking beans in the first five trials of the visible task, where either chow or beans were removed. Unlike Franco, she had no trouble switching between standard and Favorite trials. Given that the number of errors in the first and second halves of the Favorite invisible trials were not statistically significantly different, she simply may have had to adapt to the novel conditions of Experiment 2.

Overall, the data suggest that Grey parrots could track the number of treats, track where removal had occurred, and, on that basis, use or ignore exclusion, that is, remember when to avoid a cup or return to a cup even after one of their favorite treats had been removed. As in Experiment 1, exploratory behavior might explain some subsequent errors after initial successful trials.

General Discussion

The results of these experiments demonstrate that Grey parrots can reason by exclusion. They do not simply avoid an empty container, but infer the most advantageous choice based on the specific context of the trial. Four Greys, two that had previously undergone extensive laboratory testing and two that were pets, performed at essentially the same levels, demonstrating little in the way of individual differences or effects of prior experience. The data confirm the results of Mikolasch et al. (2011), who found that a single Grey, out of seven, succeeded. Notably, our task did not, like theirs, require the birds to remember a spatial cue, requiring instead remembrance of a color cue. Memory for color might be easier than right-left locations for Greys, but the change in procedure did not lessen the need for the birds to use inference to solve the task. Spatial memory is, however, likely better for birds who engage in caching (Brodbeck, 1994; Clayton & Krebs, 1994); thus, the need to depend on spatial cues may have challenged the keas (Schloegl et al., 2009), jackdaws (Schloegl, 2011), and most of the Greys in the earlier studies (Mikolasch et al., 2011), and given ravens (Schloegl et al., 2009) an advantage. Notably, however, exclusion need not be a spatial task (e.g., Markman & Wachtel, 1988; Pepperberg & Wilcox, 2000).

The success of Grey parrots when spatial cues are less important brings into question the argument that skills such as caching and stealing food are necessary in order to engage in inference by exclusion (e.g., Schloegl, 2011). Possibly the success of the Greys is a consequence of evolution for other capacities. Interestingly, Grey parrots engage in linguistic forms of the exclusion task (Pepperberg & Wilcox, 2000): Possibly in a species with a large, shared, learned repertoire (May, 2004), lack of specific notes in a call might signal the presence of a particular individual. Alternatively, one might argue that a facility for *allospecific* vocal learning—deducing novel meanings in the same way as do young children (Markman & Wachtel, 1988)—can explain Greys' success and keas' failures (Schloegl et al., 2009). Keas, a species equally as intelligent as Greys on a number of physical tasks (e.g., Werdenich & Huber, 2006) have not yet been shown to engage in allospecific vocal learning. Keas, however, have not been tested in the exclusion procedure we used for the Greys, and we suspect that they would succeed; we also suspect that keas might learn allospecific vocalizations as well. We note that other species, such as apes, who may steal food but who do not cache, and that lack significant vocal learning of any sort, also succeed on this task (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, 2004, 2006). Such findings might argue that inference by exclusion is a marker of general intelligence, an ability that underlies several different cognitive capacities and that might, as noted at the beginning of this article, be used by different species under different conditions. Selection for intelligence seems to have occurred in many species that are long-lived and exist in complex social and ecological environments (e.g., Humphrey, 1976; Jolly, 1966; Pepperberg, 1999).

We suspect that one area on which to focus might be on the role of some capacity for, and training on, symbolic reference with respect to reasoning by exclusion. Given that symbolic training, which can be independent of vocal learning, has led to success on more advanced cognitive tasks for several species (e.g., apes: Boysen, 2006; Premack, 1984; Grey parrots: Pepperberg, 1999; Pepperberg & Carey, 2012), Hill, Collier-Baker, and Suddendorf (2011b) have suggested a relationship between capacities for symbolic representation and success on the cup task used here. The rationale is that subjects having symbolic training could transfer their deductive/inferential reasoning across tasks. Griffin has undergone significant symbolic training in a laboratory situation, has learned to use a number of labels referentially, including those for color (e.g., Pepperberg, Sandefer, Noel, & Ellsworth, 2000; Pepperberg & Shive, 2001), and has demonstrated evidence for linguistic exclusion (e.g., Pepperberg & Wilcox, 2000); Arthur, in contrast, has had only limited training of this nature (e.g., Pepperberg & Wilkes, 2004), but engaged in other tasks that used representational tokens (Péron et al., 2012). Although Pepper and Franco have also had considerable training and have learned to use English speech in appropriate contexts (L. A. Hartsfield, personal communication, May, 2012; I. M. Pepperberg, personal observation, October, 2010; March, 2011), only Pepper has had training on color labeling and neither of these bird's capacities have been formally tested. Conceivably, even limited exposure to symbolic training might prepare a subject for inference by exclusion (note Carey & Bartlett, 1978), and color labels might have assisted with memory for the placement of the various treats. Franco, interestingly, the bird with the least training on symbolic representation, did seem to have the most trouble in switching between tasks in Experiment 2, although, again, exploratory behavior could have been involved.

Notably, additional exclusion tasks given ravens and keas, in which the former succeeded and the latter failed, used bent and straight tubes (Schloegl et al., 2009), and unlike tasks given to the various Greys, required birds to engage in physical examination of the hiding places—that is, to walk around and perform inspections. Such a difference in experimental design might be critical, and do not specifically involved right-left spatial cues. Greys thus need to be tested under comparable conditions to determine how they might react.

The take-home message appears to be that Grey parrots are capable of true inferential reasoning, but that details of experimental design may have significant effects on outcomes (e.g., Schloegl et al., 2012). We caution researchers that although comparative studies are likely to provide useful information about abilities across species, extreme care must be taken to avoid drawing generalizations concerning the evolutionary origins of such abilities. Comparing abilities in distantly—or even closely related—species is not a simple matter, given constraints based on different environments and even perceptual capacities.

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Received June 22, 2012
Revision received October 3, 2012
Accepted November 14, 2012 ■