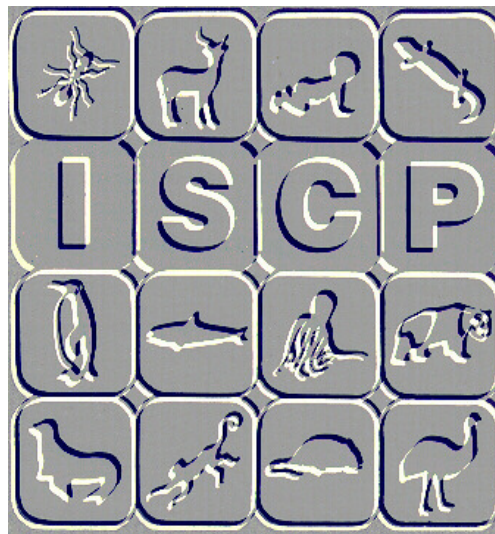


ISSN 0889-3667  
IJCP 22(2)75-126(2009)

# International Journal of Comparative Psychology



Published by the  

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International Society for Comparative Psychology

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2009, Volume 22, Number 2

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***Published quarterly.***  
ISSN 0889-3667

IJCPE822(2) 75-126 (2009)

## **Pigeons, Rats, and Humans Show Analogous Misinformation**

**Maryanne Garry and David N. Harper**  
*Victoria University of Wellington, New Zealand*

In three experiments, we show that pigeons, rats and humans can be influenced by misleading postevent information in ways analogous to findings in the human memory distortion literature. We used a delayed matching to sample analog of the eyewitness testimony procedure from Loftus et al. (1978), and varied the length of the delay between event and exposure to postevent information (PEI). We also varied the nature of PEI so that it was consistent with the event information, inconsistent, or neutral. In Experiment 1, pigeons' memory performance for colored lights was influenced by the presence of another colored light. In Experiment 2, rats' memory performance for lever position was influenced by position-related cue lights. In Experiment 3, we verified the validity of our analog procedure by having human subjects remember kaleidoscope images. Despite differences in species and the nature of the stimuli, all three experiments replicated key findings in the literature: memory accuracy was highest when consistent PEI was presented at the end of a delay, and lowest when inconsistent PEI presented at the end of a delay interval. PEI had no effect when presented at the beginning of a delay.

One of the basic tenets of animal cognition research is that many of the mechanisms that govern human behavior also govern nonhuman behavior. Animals have demonstrated the ability to form concepts (Herrnstein, 1979; Honig & Stewart, 1988), measure the passage of time (Killeen & Fetterman, 1988; Roberts, 1981) and to learn by observation (Heyes, Jaldow, Nokes, & Dawson, 1994). Some have even learned to use human forms of communication (Savage-Rumbaugh, Pate, Lawson, Smith, & Rosenbaum, 1983). But what do we know about animal memory, and how is it like human memory?

Like humans, animals can correctly remember and discriminate large quantities of visual information. Vaughan and Greene (1983, 1984) showed pigeons hundreds of pictures of various scenes, pairing some pictures with reinforcers and others with no reinforcers. Later, the pigeons were more than 90% accurate in recognizing the reinforced pictures. In fact, two years later, they were still more than 70% accurate. We also know that animals display many of the same phenomena that have been demonstrated in the human memory literature, including the ability to show object permanence (Pepperberg & Funk, 1990), retroactive interference effects (Harper & White, 1997; White, 1985), the influence of prior learning on subsequent memory performance (Edhouse & White, 1988), serial position effects (Harper, McLean, & Dalrymple-Alford, 1993; Wright, Santiago, Sands, Kendrick, & Cook, 1985), and are able to make use of mediating behavioral strategies to enhance accuracy (Harper & Bizo, 2000).

Clearly, all animal species display the ability to form accurate memories of relatively simple and even more complex experiences. However, humans are also

We are grateful to Michael Colombo, Stefanie Sharman, and two anonymous reviewers for their comments on earlier drafts of this manuscript. All research reported in this article conformed to, and was approved by, the Victoria University of Wellington Human Ethics Committee and Animal Ethics Committee. Correspondence concerning this article should be addressed to David Harper, School of Psychology, Victoria University of Wellington, Box 600, Wellington, New Zealand. (david.harper@vuw.ac.nz).

prone to memory distortion, especially when they are exposed to misleading postevent information (PEI). In this distortion, known as the *misinformation effect* (Belli 1989), when subjects are misled about a previously witnessed event they often integrate these misleading suggestions into their accounts of the event. Do animals experience eyewitness memory distortions? The answer is 'yes'. Recently, we adapted the classic Loftus paradigm (Loftus, Miller, & Burns, 1978) for pigeons. In the standard paradigm, there are three stages. First, subjects watch a visual presentation of an event (such as a simulated crime or accident). Next, after a filler task designed to thwart rehearsal, they are exposed to detailed PEI in a narrative summarizing the original event. Some of the PEI is misleading, while some is not. Finally, subjects are tested about what they saw originally. Decades of research producing hundreds of experiments have demonstrated that inaccurate PEI can bias memory reports in line with the misleading postevent suggestions. (Belli, 1989; Lindsay & Johnson, 1989; Lindsay, 1990; Loftus & Palmer, 1974; McCloskey & Zaragoza, 1985; Mitchell & Zaragoza, 2001). In our research (Harper & Garry, 2000), we showed that pigeons make eyewitness errors that mirror the ones humans make (Loftus et al., 1978). That is, misleading PEI was most likely to lead pigeons to report an incorrect target event when it was presented at the end of a delay. Our results also correspond with those found in the more recent human eyewitness memory literature (Belli, Windschitl, McCarthy, & Winfrey, 1992; Sutherland & Hayne, 2001; Vornik, Sharman, & Garry, , 2003).

The fact that pigeons and humans respond the same way to misleading PEI has at least two important theoretical implications for the study of human memory. First, our results suggest that demand characteristics play only a limited role in misinformation effects (see also Belli, 1989). After all, pigeons are somewhat unlikely to be behaving on the basis of what they believe the experimenter wants them to do. Second, our results were similar to those found with other nonverbal creatures: human infants, whose results were in turn similar to those found with children and adults (Rovee-Collier, Adler, & Borza, 1994). The striking consistency across creatures prompted us to recall Rovee-Collier's (1997) suggestion that when it comes to memory theorizing it is time to simplify our view of the universe. Such a view is similar to that put forth by Wasserman (1993), who—in reviewing a century of comparative cognition and discussing its relevance in the future—concluded that when we gather more evidence on the abilities of animals, we gather more evidence about what mechanisms drive similar abilities in humans.

In this paper, we had two broad goals. First, we wanted to examine whether an animal model of the human misinformation task would produce results consistent with the wider human misinformation literature. Second, having developed an animal analog, we wanted to evaluate the extent to which it is a good analog by subjecting it to “backward translation;” that is, by seeing if human subjects using our animal analog would perform similarly to humans from the Loftus et al. studies.

In this paper, we present three experiments in which we developed a delayed matching to sample (DMTS) analog to a misinformation task. The DMTS we used

is common in the animal memory literature. If we found that the patterns of results in all experiments were similar, and the pattern of results in Experiment 3 were similar to those found in the original Loftus et al. (1978) work from which the three experiments derived, then we would have strong evidence for the cross-species continuity of memory and memory distortions.

## **Experiment 1**

### **Method**

#### ***Subjects***

Six individually housed adult homing pigeons, who had no prior experience in conditional discrimination tasks, were maintained at 80%-85% of their free-feeding weights. They received supplementary feed after the final session each day to maintain prescribed body weights.

#### ***Apparatus***

A sound-attenuating chamber, measuring 32 x 34 x 32 cm, contained an interface panel with a centrally mounted grain hopper and three response keys. One response key was mounted directly above the hopper, and the other two keys were mounted above and to either side of the hopper. Each key could be illuminated one of three colors from behind: red, green or yellow. A ventilation fan at the rear of the chamber helped mask extraneous sounds.

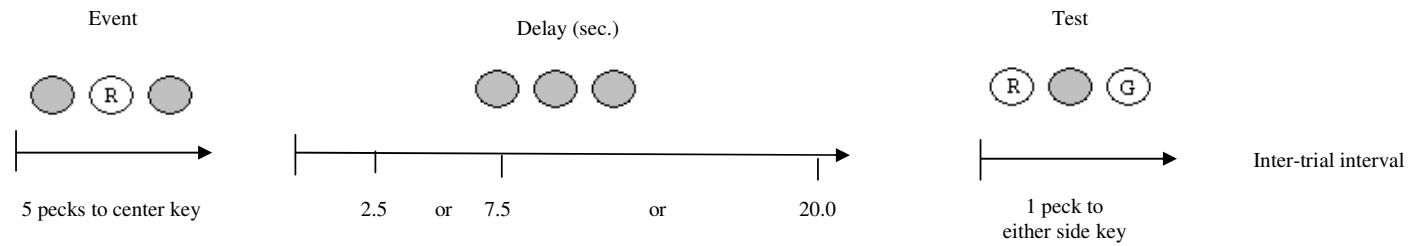
#### ***Procedure***

***Training.*** Pigeons were trained for approximately 3 months before we collected baseline data. In the preliminary training phase, they were first trained to peck when the keys were illuminated, and received access to a wheat reinforcer. Next, pigeons were trained in an abbreviated version of the adapted three stage misinformation procedure in which the postevent information (PEI) stage was omitted. That is, pigeons were trained to witness a target event stimulus and then, after a nominal 0.2 s delay, choose between this original event and another stimulus.

Figure 1 shows our specific two-stage training adaptation of the Loftus et al. (1978) misinformation procedure. The event was a central key, lit from behind by either a green light, or, as Figure 1 shows, a red light. Light color order was randomized across trials. After pigeons pecked the key five times, the light turned off and initiated a delay. During the delay, the chamber was dark and responses were ineffective. Delay intervals were randomized across trials with the constraint that a particular delay did not repeat until the other delays had occurred for a given color.

At the end of the delay, subjects were presented with the two side-key comparison stimuli and had to choose between the original event color (in this example, red) and the non-target color (in this example, green). A single peck at the key corresponding to the correct event color resulted in 3 s access to grain. An incorrect response (a peck to the non-target color) resulted in 3 s time out, in which no food was available, and all keys were darkened. Note that in this phase of training and during the subsequent experimental phase that red and green stimuli were presented equally often on either the left or right during comparison stimulus presentation.

Once subjects displayed at least 70% accuracy for at least 5 consecutive sessions, delays lengthened from 0.2 s to 2.5 s, then to 7.5, and finally to 20.0 s. The actual experiment began after all pigeons displayed consistent performance such that the overall percent correct showed no obvious trends across sessions. Sessions were conducted 7 days per week and comprised 84 trials or lasted 50 min, whichever occurred first.



**Figure 1.** Sequence of events comprising a trial in the basic DMTS recognition task used with pigeons in Experiment 1. Pigeons were trained in this task prior to examining effect of PEI as illustrated in Figure 2. Each circular disc represents a key on the front wall of a response chamber. 'R' and 'G' indicate that the key was illuminated 'red' or 'green' respectively; otherwise a given key remained unlit.

**Experiment.** In the experimental phase, we examined the effect of PEI by adding that stage to our adapted two-stage procedure by introducing a colored stimulus light either at the start or end of the delay interval. Figure 2 shows a hypothetical trial in which the to-be-remembered sample stimulus is red. Trials comprised the following sequence of events:

1. **Sample presentation.** First, the event stimulus was presented via the central sample key: it was illuminated either red or green. The subject's 5 peck response initiated the delay interval.
2. **Delay Interval.** During the delay interval, there were two conditions presented. Subjects in the *end-of-delay* condition, shown along the upper branch of Figure 2, were exposed to PEI after 2.5, 7.5, or 20.0 s. Subjects in the *beginning-of-delay* condition, shown on the bottom branch of Figure 2, were exposed to PEI was presented immediately after the fifth peck, followed by a delay of either 2.5, 7.5, or 20.0 s. In both delay conditions, a single peck was required on the center key displaying the PEI before the trial proceeded any further.
3. **Forced-Choice Test.** The two side comparison lights were illuminated (one red and the other green) for the forced-choice test after the delay interval had been completed and the subject had responded to the key with the PEI. To gain access to 3 s of grain, pigeons were required to peck once at the key corresponding to the original to-be-remembered color stimulus. An incorrect choice resulted in 3 s of time out. Both correct and incorrect responses were followed by a 27 s interval before the next trial began.

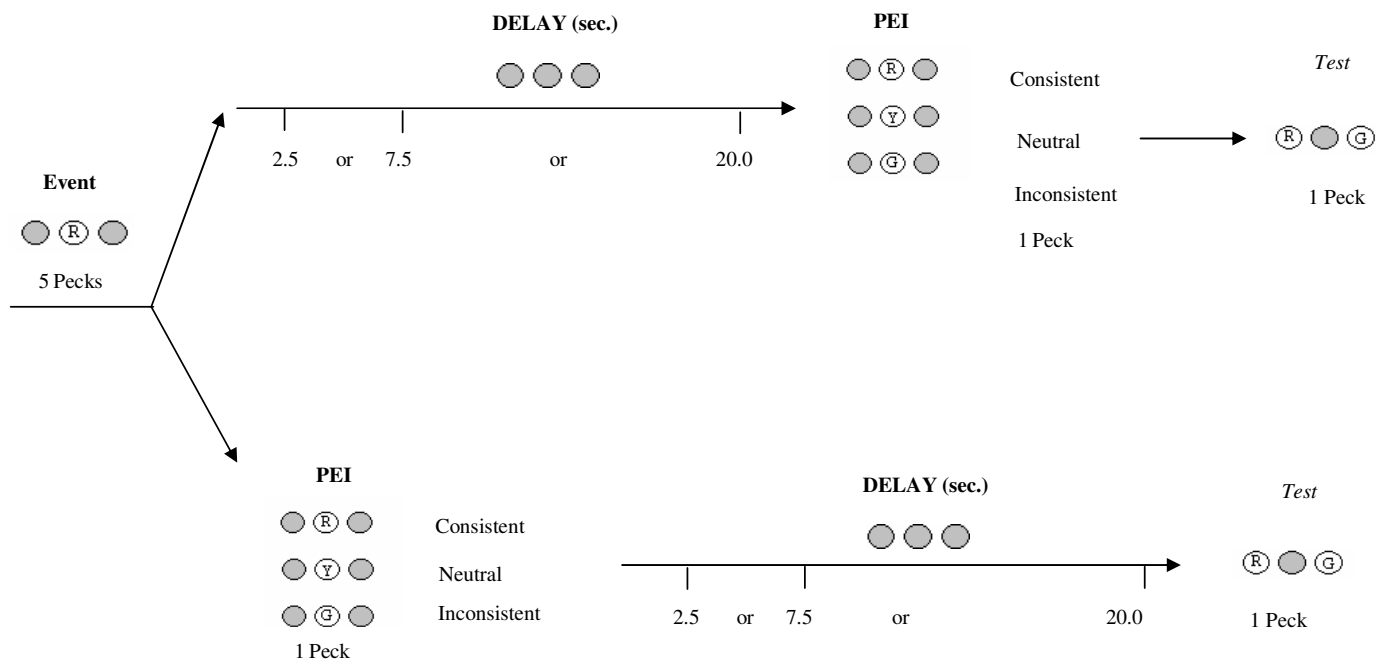
Three pigeons received the end-of-delay condition first, and the other three pigeons received the beginning-of-delay condition first. Each condition contained all three types of trials (described below); each pigeon received both conditions, and each condition lasted for 30 sessions.

In both delay conditions, we varied the relationship between event and PEI in one of three ways (cf. Loftus et al., 1978). In a *Consistent* trial, the event stimulus and the PEI were the same color. In an *Inconsistent* trial, the event and PEI were different colors. Finally, in a *Neutral* trial, the PEI was yellow, regardless of the event color (recall that yellow was never used in the event or test phases). An approximately equal number of *Consistent*, *Inconsistent* and *Neutral* trials were conducted per session in a randomized order with the constraint that no more than four consecutive trials were of the same type.

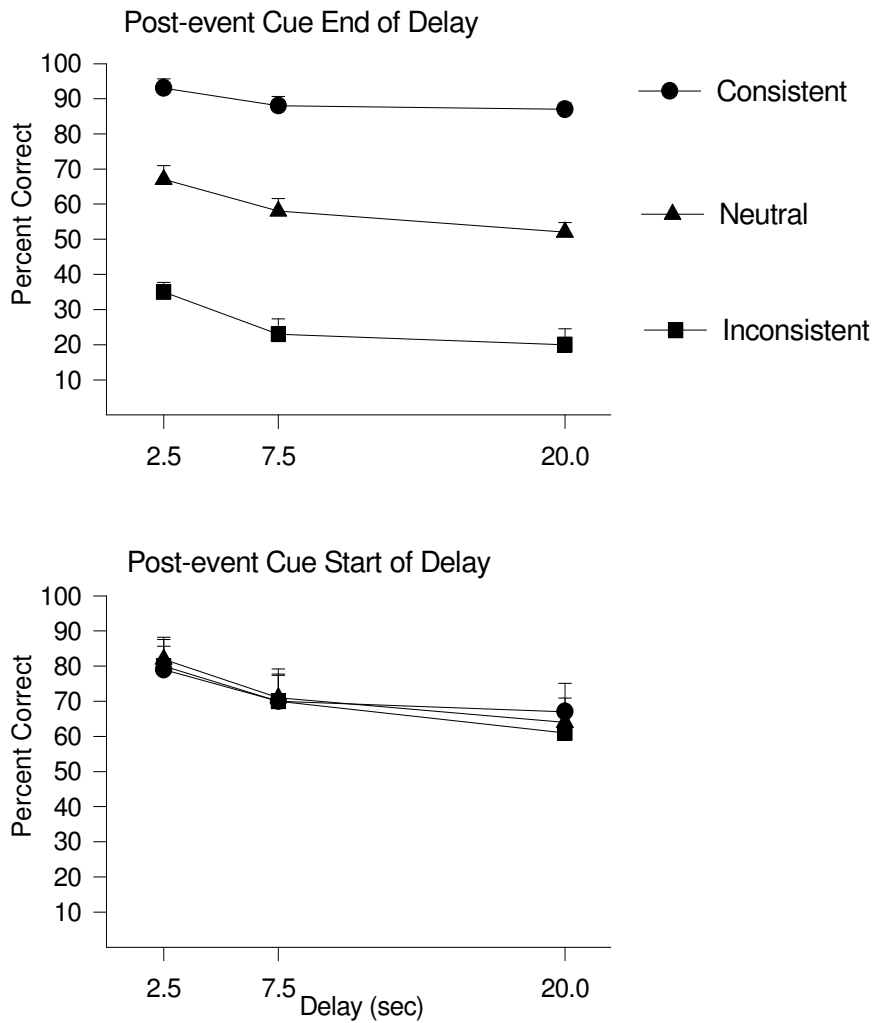
## Results and Discussion

For these analyses, we used percent correct responses made over the last 5 sessions of each condition, separated according to trial type (*Consistent*, *Inconsistent*, or *Neutral*) and delay (2.5, 7.5, or 20.0 s). Recall that the major question in this experiment was whether pigeons would be influenced by misleading PEI when assessed with a modified test. As the top of Figure 3 shows, they were. The top graph indicates a general decrease in accuracy as the delay increased, regardless of trial type. More to the point, subjects were most accurate when exposed to consistent PEI, but least accurate when exposed to misleading PEI. A repeated measures analysis of variance (ANOVA) comparing trial type by delay showed a main effect for trial type,  $F(2,10) = 240.5$ ,  $p < 0.01$ , and delay,  $F(2,10) = 11.8$ ,  $p < 0.01$ , on accuracy.

Although PEI at the end of a delay produced a misinformation effect, research suggests that PEI should have much less of an effect at the start of a delay (Loftus et al., 1974). Indeed, the bottom graph in Figure 3 shows only a general decrease in accuracy as delay length increased. A repeated measures ANOVA comparing trial type by delay showed a main effect for delay,  $F(2,10) = 14.9$ ,  $p < 0.01$ , on accuracy, but no effect for trial type,  $F(2,10) = 1.8$ ,  $p > 0.05$ .



**Figure 2.** Sequence of events comprising a trial in the adapted DMTS task used to examine the effects of PEI on pigeon recognition performance. Each circular disc represents a key on the front wall of a response chamber. 'R', 'G', and 'Y' indicate that the key was illuminated 'red', 'green', or 'yellow' respectively. The top pathway indicates the sequence of events when PEI was presented at the end of the delay interval, and the lower pathway indicates the sequence of events when PEI was presented at the beginning of the delay interval.



**Figure 3.** Mean percent correct as a function of delay in Experiment 1 when the PEI was presented at the end of the delay (top graph) or start of the delay (lower graph). Accuracy is shown separately for *Consistent*, *Neutral*, and *Inconsistent* trials. Error bars show standard error of the mean.

Overall, in both conditions, accuracy systematically decreased as the delay between the sample stimulus and subsequent recognition increased. The rate of this decrease in accuracy across delays was not affected by the different types of PEI presented either at the beginning or the end of the delay period (there was no interaction between the effect of delay and trial type on accuracy,  $F(4,20) = 0.8, p > 0.05$ ;  $F(4,20) = 1.2, p > 0.05$ , respectively). Whether PEI had an effect on overall

accuracy (regardless of delay) depended on whether it occurred at the beginning or end of the delay interval. That is, PEI had no effect on accuracy when presented at the beginning of the delay, but it had a large effect when presented at the end of the delay interval.

In short, Experiment 1 demonstrated that recognition performance in pigeons could be biased by exposure to PEI, suggesting that not only humans show a misinformation effect using a modified test. However, one criticism of Experiment 1 is that it relied on the visual mode only, whereas human misinformation effects occur when memory for event information presented in one modality (such as images) is influenced by PEI presented in another modality (such as text). Additionally, in Experiment 1, we changed the entire stimulus (in other words, the entire event), not just aspects of the stimulus array, as is the case in human misinformation research. These two aspects of the procedure used in Experiment 1 also may lead us to wonder whether the misinformation effect observed here is truly analogous to the effect observed with humans.

Another procedural concern is whether the presence of the PEI at the beginning versus end of the delay period effectively produces an alteration in other structural elements of the task beyond the intended simple alteration in temporal location of the PEI stimulus. For example, the PEI may have had no effect when presented at the beginning of the delay because the PEI was overshadowed by the target stimulus. In other words, the subject may effectively have treated the PEI as a continuation of the target stimulus, rather than as a distinct new stimulus event. Given that the target stimulus was present for 5 pecks, and the PEI only present for one peck, then we would expect the target stimulus to have a stronger representation in memory than the PEI, and cause the results we observed. By contrast, when the PEI occurred at the end of the delay, subjects may simply have treated it as the start of a new trial; that is, treated the PEI as a new target stimulus. Thus, because the PEI and target stimuli share so many characteristics, pigeons may simply not have noticed the PEI, or treated it as the start of a new trial. Despite these potential concerns it should be noted that in the 'neutral' condition accuracy at the 2.5 s delay was around 70%. However, if subjects were treating the PEI at the end of the delay as a signal for the start of a new trial, we would have expected accuracy to be around 50% in this condition - which it was not.

In Experiment 2 we sought to further explore the existence of an analogous misinformation effect in another species as well as address the issue of whether a misinformation effect would still arise in a non-human species if the PEI was only associated with (rather than identical to) the original target event. In Experiment 2, therefore, we exposed rats to a visual-spatial event in which we manipulated only a portion of the stimulus array, the position of a lever. Then we exposed them to PEI by flashing a light to cue the rat about the lever's position. Sometimes the PEI was accurate, and sometimes it was inaccurate. We chose rats as our subjects in Experiment 2 because their good visual-spatial abilities made it possible to vary aspects of the event and PEI on multiple modalities.

## Experiment 2

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## Method

### *Subjects*

Five adult Norway Hooded rats (6 months old at the start of training), with no prior experience in conditional discrimination procedures, were maintained at 80% - 85% of their free-feeding body weights. Supplementary feed was given after the final session of the day to maintain prescribed body weights. Water and untreated wood shavings were available continuously in the homecages. The housing room was maintained at a constant 22°C with lights off between 7:00 AM and 7:00 PM.

### *Apparatus*

Rats were trained individually in a single response chamber, measuring 31 x 32 x 24 cm. Three manipulanda were available; with a single 12W red light mounted above each one. Two retractable levers were located on both the left and right sides of the front interface panel. A third, non-retractable lever was located in the middle of the opposite wall. Reinforcers (0.1 ml of sweetened milk-water mixture) were delivered at floor level in the center of the panel via a dipper mechanism. All experimental events were scheduled and recorded by an IBM<sup>®</sup>-compatible computer running MED-PC<sup>®</sup> software.

### *Procedure*

Recognition performance was assessed at three different delays using an automated DMTS procedure similar to that used with the pigeons except that the event was comprised of retractable levers with a plain white light above each instead of colored lights. Sessions were conducted daily, five days per week, for 64 trials per day or until 48 minutes had elapsed. After preliminary training to respond on the levers, baseline training began. Baseline trials comprised the following sequence of events:

1. **Sample presentation.** Either the left or right lever was inserted randomly into the chamber. If the left lever was inserted, the left light was illuminated. If the right lever was inserted, the right light continuously flashed on and off (with a 0.25/0.25 s on/off cycle). Following three presses on the inserted lever, it was retracted and the corresponding light was switched off.
2. **Delay interval.** A variable delay was initiated that ended with the first rear-lever response after a predetermined time period had elapsed. The scheduled delays were 3.0, 6.0 and 12.0 s. The delays for each trial type (i.e., left or right-lever sample stimulus) were selected on a pseudo-random basis, which ensured that each duration was used equally often for each type of trial.
3. **Forced-choice test.** After the delay, both the left and right front levers were inserted into the chamber. As soon as a single response was made on either of the levers they were retracted. If the response was to the lever that was inserted as the sample stimulus at the beginning of the trial, (i.e., a correct response) a reinforcer was delivered. If the response was made to the other lever, the response was counted as an error and was not reinforced. After 2.5 s of dipper availability (following a correct response) or 2.5 s of time-out (following an error response), a 5 s inter-trial interval began during which the chamber was darkened. Upon completion of the inter-trial interval a new trial was initiated.

Approximately 80 sessions of baseline training were conducted before experimental probe sessions were introduced. During the experimental phase every fifth session was a probe session that assessed the impact of PEI on recognition performance (the remaining sessions were identical to the baseline sessions outlined above). The effects of PEI were examined across two conditions, both of which consisted of three types of trial, as outlined in Experiment 1.

Each rat received both conditions, and each condition was comprised of five probe sessions. In the end-of-delay condition, the PEI was the illumination of a light. Either the left light was

illuminated for a period of 3 s after the delay period had timed out, or the right light was flashed on and off (0.2 s on / 0.25 s off) for 3 s after the delay period had timed out. The beginning-of-delay condition was identical except that the PEI was presented prior to the start of the delay period. After the PEI was presented, the trial proceeded as outlined for baseline trials.

As in Experiment 1, both conditions consisted of approximately equal numbers of trials categorized as either *Consistent*, *Inconsistent* or *Neutral*, depending on the relationship among the sample stimulus, the PEI and the choice stimuli. If the initial sample-event stimulus (left lever plus left light) was consistent with the postevent cue (i.e., left light at the start or end of the delay), then the trial was a *Consistent* trial. If the initial sample stimulus was inconsistent with the postevent cue (i.e., flashing *right* light during in the delay), then the trial was *Inconsistent*. Finally, if the initial sample stimulus was followed by no illumination of either the left or right lights then the trial was a *Neutral* trial.

## Results and Discussion

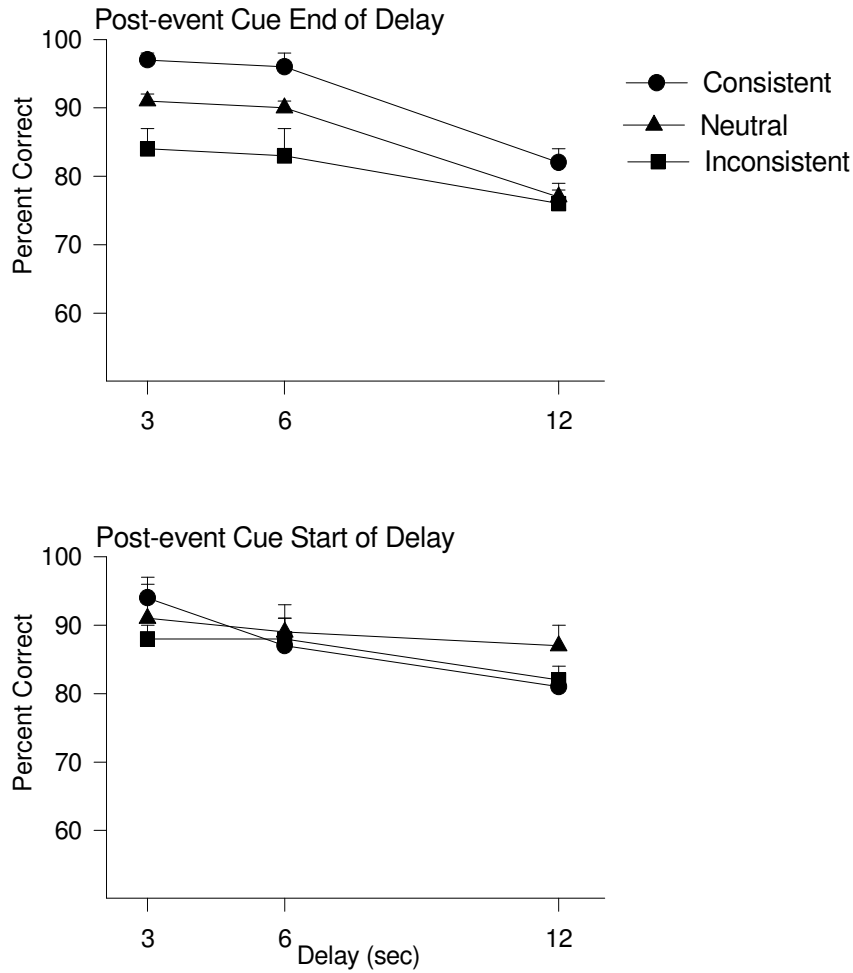
The central question in Experiment 2 was whether rats would show the same pattern of memory distortions about a visuospatial event as pigeons did about a single modality event. To answer this question, we classified percent correct responses made over the five probe sessions of each condition according to trial type (*Consistent*, *Inconsistent*, or *Neutral*) and delay (3, 6, or 12 s). The top graph in Figure 4 reveals two obvious trends in the data. First, there was a general decrease in accuracy as the delay increased, regardless of trial type. Second, accuracy was greater overall on consistent PEI trials and poorest overall on inconsistent PEI trials. A repeated-measures ANOVA comparing trial type by delay showed a significant main effect of trial type,  $F(2,8) = 19.6$ ,  $p < 0.01$ , and delay,  $F(2,8) = 33.9$ ,  $p < 0.01$ , on accuracy but no interaction  $F = 1.1$ .

As was the case in Experiment 1, the bottom of Figure 4 shows no effect for trial type, and only a general decrease in accuracy as delay length increased; an ANOVA showed an effect on accuracy as delay length increased,  $F(2,8) = 4.5$ ,  $p < 0.05$ , no interaction between delay and trial type,  $F = 1.9$ , and no clear difference on accuracy as a product of trial type,  $F = 1.2$ .

To recap, the pattern of results observed in Experiment 1 with pigeons was replicated in Experiment 2 using multimodal stimuli, and using rats. As in Experiment 1, the lowest levels of accuracy occurred when the PEI was inconsistent with the target sample stimulus, and when the PEI was introduced at the end of a delay. Taken together, Experiments 1 and 2 strongly suggest that a number of animal species can be biased towards reporting incorrectly that a certain stimulus was presented when it was not.

However, we might be criticized for having designed a poor analog of the human misinformation method, because there were at least three differences between our methods using animal subjects and the methods typically used with human subjects. First, human misinformation studies do not typically expose subjects to a large number of repeated trials, as we did in Experiments 1 and 2. Second, humans usually have a delay interval far longer than what we used in our experiments, usually on the order of 10 - 20 minutes. It may be that although pigeons and rats displayed biased performance in our analog procedures, humans would not. Perhaps given multiple trials and very short delays, they would quickly

learn to ignore the biased PEI we presented. Third, human misinformation experiments use quite complex "real life" stimuli, such as a video of a car accident, or a slide sequence of a theft. Our experiments, on the other hand, used very basic stimuli. Perhaps if we used our analog procedure with human subjects, they would fail to be misled at all by the simple abstract stimuli.



**Figure 4.** Mean percent correct as a function of delay in Experiment 2 when the PEI was presented at the end of the delay (top graph) or start of the delay (lower graph). Accuracy is shown separately for *Consistent*, *Neutral*, and *Inconsistent* trials. Error bars show standard error of the mean.

To address these differences, in Experiment 3 we took the basic elements of our tasks from Experiments 1 and 2—which we had translated from the basic elements of a human misinformation task—and "back translated" them into a simple human misinformation task. That is, we exposed human subjects to repeated trials, using a limited pool of kaleidoscope images and relatively short delays. Our aim was to create a task that was more like the animal tasks, but still complex enough so that our human subjects could not assign verbal labels to aspects of the stimulus array. After all, pigeons do not have the advantage of labeling a stimulus as "red light" to facilitate encoding and retrieval. The main question we ask in Experiment 3 is whether the patterns we observed in Experiments 1 and 2 would also emerge with our human adaptation. If the answer is yes, then we have evidence that misinformation effects occur across species.

### Experiment 3

#### Method

##### *Subjects*

Thirty students (age range 18 to 38 years) responded to recruiting fliers. They were equally allocated to one of two conditions (described below), and were given \$5 for their participation.

##### *Apparatus*

All experimental events were presented on IBM®-compatible 486 computers using SuperLab® software. The background screen color was white at all times.

##### *Procedure*

Recognition performance was assessed at two delays using a computerized DMTS procedure similar to that used in the previous experiments with the following exceptions. First, instead of either colored lights or lever position serving as target stimuli, we used black and white kaleidoscope images. Second, we collected data in a single session comprised of 70 trials and lasting approximately 25 minutes. Before starting the experiment participants were told that they would be performing a memory task and that they were required to remember kaleidoscope images. They were asked to pay careful attention to the screen and the images that appear on it at all times. Subjects were asked to remember the four images presented simultaneously at the beginning of the trial. They were told that their task was to report which of the two images presented after a short delay was the same as one of the images seen at the start of the trial.

Our three-stage adaptation of the DMTS/misinformation procedure involved the following sequence:

1. **Sample presentation.** At the start of a trial, subjects saw an array of four black and white kaleidoscope images on the screen for a total of 1.5 s. The four images were arranged equidistantly around the center point of the computer screen with a boundary of 1 cm of white space separating the edges of the individual images. Each image in the array was 5 cm high by 5 cm wide.
2. **Delay and PEI.** After the sample image disappeared, a delay period began. The delay lasted for either 4 s or 12 s, randomly determined. Subjects were asked to pay attention to the screen at all times. During the delay, the PEI appeared in the center of the screen. It was a single

kaleidoscope image (5 cm x 5 cm), and remained on the screen until the participant pressed a labeled key on the keyboard. The appearance of PEI during the delay was varied across two conditions, either at the end of the delay (immediately after either 4 s or 12 s of delay interval had timed out) or at the start of the delay interval (immediately after presentation of the array of four images but before the delay interval commenced).

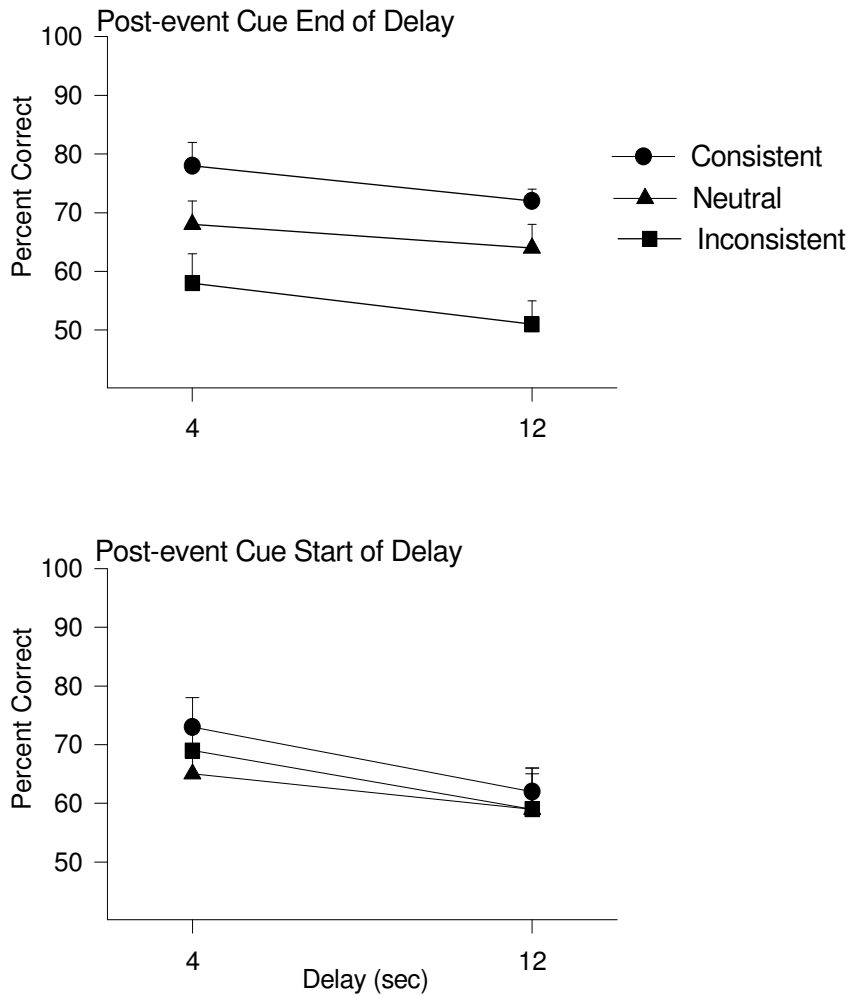
3. **Forced-choice test.** After the delay interval had timed out, two kaleidoscope images (each 5 cm x 5 cm) appeared on the screen. One image was positioned 0.5 cm to the left of center and the other image was 0.5 cm to the right of center with both images centered on the vertical plane. Participants were instructed to press the 'LEFT' button on the keyboard if they thought the left image was the one from the original array of four images at the start of the trial and the 'RIGHT' button if they thought it was the right image. The LEFT and RIGHT response options were labeled with stickers and corresponded to the letters 'Z' and 'M' on a standard keyboard. As soon as a single response was made on either of the keys, the images disappeared and a 1 s intertrial interval occurred before the next trial was initiated. A response was labeled as correct if it corresponded to the target image presented among the array of four at the start of the trial. There were sixteen different kaleidoscope images used. Across trials all images were used as target stimuli, postevent cues, and incorrect recognition options. Across trials the position of any given kaleidoscope image in the original array of four varied, as did the four separate images that were combined in to a single array, and the position of the correct target image varied (both with respect to its position among the original array of four images and its position either on the left or right of the screen at recognition).

In all conditions there were three types of trial: *Consistent*, *Inconsistent* and *Neutral*. These trials were defined in the same way as in Experiments 1 and 2. However, the first 10 trials scheduled in a session were all of the Consistent type and were not included in subsequent analyses. We manipulated the first 10 trials in this fashion because in our pilot research, where we randomized the three trial types right from the first trial, we found that subjects quickly learned to mistrust the PEI, and avoided selecting it at test. Of course, in real world situations, PEI has the power to misled precisely because we learn to trust sources of information that are ostensibly faithful records of an event. Thus, we included the 10 consistent trials to encourage subjects to trust the PEI. The remaining 60 trials were comprised of 20 Consistent, 20 Inconsistent and 20 Neutral trials arranged in random order.

## Results and Discussion

The main research question in Experiment 3 was whether human subjects would show the same pattern of memory distortions using our DMTS analog as pigeons and rats did in the two earlier experiments. Figure 5 shows that the answer is yes. The top panel in Figure 5 shows the mean percent correct (averaged over all subjects) across delays for the three trial types when PEI was presented at the end of each delay. More to the point, it shows the same trends that emerged in the equivalent condition in Experiments 1 and 2. Specifically, consistent PEI trials produced the greatest accuracy, and inconsistent PEI produced the lowest accuracy,  $F(2,28) = 16.3, p < 0.01$ . There was no interaction between delay and trial type,  $F = 0.1$ .

The bottom panel in Figure 5 shows the mean percent correct when PEI was presented at the start of each delay. Although accuracy decreased as delay increased,  $F(1,14) = 7.65, p < 0.05$ , the PEI had no effect on accuracy,  $F = 0.7$ . There was no interaction between delay and trial type,  $F = 0.5$ .



**Figure 5.** Mean percent correct as a function of delay in Experiment 3 when the PEI was presented at the end of the delay (top graph) or start of the delay (lower graph). Accuracy is shown separately for 'consistent', 'neutral', and 'inconsistent' trials. Error bars show standard error of the mean.

In summary, the pattern of results observed in Experiment 3 with humans replicated the four basic patterns observed in Experiments 1 and 2 using pigeons and rats. First, accuracy systematically decreased as the delay between the sample stimulus and recognition increased. Second, the rate of this decrease in accuracy across delays was not affected by the different types of PEI presented either at the

beginning or the end of the delay period. Third, whether PEI had an effect on overall accuracy depended on whether it was presented at the beginning or the end of the delay interval. Fourth, only when the PEI occurred at the end of the delay interval was there an effect on recognition performance. In such a condition accuracy was greater, relative to the neutral baseline condition, when the PEI was consistent with the target sample stimulus. However, lowest levels of accuracy occurred when the PEI was inconsistent with the target sample stimulus.

### **General Discussion**

Does the misinformation effect occur across species? We believe the answer is 'yes'. We base our answer on three important results across our experiments. First, we used a DMTS analog of the classic three-stage procedure used in human research with pigeons, and produced a pattern of results very similar to that found by Loftus et al. (1978): misleading PEI lowers memory accuracy; consistent PEI increases memory accuracy. In both cases the effect increases as delay between the event and exposure to PEI increases. Second, we refined our analog with rats so it was more like the human misinformation methods; we used an event with visual-spatial information, and altered details in that event. Again, we found a pattern of results in line with Loftus et al. Third, we back translated our DMTS analog for use with human subjects, developing a complex event they would have found difficult to embellish with verbal labels. They too showed the misinformation effect.

Before exploring the reasons why the misinformation effect may arise, it is worth noting that the current paradigm and results correspond very well with an even older and parallel line of research in the animal literature concerning 'retroactive interference effects'. Retroactive interference studies also involve the presentation of stimuli after an original target even has been presented (see for example, Harper & White, 1997; White, 1985). The emphasis of retroactive interference studies, in contrast to the misinformation literature, has been in terms of the disruptive effects of PEI on memory-task performance (essentially one side of the misinformation phenomenon). The current results not only show that memory is disrupted by PEI (as in the retroactive interference literature), but that accuracy can also be enhanced. Furthermore, the current findings are quite consistent with the retroactive interference findings. For example, as shown here, Miller, Greco, Marlin and Balaz (1985) found that inconsistent PEI had a greater negative impact on accuracy the more similar it was to the incorrect response option and the further it was away (temporally) to the original event in a maze task with rats.

Why should both humans and nonhumans be similarly influenced by misleading PEI? One possible answer to this lies with the possibility that errors that occur as a result of exposure to PEI are not errors at all. Perhaps they are simply the byproduct of an adaptive mechanism that—in certain contrived situations—produce unwanted effects. What could possibly be adaptive about memory influences caused by PEI? Schacter (1999) has speculated that they are

the price we pay for being able to spend time on what he calls the psychological equivalent of autopilot. Put another way, humans and animals alike have little need to remember all details great and small, so it is easy—perhaps even essential—that we rely on multiple, supplemental sources of information for understanding something.

In fact, it is often necessary to rely on supplemental sources of information, and thus we do not expect them to mislead us. Kugler, Shaw, Vincente, and Kinsella-Shaw (1990) argued that these supplemental postevent sources of information have the ability to fill in and update our "persisting knowledge" of an event or the environment (p.76). In other words, all PEI—whether misleading or not—allows organisms to remain coordinated with some information that is not perceivable now. For example, we refer to our notes when we want to recapture information from a lecture, and we rely on maps when we are lost. Animals may not be that different. Take the shark, for instance. According to Turvey, Shaw, Reed, and Mace, (1981), sharks detect food and locomotive obstacles electronically. One of its favorite foods, the flatfish, produces a distinctive bioelectric field that is detectable when the shark swims over it. The shark uses this electric field to remain coordinated with its environment. When researchers bury electrodes in the sand and reproduce the electric field patterning, the shark looks for flatfish, even digging around the electrodes. What are we to make of the shark's behavior? One might say that the shark has made a mistake, behaving as though a flatfish will soon appear. But Turvey et al. (1981) make a different interpretation of the same data: given that the instrument duplicated information that points to a flatfish, the shark would have made an error only if it had *not* searched. Would we really expect the shark to be able to know that the electronic information had been planted by scientists? We would no more expect the shark to know that the electronic field was an electrode dressed up as a flatfish than we would expect people in an experiment to know that the postevent narrative was a collection of mistakes dressed up as a summary, or that the questions the police officer put to eyewitnesses were inaccurate and would later distort their memories for the event.

Deleted:

The traditional study of misinformation effects has similarly viewed the effect as the result of error; the standard parlance of misinformation research uses words such as *error* and *misremembering*. In light of the experiments we have presented here, we urge researchers to reconsider what they mean by a memory error and to consider theoretical perspectives that conceptualize memory 'errors' in the context of environmental information currently available to the organism (such as White's theory of 'direct remembering,' 2001).

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## **Individual Recognition in Japanese Quail Requires Physical and Behavioral Cues**

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Individual recognition is a complex social learning process in which idiosyncratic characteristics of a conspecific are learned and later used to discriminate this conspecific from others. Many social species of birds appear to be capable of individual recognition. However, it is possible that at least under some circumstances these and other species discriminate conspecifics not based on individual recognition but instead, by recognizing them as members of one or more social categories. Many references to individual recognition in the literature have neglected to address this distinction. For example, Ritters and Balthazart (1998) reported that male quail were capable of recognizing individual females with which they had and had not copulated, but their experimental design may have unintentionally created two social categories of females (sexually receptive and non-receptive). The present set of experiments replicated Ritters' and Balthazart's findings (Experiment 1) and then tested male quail for their ability to recognize females based on physical cues only (Experiment 2), physical and behavioral cues (Experiment 3), and the social categorization cues associated with female receptivity (Experiment 4). The results suggested that male quail are capable of recognizing individual females with which they have and have not copulated, but this recognition is not based on physical, non-sexual, or sexual receptivity behaviors in isolation. Instead, individual recognition occurred only when the males were able to utilize all of these potentially distinctive female attributes in combination. The results also suggested that female receptivity responses may be unique and idiosyncratic, varying along one or more dimensions.

Recognition of conspecifics is important to the survival and reproductive success of many species of social animals. The maintenance of dominance hierarchies, territories, pair-bonds, and parent-offspring relationships all depend upon remembering information associated with specific individuals. The recognition of one particular individual of an animal's own species is referred to as individual recognition. This specific form of conspecific recognition requires that the observer process and remember the idiosyncratic cues of a conspecific (Gheusi, Goodall, & Dantzer, 1997; Sherman, Reeve, & Pfennig, 1997). The evolution of individual recognition has been documented in wide variety of animals including insects (Tibbetts, 2002), fish (Johnsson, 1997) rodents (Johnston & Bullock, 2001), aquatic invertebrates (Karavanich & Atema, 1998), horses (Proops, McComb, & Reby, 2008), dolphins (Janik, Sayigh, & Wells, 2006) and both non-human and human primates (Seyfarth & Cheney, 2009).

The ability to recognize individuals also has evolved in a variety of avian species including spectacled parrotlets (Wanker, Apein, Jennerjahn, & Waibel, 1998), penguins (Clark, Boersma, & Olmsted, 2006), pigeons (Watanabe & Ito, 1991) chickens (Ryan, 1982; Ryan & Lea, 1994), and flycatchers (Lovell & Lein, 2005). However, the specific signature traits that form the basis of individual

This work was funded by grants from the National Institutes of Health, MH39940 and R15 HD051622-01A1. We would like to thank Michael Domjan for his advice during the early stages of this study and comments on an earlier draft. We would like to thank Meena Dershin, Robert Ervin, and Jasmin Kaeser for their contributions to the project. All animals were treated in accordance with the guidelines set forth by the American Psychological Association. Correspondence concerning this article should be addressed to Brian Cusato, Department of Psychobiology, Centre College, 600 West Walnut Street, Danville, KY 40422, U.S.A. (b.cusato@centre.edu).

recognition vary among these birds. Penguins and spectacled parrotlets, for example, recognize individuals based on vocalizations, (Jouventin, 1982; Wanker et al., 1998; Wanker & Fischer, 2001) while turnstones and pigeons rely more on idiosyncratic visual and behavioral cues (Jitsumori, Natori, & Okuyama, 1999; Whitfield, 1987).

Many adaptive social behaviors rely on an animal's ability to recognize individual conspecifics (see Tibbetts & Dale, 2007 for a review). In territorial species, for example, it allows animals to discriminate neighbors from non-territorial floaters (Temeles, 1994). It also can play an important role in the maintenance of dominance hierarchies, reducing the need for aggressive interactions once the hierarchies have been established (Benard & Burk, 1979). In mating interactions, the ability to recognize individuals of the opposite sex can help maximize outbreeding.

Although it is pervasive and highly adaptive (Seyfarth & Cheney, 2009), individual recognition in social situations is a challenging cognitive task. It requires that animals attend to, remember, and then accurately recall the idiosyncratic characteristics of the individuals with which they interact. The challenge becomes more difficult as the size of the social group increases so some species have evolved alternative identification strategies to compensate. For example, under conditions when individual recognition is not possible, large flocks of domestic hens shift from a dominance hierarchy system based on actual aggressive encounters to a more passive social organization, likely making use of reliable markers highly correlated with dominance such as large body and comb size (Pagel & Dawkins, 1997). Situations like this when animals rely on species typical physical or behavioral characteristics to successfully interact with conspecifics require a simpler form of learning, social categorization.

Unlike individual recognition, social categorization requires that animals need only recognize the species-typical characteristics of particular categories and then identify these characteristics in the individuals they encounter (Gheusi et al., 1997; Payne, Payne, Rowley, & Russell, 1991; Tibbetts & Dale, 2007). The unique attributes of individual conspecifics within each category may in fact never be learned or even attended to. There is substantial evidence that birds recognize many social categories including familiarity (Bradshaw, 1992; Dawkins, 1982), dominance (King, 1965; Syme, Syme, & Barnes, 1983), sex (Domjan & Nash, 1988), and kin (Bateson, 1982). For social categorization to occur, species typical characteristics must be highly stereotyped within the individuals of each social class and vary noticeably between social classes (Wanker & Fischer, 2001). Under some circumstances, a categorical distinction such as male–female, or dominant–submissive, is sufficient to successfully interact with a particular individual even during a first encounter. Social categorization is likely to occur in species that maintain relatively simple social structures where individual recognition is not necessary (Jitsumori et al., 1999) or in very large groups of animals where individual recognition is not possible.

Individual recognition and social categorization can be easily confused, especially in the study of non-human behavior. For example, Ryan and Lea (1994)

used a dishabituation procedure in an attempt to demonstrate individual recognition in pigeons. Subjects were repeatedly exposed to a stimulus bird for short periods of time. Once the subject bird's agonistic behaviors decreased the presentation a novel stimulus bird caused the agonistic behaviors to return. The authors concluded that the return of agonistic responding was evidence of individual recognition (Ryan & Lea, 1994) even though sorting the stimulus pigeons into familiar and unfamiliar categories would have resulted in the same behavior. Other researchers have tested for individual recognition by presenting visual or auditory stimuli associated with a mate or a stranger, creating a similar familiarity confound (e.g., Clark, Boersma, & Olmsted, 2006).

Riters and Balthazart (1998) conducted a similarly ambiguous experiment using male Japanese quail as subjects and live female quail as discrimination cues. Males were permitted visual access to a female before being allowed to copulate with her. The same males also were exposed to a different female with which they were not permitted to copulate. The males spent significantly more time viewing the copulation female, a result suggestive of individual recognition. However, the copulation females may have displayed sexual anticipatory squatting responses that distinguished them from the non-copulation females. If this occurred, a categorization strategy using female sexual receptivity responses also would have allowed the males to successfully discriminate between the two females. Therefore, as in the Ryan and Lea (1994) experiment, the results of the Riters and Balthazart (1998) experiment may not have represented individual recognition.

The present experiments were conducted to identify the mechanisms by which male Japanese quail discriminate between the females with which they have and have not copulated. Evidence of true individual recognition would suggest a level of cognitive complexity not yet documented in this species. The experiments also were designed to provide information about the mating strategies used by male quail in their natural environment, and which particular female cues are most salient to males as they make their mating decisions.

Experiment 1 replicated the procedures used by Riters and Balthazart (1998) with slight modifications to regulate the male subjects' familiarity with each stimulus female. Experiment 2 used taxidermic models of female quail to examine whether males were capable of recognizing females based only on their physical characteristics. Experiment 3 examined the ability of males to recognize live females based on their idiosyncratic, non-sexual characteristics. The design of Experiment 4 tested the extent to which males utilize social categorization to regulate their social interactions. In this experiment the male subjects had to discriminate between live females based on the presence or absence of sexual anticipation behaviors.

## **General Method**

### ***Subjects and Stimulus Birds***

Forty-eight male Japanese quail served as subjects and 58 female Japanese quail served as stimulus birds. The birds were raised from eggs randomly selected from a colony of quail maintained at The University of Texas and housed in mixed sex brooders until 30 days of age. The birds were

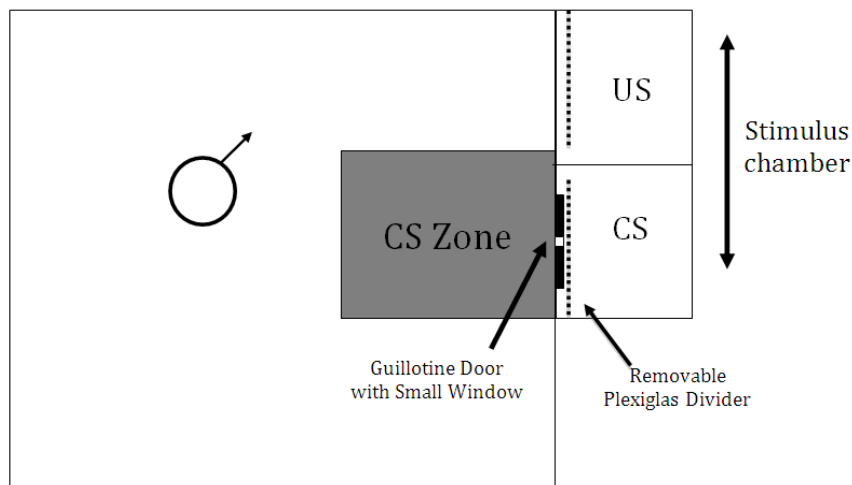
then sexed and transferred to smaller wire cages (GQF Manufacturing, 55 cm long x 25.4 cm wide, with a sloping floor creating a height of 20 cm at the back and 25.5 cm at the front of the cage). Males were housed individually and females were housed in pairs.

Potential male subjects were screened for abnormally low sexual motivation with a 5 min copulatory pretest at 6 month of age. Only males that achieved cloacal contact during the pre-test were selected as subjects. The copulatory pretest was the only sexual experience the male subjects had prior to beginning the experiments and none of the males were previously involved in any other experiments. Sexually and experimentally naïve female quail that were at least 4 months of age served as the conditioned and unconditioned stimuli.

The lights in the colony and experimental rooms were set on a 16 hr light: 8 hr dark cycle. This simulation of long days allowed the birds to remain in reproductive condition throughout the experiment. Food (Purina Poultry Chow) and water were available at all times.

### *Apparatus*

Twelve identical experimental chambers were used (Figure 1). Each subject was housed in a large test chamber (90 cm wide x 90 cm deep x 50 cm high). The top, bottom, back, and side walls of each large test chamber were constructed of sealed plywood. The front of the chamber was made of wire mesh to allow for behavioral observations and hinged to act as a service door. Two side-by-side stimulus chambers, also constructed of sealed plywood, rested on a sliding track that was mounted just outside the large test chamber. They were used for presentation of the conditioned and unconditioned stimuli. Each stimulus chamber measured 20 cm wide x 15 cm deep x 15 cm high. The stimulus chamber wall that faced the large test chamber was made of opaque Plexiglas. It could be removed to reveal the contents of the stimulus chamber. A doorway (14 cm wide x 16.5 cm high) with a guillotine-style door (stimulus door) separated the large test chamber and the small stimulus chambers. The door contained a narrow Plexiglas viewing window (1.3 wide x 15.2 cm high) that allowed visual access into only the stimulus chamber that was aligned with the doorway. During most experiments the CS presentations began by removing the stimulus chamber's opaque Plexiglas wall so that the subject male could view the CS through the viewing window. Sliding the stimulus chambers and/or raising the stimulus door allowed for the presentation of the unconditioned stimulus. The configuration of the test enclosures did not permit the experimenters to regulate the degree to which the subject and stimulus birds could hear one another. Although the vocalizations in this species are sex-specific there is no evidence that either sex uses vocal cues to discriminate individuals.



**Figure 1.** Experimental Apparatus – Stimulus chambers slid along a track so that the contents of only one of the stimulus chambers (CS or US) was visible through the window in the guillotine door.

**Procedure**

One week prior to starting an experiment, subjects were housed in the large test chambers to facilitate habituation to the testing environment. Food and water were available in the test chambers at all times. The experiments utilized a Pavlovian discrimination procedure in which one conditioned stimulus (CS+) was paired with sexual opportunity and another conditioned stimulus (CS-) was not. The nature of the conditioned stimulus differed between experiments (see Table 1) but all of the conditioned stimuli were presented in a similar fashion.

**Table 1**

*Conditioned Stimuli (CS+ & CS-) and Unconditioned Stimuli (US+ & US-) for each experiment. Letters indicate whether the same or different females served as CS and US for each subject within an experiment. The plus and minus signs used in the boxes for Experiment 4 indicate female categories (CS+, CS-)*

	CS+	US+	CS-	US-
Exp 1	Window Viewing of Live Female (A)	Full Access to Live Female (A)	Window Viewing of Live Female (B)	Visual Access to Live Female (B)
Exp 2	Window Access to Taxidermic Model (A)	Full Access to Live Female	Window Access to Taxidermic Model (B)	No Access to Female
Exp 3	Window Access to Live Female (A)	Full Access to Live Female (B)	Window Access to Live Female (C)	Visual Access to Live Female (D)
Exp 4 (Disc)	Window Access to Live Female (A+)	Full Access to Live Female (A+)	Window Access to Live Female (B-)	No Access to Female
Exp 4 (Transfer)	Window Access to Live Female (C+)	---	Window Access to Live Female (D-)	---

During reinforced trials the CS+ was placed in one stimulus chamber and then revealed to the subject by removing the opaque Plexiglas wall. The subject could then view the CS+ through the window in the stimulus door for 5-min. At the end of the CS+ period the stimulus door was raised in order to release a sexually receptive female quail (the unconditioned stimulus or US+). The subject was permitted to interact with the female in the large test chamber for 5 minutes, during which copulation invariably occurred. In some experiments the CS+ and US+ were the same female, but in others, the CS+ and US+ females were different. To achieve the latter, immediately after the CS+ period the other stimulus chamber containing a female was shifted to align with the doorway and the stimulus door was raised, simultaneously hiding the CS+ and allowing the male and the US+ female to interact.

During CS- trials, the opaque Plexiglas wall was again removed to reveal the CS- in one of the stimulus chambers. After 5 min, the stimulus chambers were shifted to reveal the US- condition. There was some variation in the US- across experiments (see Table 1), but the US- never involved the opportunity to copulate with a female.

Every subject received one CS+ and one CS- trial each day for 10-14 consecutive days in Experiments 1, 2, and 3. The CS+ and CS- trials were conducted at least 2 hours apart and the order of CS+ and CS- presentations was randomized with the single constraint that no subject experienced the same type of trial first on more than three consecutive days. In Experiment 4, trial type was randomized such that two trials of the same type could occur on the same day. Each trial was video recorded for subsequent scoring and two behaviors were measured to assess the effects of discrimination training: time in the CS zone and orientation towards the viewing window. The CS zone (30 cm<sup>2</sup>) was marked on the floor of the cage directly in front of the viewing window. A subject

was considered to be in the CS zone when both feet were within the marks. Orientation was measured using a point sample technique. Orientation of the subjects beak (towards or away from viewing window) was recorded every 5 sec for the 5 min CS period.

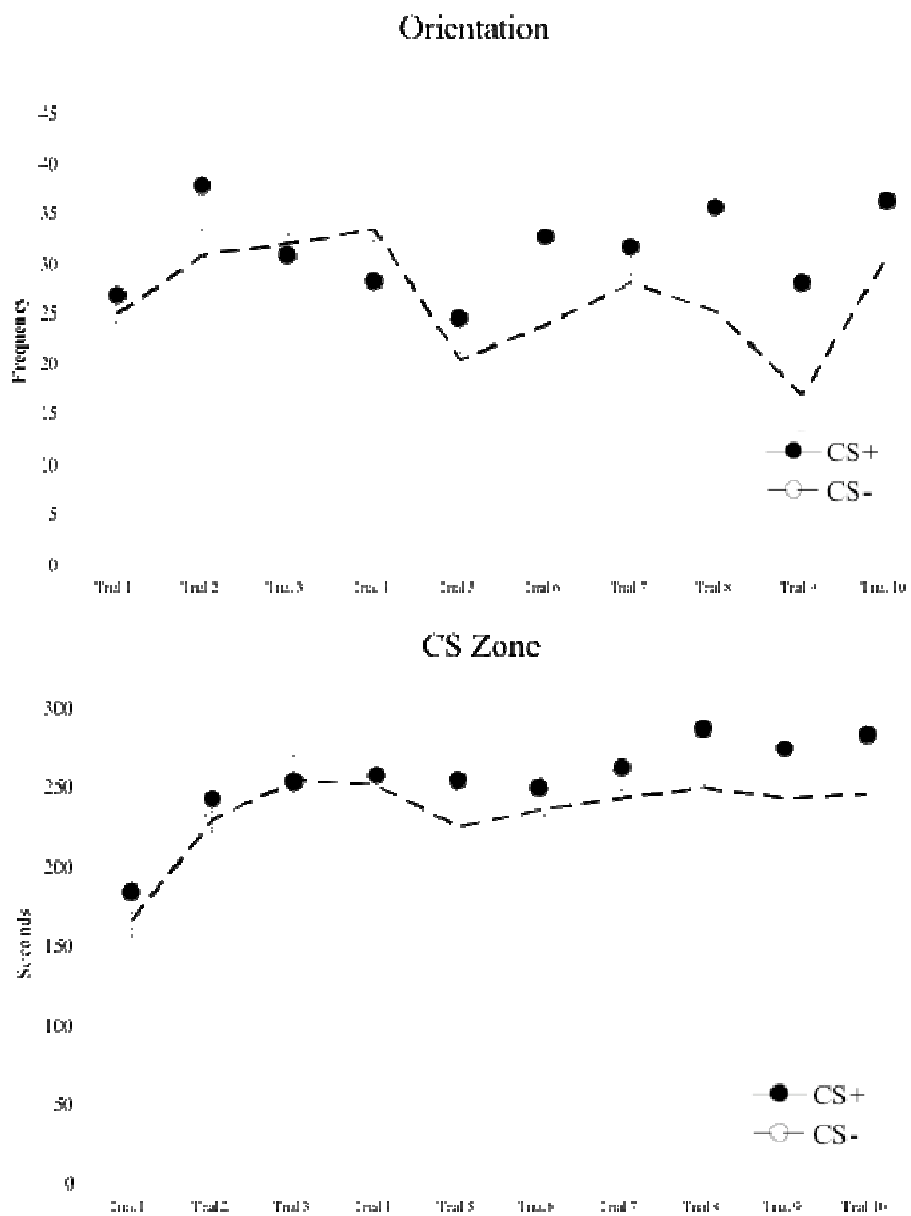
### **Experiment 1: Social Categorization or Individual Recognition**

Experiment 1 was conducted to replicate the previous finding that male quail can discriminate between females with whom they have and have not copulated (Riters & Balthazart, 1998). Twelve live females served as conditioned and unconditioned stimuli. Each male subject ( $n = 12$ ) was assigned a pair of stimulus females. One female served as the CS+ and one as the CS- throughout the experiment. During CS+ trials, subjects could see a live female (the CS+) through the viewing window for a 5 min period then were allowed to copulate with the same female during the 5 min US+ period. During CS- trials, a different female (the CS-) was visible in the stimulus chamber. The CS- period lasted for 5 min and was immediately followed by the US- period when the door was raised to reveal the CS- female behind a transparent Plexiglas wall. During the 5 min US- period, the subject had visual access to the female but no physical access. Each stimulus female served as a CS+ for one subject and a CS- for a different subject. Subjects received one CS+ and one CS- trial per day for 10 consecutive days. Like the experiment conducted by Riters and Balthazart (1998) this procedure did not distinguish between social categorization and individual recognition. Either identification strategy would permit the subject males to successfully discriminate between the CS+ and CS- female.

### **Results and Discussion**

The average amount of time that subjects spent in the CS zone during the 5 min CS period increased across trials (Figure 2, top panel). Furthermore, there was a consistent trend for subjects to spend more time in the CS zone during CS+ trials than CS- trials. These impressions were supported by a repeated measures analysis of variance (ANOVA) with Days (1-10) and CS type (CS+ and CS-) as within subject variables. The analysis revealed significant effects of Days ( $F(9,99) = 4.13$ ,  $p = 0.0002$ ) and CS Type ( $F(1,11) = 11.70$ ,  $p = 0.0057$ ) but the Days X CS Type interaction was not statistically reliable,  $F < 1.0$ .

Orientation towards the CS window (Figure 2, bottom panel) tended to occur more frequently on CS+ trials than CS- trials. However, when the data were analyzed with a repeated measures ANOVA with Days and CS Type as independent variables, the main effect of CS Type was marginally significant,  $F(1,11) = 4.50$ ,  $p = 0.058$ . The main effect of Days was significant,  $F(9,99) = 2.088$ ,  $p = 0.038$ ; but the Days X CS Type interaction was not,  $F(9,99) = 1.28$ ,  $p = 0.256$ .



**Figure 2.** Mean time ( $\pm$ SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). Subjects were allowed to copulate with CS+ females after the 5 min exposure but were not allowed to copulate with CS- females.

In discrimination tasks that require one or more trials for subjects to become familiar with the stimuli and the nature of the task, evidence of successful discrimination by the end of the experiment can often be diluted by poor performance early in training when learning was still occurring. Therefore, it was necessary to isolate behavior during the last few trials to assess whether subjects

were able to truly discriminate between the identities of the female stimuli. Subsequent analyses examined data from the final 3 days of training to assess the extent to which learning had occurred independent of the early phase of learning (Figure 2). A repeated measures analysis of time spent in the CS zone during CS+ and CS- trials on days 8, 9, and 10 revealed a significant main effect of CS Type ( $F(1,11) = 7.77, p = 0.018$ ) indicating more time spent near the CS+ than the CS-. Neither the main effect of Trials nor the Trials x CS Type interaction were significant ( $F_s < 1.0$ ), suggesting that learning may have been complete at that point. Evaluation of orientation data during the last 3 days of training also revealed a significant main effect of CS type,  $F(1,11) = 8.32, p = 0.015$ . Subjects spent significantly more time in the CS zone when the CS+ was visible through the viewing window than when the CS- was visible. The main effect of Trials was also significant,  $F(2,22) = 7.56, p = 0.003$ , but the Trials X CS Type interaction was not,  $F < 1.0$ .

These results were very similar to those obtained by Ritters and Balthazart (1998). The male subjects learned to discriminate between the females with which they had and had not copulated. However, it remained unclear from these results what type of cues the males were using to make this discrimination. One possibility is that they relied on the physical characteristics of the females like overall size or plumage variations to identify individuals. This possibility was tested in Experiment 2.

## **Experiment 2: Individual Recognition Using Only Physical Cues**

Experiment 2 was designed to determine if male quail could recognize individual females based solely on their physical attributes. In a small pilot study, it was determined that human observers were able to easily distinguish same-sex quail based only on their physical characteristics (shape, size, plumage variation, etc.) so it was theorized that male quail would be capable of doing the same. The contribution of idiosyncratic behaviors to individual recognition was eliminated by using taxidermic models of female quail as the CS+ and CS- and all of the models were placed in a squatting position to eliminate the use of sexual receptivity as a categorical cue. In the absence of behavioral and categorical cues, the male subjects had to rely on their ability to recognize individual females based solely on their physical characteristics. Twelve naïve males participated as subjects and 12 naïve female quail served as unconditioned stimuli.

Six female quail were prepared as taxidermic models to serve as conditioned stimuli. Each model was a CS+ for four subjects and a CS- for four different subjects. During CS+ trials, the CS+ model was visible through the viewing window for 5 min before a live female (US+) was released into the test chamber by shifting the stimulus chambers. During CS- trials, the subject could see a different model (CS-) through the viewing window for a 5 min period, but no US- was presented. In order to avoid subjects discriminating CS+ from CS- conditions based on the presence of cues produced by the US+ female (e.g., vocalizations, movement), a live female was placed in the concealed stimulus

compartment during CS- trials as well. Subjects did not see or interact with the concealed female at any time. However, as was the case during the CS+ model presentations, males were able to hear the live females when the CS- model was visible. Sliding the opaque Plexiglas wall between the viewing window and the stimulus chamber ended the CS- period. Because subjects failed to show evidence of discriminating between the CS+ and CS- conditions after day 10, discrimination training was extended for an additional 4 days to determine if the difficult nature of the task required additional training sessions before individual recognition was evident.

## Results and Discussion

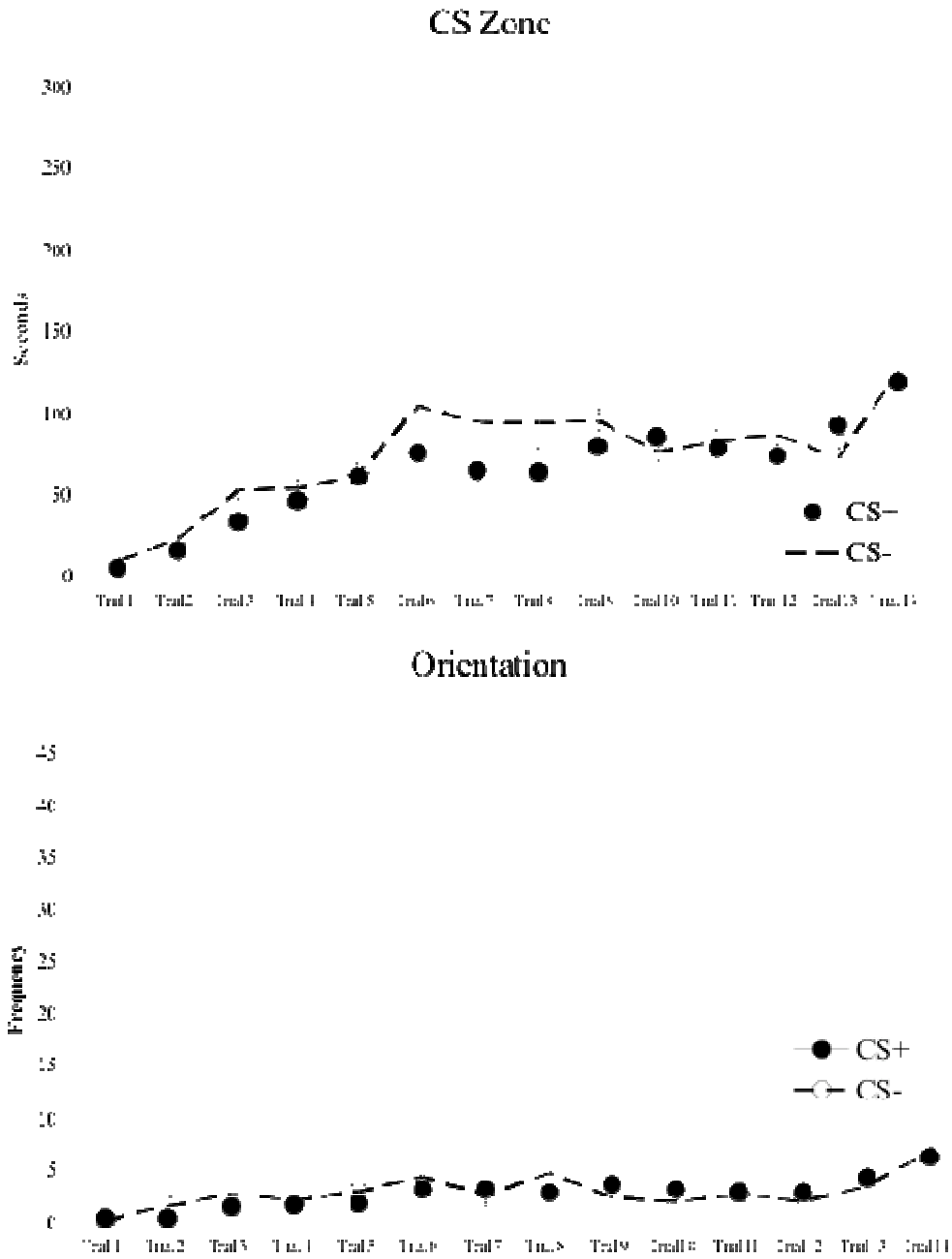
Time in the CS zone and orienting towards the CS window during the 5 min CS periods are represented in the top and bottom panels of Figure 3. Subjects showed an increase in both behavioral measures across trials, indicating that learning occurred with training. However, the subjects showed similar amounts of approach to the CS window and orientation towards the CS window regardless of whether the CS+ or CS- taxidermic model was visible.

The CS zone data was evaluated using a repeated measures ANOVA with Trials (1-14) and CS Type (CS+ and CS-) as within group variables. The analysis revealed a significant effect of trials,  $F(13, 91) = 6.498, p < 0.0001$ , reflecting increased time spent in the CS zone with training. However, the main effect of CS Type was not significant,  $F(1,7) = 2.13, p = 0.188$ . Subjects did not discriminate between the taxidermic models that predicted copulatory opportunity and the models that did not. The Trials X CS Type interaction also did not reach significance ( $F < 1.0$ ).

The orientation data was analyzed with the same statistical tests and similar results were found. Orientation towards the CS window during the 5 min exposure period increased significantly across trials,  $F(13,91) = 4.746, p < 0.0001$ . However, neither the main effect of CS Type nor the Trials X CS Type interaction were significant ( $F_s < 1.0$ ) indicating that the subjects did not react differently to the CS+ and CS-.

These results suggest that male quail are not capable of recognizing female quail based solely on their physical characteristics. The lack of discrimination in Experiment 2 was not likely due to insufficient training. Unlike the 10 days of discrimination training used in Experiment 1, this experiment used 14 days of discrimination training. This was done to increase the opportunity for subjects to learn the association between the CS+ and copulation, and this length of training has been more than sufficient to sexually condition male quail in previous experiments (Crawford, Holloway, & Domjan, 1993).

The results of Experiment 2 also suggest that the males in Experiment 1 were relying on behavioral cues to successfully discriminate between individual females. Experiments 3 and 4 were designed to determine whether sexual or non-sexual female behaviors were more important to the males during their discrimination training.



**Figure 3.** Mean time ( $\pm$ SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). The presentation of the CS+ taxidermic model preceded opportunity to copulate whereas the CS- taxidermic model was never paired with copulation.

### **Experiment 3: Individual Recognition Using Physical and Behavioral Cues**

Female quail that are sexually receptive show species-typical squatting behavior (Gutiérrez & Domjan, 1997; Domjan, Mahometa, & Mills, 2003). This species-typical, sex-specific response consists of the female remaining immobile while at the same time bringing her body in contact the ground. Thus it is possible that the males in Experiment 1 were using this squatting behavior to separate females into social categories – those that are sexually receptive and those that are not. In contrast, female quail also exhibit individual variation with respect to their non-sexual behaviors. Males could presumably use these unique non-sexual behaviors to distinguish one female from the next. It is unclear what female behaviors to which the males were attending in Experiment 1 but the distinction is important because only the use of the idiosyncratic behaviors, physical cues, or some combination of the two would represent true individual recognition.

Experiment 3 was designed to determine if male quail could recognize individual females in the absence of the categorical cues associated with sexual anticipation. This was accomplished by using the presentation of a live female bird (the CS+) to predict copulation with a different female (US+). A similar procedure in which a live rat acted as a CS to signal impending food was used by Timberlake and Grant (1975). In our CS+ trials, the CS+ female was visible through the viewing window for 5 min before a different female (US+) was released into the test cage for copulation. The presentation of yet another live female (the CS-) predicted non-copulation with a different female (US-). During CS- trials, the CS-female was presented in the stimulus chamber for 5 min then the stimulus chamber was shifted to expose a different female (US-) behind transparent Plexiglas. The Plexiglas partition prevented physical contact but allowed visual access to the female US-. As in Experiment 2, each male subject experienced two trials daily for 14 consecutive days. Twelve male quail served as subjects and 24 females served as stimuli (12 as CSs and 12 as USs). Unlike Experiment 1, the CS+ and CS-females in the present study remained sexually naïve for the duration of the experiment, and therefore, were prohibited from anticipating sexual opportunity during discrimination training. Periodic observations of the female stimulus birds during discrimination training confirmed that the females did not engage in squatting behavior while in the stimulus chambers. In the absence of such categorical information, the males needed to rely on the unique physical and non-sexual behaviors of the females to successfully discriminate.

### **Results and Discussion**

The average amount of time that the subjects spent in the CS zone on CS+ trials and on CS-trials across the 14 days of discrimination training is represented in the top panel of Figure 4. In general, time spent near the CS female increased across trials regardless of whether or not the stimulus predicted impending sexual opportunity. Analysis of the data using a repeated measures ANOVA with Trials and CS Type as independent variables revealed a significant main effect of Trials,

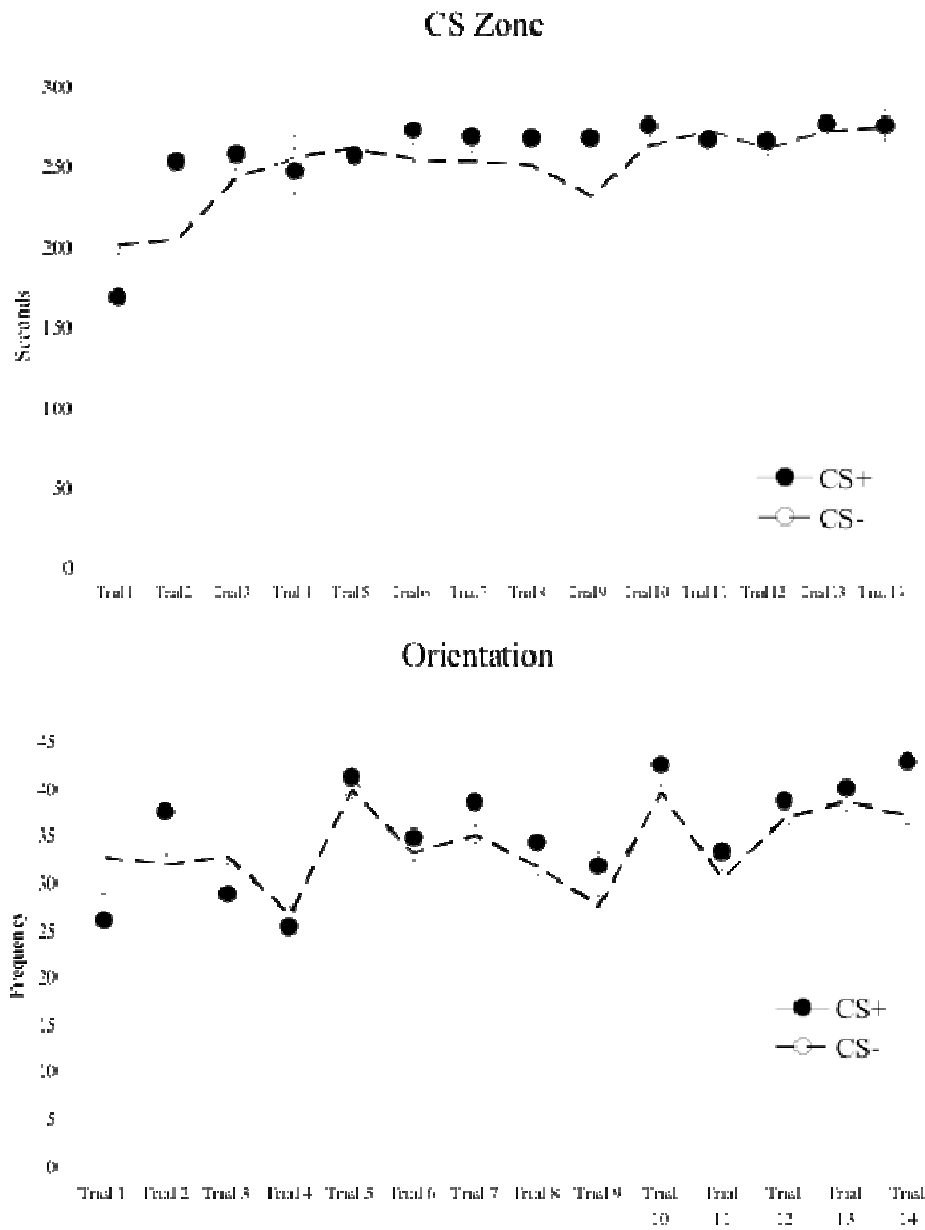
$F(13, 143) = 4.70, p < 0.0001$ , but neither the main effect of CS Type,  $F(1,11) = 2.88, p = 0.118$ , nor the Trials X CS Type interaction  $F(13, 143) = 1.54, p = 0.111$ , were significant. The subjects did not discriminate between the CS+, which predicted sexual opportunity, and the CS-, which predicted no sexual opportunity.

The orientation data (bottom panel of Figure 4) also was analyzed with a repeated measures ANOVA. Orientation towards the CS window during the 5 min exposure period increased significantly across trials,  $F(13, 143) = 4.00, p < 0.0001$ . However, neither the main effect of CS Type ( $F(1,11) = 1.94, p = 0.188$ ) nor the Trials X CS Type Interaction ( $F(13, 143) < 1.0, p = 0.774$ ) were significant indicating that the subjects did not learn to discriminate between the CS+ and CS-females.

By using virgin females as conditioned stimuli, the males in this experiment were forced to rely on general behavioral cues such as overall activity level or idiosyncratic behavior patterns to discriminate between individual females. Without the benefit of sexual anticipation cues, the males failed to recognize the differences between the CS+ and CS- females, even after 14 days of discrimination training. These results suggest that female sexual anticipatory responses were important in the recognition exhibited by the male subjects in Experiment 1 and that these males may have simply separated females into receptive and nonreceptive categories. This possibility motivated the design of Experiment 4.

This change in procedure created a difference in the amount of time that a subject was exposed to the CS/US+ female (5 min CS period + 5 min US period per trial) compared to the CS- female (5 min CS period only per trial) allowing for the possibility that the subjects would be more familiar with the CS+ female than the CS- female. To eliminate this inequality, the number of CS- trials was doubled so that by the end of training, subjects had visual exposure to each stimulus female for 140 min (CSs+: 10 min on 14 trials; CS-: 5 min on 28 trials). Eight stimulus females served as either a CS+ or as a CS-, but not both. Additionally, each female was used to train three different subjects to ensure that the female's sexual anticipation would develop in response to cues associated with the stimulus chamber rather than in response to the individual identity of the subject.

A transfer test was conducted immediately following discrimination training to determine if males were utilizing social categorization to discriminate between the CS+ and CS- females. On this day, each subject received a 5 min CS+ trial and a 5 min CS- trial with, respectively, a CS+ female and a CS- female that were used in the discrimination training of another male. Therefore, the physical characteristics and individual behaviors of each female were unfamiliar to the subject male, but the sexual anticipation behaviors of the CS+ females (i.e. immobility and squatting) were similar to those the male observed during the discrimination training. If males categorize females using the presence or absence of anticipatory squatting behavior, the subjects during the transfer test should successfully discriminate between unfamiliar receptive and nonreceptive females even when seeing them for the first time.



**Figure 4.** Mean time ( $\pm$ SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). The CS+ (a live female) predicted an opportunity to copulate with a different live female whereas the appearance of the CS- (yet another live female) was not followed by sexual opportunity.

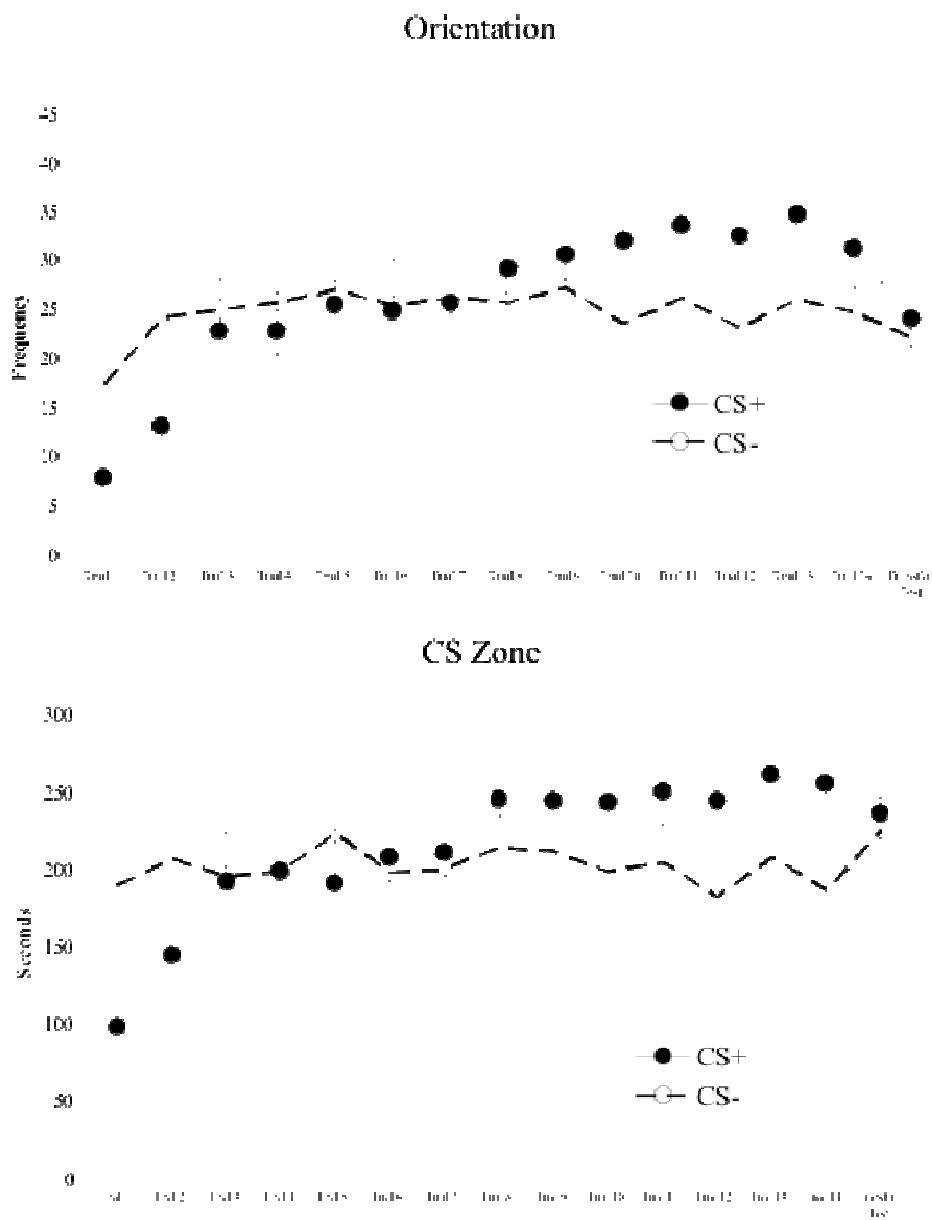
## Results and Discussion

Prior to statistical analyses, data from sequential pairs of CS- trials were averaged to equate the number of CS- data points with CS+ data points. Time spent in the CS zone and orientation toward the viewing window during discrimination training were analyzed separately with two-way repeated measures ANOVAs. Trials (1-14) and CS Type (CS+ and CS-) were within subject variables. The top panel of figure 5 represents the average amount of time subjects spent in the zone near the CS window during the 5 min period when the female was visible. The males initially spent more time looking at the CS- female than the CS+ female but this trend reversed with training. During the last 5 training trials, males showed a clear preference for the CS+ female over the CS- female. This change in preference across trials was reflected in the results of the analyses: the main effect of CS type was not significant,  $F(1,11) < 1.0$ , but the CS Type X Trials interaction was significant,  $F(13, 143) = 5.99$ ,  $p < 0.0001$ . The main effect of Trials also was statistically reliable,  $F(13, 143) = 4.85$ ,  $p < 0.0001$ , indicating a substantial increase in time spent in the CS zone across trials.

The pattern of orientation behavior was very similar to time spent in the CS zone (figure 5, bottom panel). Subjects looked at the CS- more often than the CS+ at the beginning of training but spent more time looking at the CS+ than the CS- at the end of the experiment. As a result, the main effect of CS type failed to reach significance,  $F < 1.0$ , but the main effect of Trials and the Trials X CS Type interactions were both significant,  $F(13, 143) = 9.56$  and  $4.84$ , respectively,  $p$ 's  $< 0.0001$ .

Analysis of behavior during the transfer test failed to show any evidence of discrimination between the novel CS+ and CS- females (see figure 5). Both behaviors were evaluated using separate paired t-tests yet neither time in zone ( $t(11) = 0.50$ ,  $p = 0.630$ ) nor orientation ( $t(11) = 0.52$ ,  $p = 0.617$ ) were significant.

The behavior of the male subjects during the training phase confirmed that male quail are capable of discriminating between females with which they have and have not copulated. However, the males spent similar amounts of time near and orienting towards the novel CS+ and CS- females during the transfer test. These results suggest that social categorization based on sexual anticipation alone is insufficient for males to discriminate between individual females.



**Figure 5.** Mean time ( $\pm$ SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). Subjects were allowed to copulate with CS+ females after the 5 min CS period but were not allowed to copulate with CS- females. On the first 14 trials, CS+ data represents single trials and the CS- data represents blocks of two trials. During the transfer test, subjects were exposed to unfamiliar females that had served as either CS+ or CS- females to other males.

## General Discussion

Individual recognition and social categorization represent two different ways animals draw on their past experiences with conspecifics to help determine their behavior during social interactions. Both mechanisms are pervasive throughout the animal kingdom and have obvious adaptive value (Seyfarth & Cheney, 2009), but only individual recognition requires that the unique traits of individuals be remembered in association with each individual's identity. In contrast, social categorization is a simpler task requiring only the recognition of the defining characteristics of two or more distinct social groups (e.g., receptive vs. non-receptive females). Only a relatively few distinguishing characteristics need be remembered, and no previous interactions with the target conspecific are necessary for categorizations to be swift and accurate.

There is evidence that some bird species are capable of true individual recognition (e.g., D'Eath & Keeling, 2003; Lovell & Lein, 2005; Watanabe & Ito, 1991). But even in these species it is possible that individuals utilize social categorization to narrow the possible identities of a conspecific. Since the two strategies may be used concurrently, experimental findings that have the appearance of individual recognition may actually represent social categorization (Riters & Balthazart, 1998).

The present experiments were conducted to identify the mechanisms by which male Japanese quail discriminate between individual females. The results of Experiment 1 indicated that male quail are capable of discriminating between female quail with which they have and have not copulated. The results of the subsequent experiments helped clarify the extent to which the males in Experiment 1 discriminated the females using their unique physical cues (Experiment 2), non-sexual behaviors (Experiment 3), or sexual anticipatory responding (Experiment 4). Unlike Experiment 1, the males in these subsequent experiments were unable to discriminate between the female stimulus birds using the limited physical and behavioral cues they were provided.

The fact that the males in Experiment 2 failed to recognize the differences between the 2 female models was somewhat surprising since the results of a pilot study indicated that human observers performed well on a similar task. However, poor performance on a discrimination task using taxidermic CSs is not without precedence. Ryan and Lea (1994) found that pigeons were unable to discriminate between two taxidermically prepared pigeon models when one model predicted food and the other did not. Perhaps the artificial nature of the taxidermic females in the present study prohibited the males from processing the relevant distinctions between the two models. This seems unlikely since male quail in a previous experiment responded to the visual aspects of live females and taxidermic females in a similar way (Hilliard, Nguyen, & Domjan, 1997).

Moreover, the failure of the males to discriminate between the two taxidermic models does not mean that the visual features of females are unimportant to male quail. Instead, these results suggest that visual features alone,

*in the absence of other cues*, are insufficient for males to make accurate female identifications. In fact, numerous sexual conditioning experiments with male quail have shown that the visual characteristics of live birds contribute substantially to conspecific and sex recognition (Domjan & Hall, 1986; Nash & Domjan, 1991; Nash, Domjan, & Askins, 1989;). But in all of these studies, the discrimination tasks were far less subtle (e.g., discriminating between different color strains of quail, recognizing males vs. females) and live stimulus birds provided the males with distinguishing behavioral cues to complement their static visual features.

The combined results of Experiments 1 and 2 suggest that male quail rely on behavioral cues to successfully discriminate between individual females. However, the results of Experiments 3 and 4 indicate that males are incapable of discriminating between individual females using non-sexual and sexual female behaviors when they are presented independent of one another.

How do these results clarify the extent to which male quail use either social categorization or individual recognition to discriminate female conspecifics? The inability of the males to discriminate between the taxidermic models in Experiment 2 suggests that unique physical cues alone are insufficient for individual recognition to occur. Likewise, individual recognition did not occur when the males in Experiment 3 were limited to using idiosyncratic physical and non-sexual behaviors. This suggests that male quail are incapable of discriminating individual females in the absence of differing levels of sexual receptivity responding. However, the males during the transfer test in Experiment 4 also failed to discriminate between individual females when sexual receptivity behaviors were provided as distinctive female cues. This latter finding suggests that, much like the physical and non-sexual behavioral cues of females, the social categorization cues of female receptivity are, at least by themselves, insufficient for males to use as discriminative stimuli.

The failure of the males to discriminate between the two stimulus females during the transfer test in Experiment 4 suggests that the male discrimination behavior observed in Experiment 1 and in the experiment conducted by Ritters and Balthazart (1998) represents true individual recognition. This is of particular importance since quail are a polygynous species that lack biparental care (Tibbetts & Dale, 2007). Given the cognitive complexity that individual recognition requires (Beecher, 1989), identifying and remembering previous mating partners is likely to be important for the reproductive success of male quail in their natural environment. Why this is the case has yet to be empirically determined, but males would certainly benefit from avoiding females that were consistently nonreceptive. At the same time, males that consistently returned to females that were receptive to their previous mating attempts would have difficulty competing with males attracted to novel females. Perhaps male quail are capable of balancing between these two strategies to optimize their reproductive success. Future experiments should address this possibility.

The present findings also suggest that male recognition of individual females in this species is not accomplished by focusing on physical, non-sexual, or sexual receptivity behaviors in isolation. Instead, individual recognition is likely to

occur only when males are able to utilize all of these potentially distinctive female attributes at the same time. Such was the case in Experiment 1 and in the training phase of Experiment 4, as well as the experiment conducted by Ritters and Balthazart (1998).

Another potential explanation for the present findings is that female Japanese quail receptivity responses are themselves unique and idiosyncratic, varying along one or more dimensions from one female to the next. One female may squat while looking toward the male, while another female may squat while looking away. Or perhaps individual female squatting responses vary in frequency and duration. Gutiérrez and Domjan (1997) observed group differences in the duration of female squatting as a result of sexual conditioning. If this occurred in the present set of experiments, it is not surprising that males were unable to discriminate between the CS+ and CS- females they observed during the transfer test of Experiment 4. During this test the stimulus females no doubt displayed species-typical behaviors that were generally indicative of receptivity, but the idiosyncratic female receptivity responses the males were able to use during their previous discrimination training were absent. Thus, the lack of male discrimination during the transfer test suggests that each female's receptivity responses are unique, and these unique features are important for males to recognize one female as being distinct from another. The design of future experiments should directly investigate this possibility. Future experiments also need to further explore the cognitive and behavioral differences between social categorization and true individual recognition. It is likely that some species utilize both forms of recognition. Thus, distinguishing between these two forms of social learning in future experiments will be both challenging and important to the understanding of what regulates animal social interactions.

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## **Magnitude Effects of Sexual Reinforcement in Japanese Quail (*Coturnix japonica*)**

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The effect of the magnitude of sexual reinforcement on the extinction of a running response was studied in quail. In Experiment 1, a group of subjects (L) received copulatory access to eight females, whereas a second group (S) received access to a single female. Both groups acquired the running response. During extinction, Group S showed a fast decrease in responding, whereas Group L persisted longer. In Experiment 2, males were allowed a choice between one or eight females. Preference for eight females demonstrated that males discriminated between the two reward magnitudes and that access to eight females had a larger reinforcing value than access to one female. The results are discussed within the context of the paradoxical reinforcement effects and the divergence in learning mechanisms in birds.

The origin of learning processes has been a traditional topic for comparative psychology. Thorndike (1911) assumed that learning principles were general to all species and differences between species were the result of quantitative rather than qualitative divergence, as Darwin suggested in his hypothesis of continuity of mental processes (Darwin, 1871). The question of whether learning depends on general mechanisms common to all species or on species-specific mechanisms has been approached from an evolutionary perspective. This implies that research in the area should use a comparative strategy with current species, since behavior does not leave a fossil record that would allow researchers to track its evolution (Bitterman, 1986). Thus, it is important to provide answers to questions about types of learning, the mechanisms that support such types of learning, and the origin of those mechanisms (Bitterman, 1975).

Following Thorndike, authors supporting a general-processes theory consider that differences among species in associative learning are more of degree than of type (Bitterman, 2000). According to this vision, it has been found that some basic learning processes, such as gradual and asymptotic acquisition and extinction with spontaneous recovery, as well as reversal discrimination among others, appear in different species of vertebrates. In addition, it has been observed that the same physiological properties of the neurons of cnidarians, animals that possess the simplest nervous system, also appear in the neurons of mammals and other animals (Papini, 2002a).

Despite the generality of the aforementioned processes, some phenomena related to behavioral adjustment to changes in the conditions of reward that are present only in some species. These phenomena are known as paradoxical effects of reinforcement because they contradict an assumption derived from the Law of Effect according to which a larger frequency and magnitude of reward would lead to stronger response and, therefore, a stronger persistence of performance during

extinction (Amsel, 1958, 1992). It has been observed that the paradoxical effects of reinforcement show a high degree of covariation in their occurrence across species, a fact allowing for the identification of evolutionary divergence in associative learning mechanisms across species (Papini, 2002b).

Some of the most commonly studied paradoxical effects are the magnitude of reinforcement extinction effect (MREE), successive negative contrast (SNC), and partial reinforcement extinction effect (PREE). In the MREE, a small magnitude of reward during acquisition is associated with a stronger persistence of response during extinction, in comparison with a large reward. In SNC, a sudden reduction of reinforcer magnitude generates an abrupt deterioration in performance compared to that of a group always trained with a small magnitude. In the PREE, intermittent reinforcement during acquisition leads to a stronger persistence of responding during extinction, in comparison with a continuously reinforced group (Domjan, 2003).

In studies with rats, the MREE, SNC, and PREE have been observed under different experimental conditions of training (Cándido, Maldonado, Mejías, & Catena, 1992; Flaherty, Greenwood, Martin, & Leszczuk, 1998; González & Bitterman, 1969; Pellegrini, & Mustaca, 2000). SNC has been observed in marsupials (Papini, Mustaca, & Bitterman, 1988). In humans, there is evidence of both SNCE (Kobre & Lipsitt, 1972) and PREE (Svartdal, 2000). In other taxonomic groups, including reptiles (Papini & Ishida, 1994), fish (González, Behrend, & Bitterman, 1965; González, Potts, Pitcoff, & Bitterman, 1972; Longo & Bitterman, 1960; Lowes & Bitterman, 1969; Schutz & Bitterman, 1969) and amphibians (Muzio, Segura, & Papini, 1992; Papini, Muzio, & Segura, 1995), performance is consistent with the basic assumptions of the Law of Effect.

When these phenomena are studied in pigeons, the results show an interesting dissociation: The PREE is observed, but the MREE and SNC are not recorded (Papini, 1997; Papini & Thomas, 1997; Papini, Thomas, & McVicar, 2002; Thomas & Papini, 2003). In general, each taxonomic group counts with more than one representative species in these studies. Nevertheless, most of the studies have been made with rats. Thus, it is important to study these phenomena in species other than mammals. Studies using birds have concentrated in pigeons, so studies with another avian model would help clarify the dissociated results found in pigeons and mentioned above. Given the apparent phenotypic similarity between birds and mammals attributable to evolutionary convergence or parallelism, it is plausible that similar behavioral effects in situations involving reinforcement downshifts could be generated by different underlying learning mechanisms (Papini, 2006).

If the focus on general-process theory is retaken, this does not only refer to the generality of learning principles in a comparative sense, but also to the application of these principles to different stimuli, responses, and reinforcements (Papini, 1998; Papini, Salas, & Muzio, 1999). However, as shown by the selective-association effect in aversive conditioning (Domjan, 1997; García & Koelling, 1966), animals in an experimental situation learn more easily certain relationships between stimuli and responses. Such discovery challenged the concept of equipotentiality, which had a wide influence in the study of learning until the

1970s (Domjan, 1997). Most of the research in this area centers on the study of paradoxical effects of reinforcement in ingestive behavior and, for that reason, they use solid food and sucrose solutions, both in varied quality and quantity. However, there is little research about paradoxical effects based on the use of sexual reinforcers or on any type of reinforcer other than food and water.

Domjan and Crawford (1998) argue that it is necessary to investigate the effects of reinforcement specifically in the sexual behavior system for two basic reasons. First, to determine empirically if the effects of sexual reinforcement are similar to the feeding reinforcers, thus avoiding generalizations based on extrapolations. Second, given that sexual reinforcement is part of a nonregulatory behavior system (not indispensable for the individual's survival) it could work in a different way from reinforcers that are part of a regulatory system, such as the consumption of water, food, or the maintenance of the temperature. In such cases, deprivation affects the metabolic process and compromises the individual's survival.

Based on the discoveries of comparative research on learning and on concerns about the reproductive behavior system (Domjan, 1994), this article presents the results of a first approach to the study of paradoxical effects of reinforcement in a sexual conditioning paradigm. The manipulated variable was the magnitude of sexual reinforcement, defined as copulatory access to different numbers of females, in male Japanese quail during a limited period of time and under widely spaced training trials (24 h). The effect of reward magnitude on performance was explored in a straight alley during the acquisition and extinction of sexual approach.

### **Experiment 1: Magnitude of Reinforcement Extinction Effect**

Magnitude of reinforcement can affect performance in instrumental tasks (Bonem & Crossman, 1988). Despite this, there seems to be no parametric studies establishing high and low magnitudes of sexual reinforcement. For this reason, Experiment 1 involves what a priori seemed extreme values: one female for the small magnitude and 8 females for the large magnitude. The effects of this manipulation were observed in both acquisition and extinction.

Experiment 1 aimed to establish the occurrence of the effect of magnitude of reward in extinction. Studies about paradoxical effects in birds have found that these phenomena happen when the probability of reinforcement is manipulated, but not when the variable is quantity or quality of reinforcement (Papini, 1997; Papini & Thomas, 1997; Papini et al., 2002; Thomas & Papini, 2003). These discoveries have not been generalized to other response systems; thus, there is no empirical evidence about how the MREE may work in the reproductive behavior system. Male Japanese quail were used as subjects for two reasons. First, pigeons are used as subjects in most studies with birds and the results are generalized to the whole taxonomic class, which may not be appropriate. Second, Japanese quail have proved suitable as a laboratory model to study sexual conditioning.

Running in a straight alley was reinforced with copulatory access to female Japanese quail. This task was chosen because it has been used in studies

about paradoxical effects, with both birds and other species. Also, because the locomotion responses make part of the appetitive component of focal and general search, related with the consummatory component of sexual behavior (grab, mount, and cloacal contact; Domjan, 1994).

## Method

### *Subjects*

Twenty-four sexually mature and experimentally naive male Japanese quail (*Coturnix japonica*) were selected from the colony at the Animal Learning and Behavior Lab of the Universidad Nacional de Colombia, after a 5-min copulation test. Only subjects who copulated during that period were selected for the experiment. They were housed in a metallic 6-level stand. Each level had 4 compartments, each 61 cm deep, 22 cm wide, and 35 cm high, and each with an independent door.

The birds had free access to water and food, and were exposed to a photoperiod of 16 h of light and 8 h of darkness (lights on at 06:00 h). All the subjects were deprived of sexual access to females, except during the experimental sessions according to the design.

### *Apparatus*

A wooden straight alley, divided in 3 compartments, a start box, a straight runway, and a goal box, was used. The alley was 300-cm long, 15-cm wide, and was surrounded by 15-cm high walls. Both the start box and the goal box were located on each side of the alley and they were separated from the runway by a vertical sliding door 10-cm wide and 15-cm high. The door was operated by a string and pulley system. In addition, there was another door located 15 cm before the end of the runway to retain the subject while the entrance door was opened, in order to avoid the females to escape from the goal box. The measures of the start box were 30-cm wide, 30-cm long, and 15-cm high. The goal box was 49-cm wide and 65-cm long. The alley was covered with a wire mesh, to prevent the experimental and the stimulus subjects to escape from the instrument.

Three infrared sensors were located at different points of the runway. The first sensor was located within the straight alley, at 15 cm from the start box. The second sensor was located 180 cm from the first one and the last pair was located 270 cm from the first sensors and 15 cm before the goal box. The infrared sensors were connected to a computer where a program (written in Visual Basic 6.0) registered the time that each animal took to run the different sections of the alley (in 0.01-s units).

### *Procedure*

Subjects were randomly assigned to two different groups. The first group received a large reinforcer (Group L), that is, copulatory access to 8 females. When the male entered the goal box, it found a female. After 1 min, a new female was introduced and the previous one was taken away. The same procedure was followed until 8 females were presented.

The second group received a reinforcer of small magnitude (Group S), that is, copulatory access to a single female. Each subject of this group was kept in the goal box until it copulated with the female. If it did not achieve cloacal contact within 180 s, it was taken to its housing cage.

Experiment 1 consisted of 3 phases: pretraining (1 trial), acquisition (10 trials), and extinction (45 trials). During pretraining, subjects were exposed to the apparatus in a single 5-min trial while the doors of the runway were lifted. The subjects were free to leave the start box and move about in the runway.

During the training phase, subjects received 1 trial per day. The structure of each trial was the following: A subject was placed in the start box; 30 s later the door was opened, and the subject had 60 s to start running. If the subject did not begin running the alley in the specified time or if after having initiated, it stopped for more than 60 s, it was gently pushed to the goal box, to provide exposure to the female and facilitate acquisition. When the subject reached the end of the alley, the

front door was closed behind the subject and, simultaneously, the lateral door was opened, allowing the subject to enter the goal box.

In the following phase, subjects were exposed to an extinction procedure. Each group of 12 subjects was divided at random in two groups of 6 subjects, in order to balance the amount of time subjects remained in the goal box. This time could differentially affect extinction performance and be confounded with the effect of training with two distinct reward magnitudes, so we decided to provide and compare different intervals of permanence in the goal box during extinction.

Table 1 shows the distribution of each group during the acquisition and extinction phases. Group L was divided in two subgroups. Group LT (Large-Total), remained in the goal box the average time all 24 subjects spent in the goal box with females during the last trial of acquisition (Mean = 253 s). Group LL (Large-Large) remained in the goal box the average time spent by subjects of Group L during the last trial of acquisition (Mean = 480 s).

**Table 1**  
*Duration and Distribution of the Groups in each of the Experimental Phases*

Phase and Duration (sessions)	Groups			
<b>Acquisition (10)</b>	Large: 8 females n: 12 males		Small: 1 female n: 12 males	
<b>Extinction (45)</b>	Large-Large (LL): Average time of group L in goal box during acquisition n: 6 males	Large-Total (LT): Average time of all subjects in goal box during acquisition n: 6 males	Small-Small (SS): Average time of group S in goal box during acquisition n: 6 males	Small-Total (ST): Average time of all subjects in goal box during acquisition n: 6 males

Likewise, Group S was divided in 2 subgroups. Group ST (Small-Total) remained in the goal box the average time spent by all subjects during the last trial of acquisition (Mean = 253 s). Group SS (Small-Small), remained in the goal box the average time spent time by subjects of group S during the last trial of acquisition (Mean = 26 s).

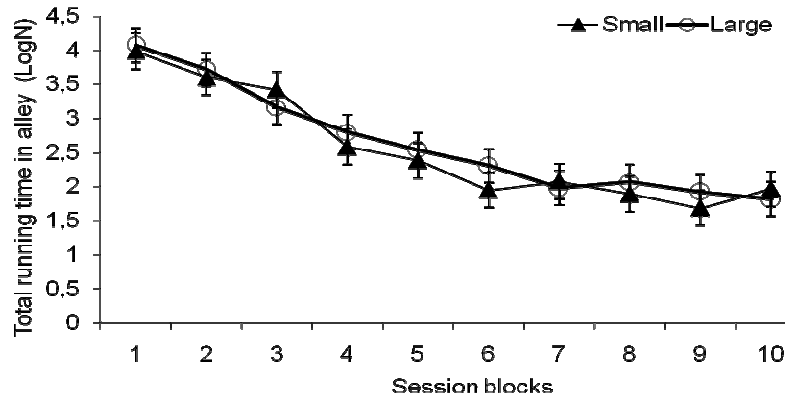
Ten females in reproductive condition were used as reinforcers. They were maintained under the same feeding and illumination conditions as males, but they were group-housed in a cage. All females used as reinforcing stimuli during the acquisition phase were rotated at random to minimize exposure to the same female in subsequent trials.

## Results

To improve the normality and allow the use of parametric statistics, the arrival latencies to the goal box were transformed to their natural logarithm. Transformed data were grouped in blocks of 5 trials and a repeated-measure analysis of variance was applied. The data of the first and second partial measures are not presented because they did not show significant differences.

The results of the acquisition phase are illustrated in Figure 1. The statistical tests reveal that there is an effect of blocks of trials,  $F(3, 10) = 351.43$ ,  $p < 0.05$ , but not of group,  $F = 0.44$  (3, 10),  $p > 0.05$ , or interaction of Blocks X Group,  $F = 0.09$  (3, 10),  $p > 0.05$ . This demonstrates that subjects trained with a small reward did not differ in their rate of acquisition from those trained with a large reward. In comparison with other vertebrate species, male quail show a

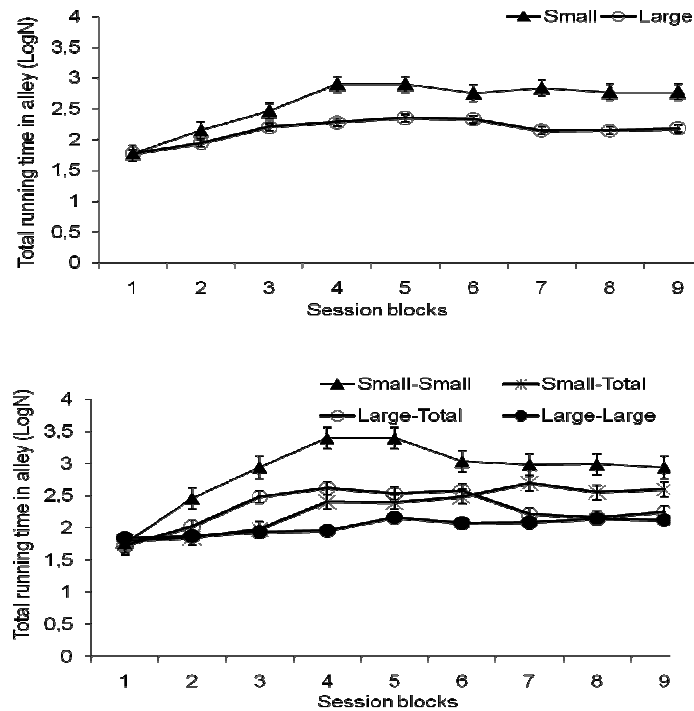
quicker response acquisition to run the straight alley for reinforcement. It has been reported that the duration of acquisition ranges between 40 and 50 daily trials for fish (Lowes & Bitterman, 1967; Schutz & Bitterman, 1969) and 24 daily trials for pigeons (Thomas & Papini, 2003), using food as reinforcement. In this experiment, asymptotic responding was reached on trial 7 and remained stable until trial 10.



**Figure 1.** Total running time (and SE) in the runway during acquisition. Data were transformed to natural logarithm.

When data from Groups ST and SS were combined and compared with combined data from Groups LL and LT during extinction, a significant effect of blocks of trials was observed,  $F = 7.54 (8), p < 0.05$ . A significant Blocks X Group interaction effect in extinction was also observed,  $F = 1.30 (8), p < 0.05$ ; however no group effect was identified,  $F = 3.25 (8), p > 0.05$ . The large reward magnitude groups showed stronger persistence in their running time at the alley, in comparison with the performance of the small reward magnitude groups. This is confirmed with test of contrasts in Block 7 where there is a significant difference among the groups. These results are shown in the top panel of Figure 2.

When the performance of all groups during extinction was compared, there was an effect of blocks,  $F = 13.29 (11), p < 0.05$ , and of blocks X group interaction,  $F = 1.75 (33), p < 0.05$ , but not of group,  $F = 2.06 (3), p > 0.05$ . Post hoc tests (LSD) reveal significant differences between Group SS and Group ST in blocks 2 to 4, and between Group SS and Group LL in blocks 2 to 5. No significant differences were found between SS and LT groups, LT and ST groups or LT and LL groups during extinction. This indicates a reversed MREE; that is, a performance according to the law of effect. As shown in the bottom panel of Figure 2, Group SS showed a faster extinction than the other groups; Group ST also showed an increase in arrival latencies but this process is slower. On the other hand, Group LT showed a slight increase in latencies during the initial sessions, which would indicate the beginning of extinction; later, however, its performance overlapped with group LL; this last group did not show a decrease in the running response to the goal box.



**Figure 2. Top:** Total running time (and SE) in the runway during extinction grouping data according to acquisition groups. **Bottom:** Total running time (and SE) in the runway during extinction. SS: Small reward during acquisition/Small reward (time) during extinction; ST: Small reward during acquisition/Mean time of extinction; LT: Large reward during acquisition/ Mean time of extinction; and LL: Large Reward in acquisition/Large Time in extinction. Data were transformed to natural logarithm. Each session block includes five individual sessions.

### Discussion

The obtained results show that the manipulation of magnitude of sexual reinforcement did not affect the running response of quail during acquisition. This discovery is interesting because studies with other species, including pigeons, have shown that a larger reward magnitude yields a quicker acquisition in comparison with a smaller reward magnitude. Although the reported studies with pigeons use food as reinforcement, the magnitude effect persists when reinforcers associated with other behavior systems are used (e.g., defense behavior). In this vein, Cándido, Catena, and Maldonado (1984) varied the duration of safety signals in an avoidance learning experiment with rats and found that acquisition rate was directly related to the quantity of reward (safety time).

During the extinction phase, a reversed MREE was observed, that is, resistance to extinction was directly related to reinforcer magnitude during acquisition. The small magnitude groups exhibited considerable extinction, whereas the large magnitude groups continue persisting in their responses during extinction trials. These results are attributable to training with different magnitudes of reward. The persistence observed in the large magnitude groups demonstrates a strong biological predisposition of animals of this species to approach contextual cues that signal copulatory access to a female even after considerable exposure to extinction (Domjan, Lyons, North, & Bruell, 1986; Krause, Cusato, & Domjan, 2003).

When we separate the possible effects of confinement time in the goal box during extinction, no differences were observed in extinction between groups with the same retention time in the goal box (ST vs LT). Despite a graphic suggestion of an actual MREE effect in the first 4 blocks of extinction of groups ST and LT, followed by a reversed MREE, these suggestions are not supported statistically.

Significant differences were observed in extinction between two groups with the same retention time in the goal box during the acquisition phase, (SS vs. ST). Group ST was confined in the goal box longer than Group SS. It is possible that goal box cues served as conditioned reinforcers, maintaining the performance of subjects in Group ST during extinction for a longer period (blocks 2 to 4; see Williams, 1994).

Everitt, Fray, Kostarczyk, Taylor, and Stacey (1987) suggest that the performance shown by rats during instrumental extinction is affected by the level of sexual deprivation during the experiment. Such effect cannot be determined in the present experiment, because all groups were exposed to the same deprivation conditions. However, it would be interesting to observe performance when extinction is prolonged using sexual reinforcers. Lastly, although it may be argued that access to 8 females in the large group produced satiation in male quail, a dissociation between appetitive and consummatory sexual responses has been observed. Hilliard et al. (1998) exposed male quail to successive presentations of conditioned stimuli followed by female conspecifics and found that although the subjects decreased their copulation responses over time, they continued exhibiting approach responses to the conditioned stimuli and females. They argued that appetitive and consummatory sexual responses might be differentially affected by motivational changes.

## **Experiment 2: Preference for Reinforcers of Different Magnitude**

In Experiment 1, the subject's extinction performance reflected a reversed MREE. Large and small groups differed significantly in some extinction sessions, but did not differ graphically or statistically in acquisition. The acquisition results did not provide evidence that the subjects discriminated large and small reinforcers used in this study. To evaluate this possibility, an experiment comparing the response of males to two different magnitudes of reward was designed. The discovery of a significant preference for one of two reward magnitudes would imply that the subjects discriminate between the alternatives. Therefore, the results

reported in Experiment 1 would not reflect a lack of discrimination of actual reward magnitudes.

## Method

### *Subjects*

Four sexually mature, experimentally naive male Japanese quail (*Coturnix japonica*), from the colony at Universidad Nacional de Colombia were used. The subjects were maintained under the same conditions of the previous experiment.

### *Apparatus*

A straight alley similar to that used in Experiment 1 was used. The two boxes at each end of the alley had the same dimensions (30-cm wide, 30-cm deep, and 15-cm high). In addition, two guillotine doors at the center of the runway and separated by 15 cm from each other controlled access to the two boxes. These doors formed a central compartment that served as the start box. After leaving the start box, the subjects had to walk a distance of 127.5 cm to reach anyone of the choice boxes.

### *Procedure*

The experiment consisted of 3 phases. In the habituation phase, subjects were placed in the start box, with all the doors of the runway lifted and they were allowed to move about freely during 5 min. In this phase, no reinforcement was provided. In the forced-election phase, each subject was placed in the start compartment for 30 s; then, one of the doors was opened and the subject was gently guided to one of the goal boxes in a series of 8 trials, 4 toward each box. When the subject crossed the goal line, in one of the ends of the runway, the goal box door was raised. Reinforcement consisted of copulatory access to one female during 1 min or to 8 females, presented one per minute, as done in Experiment 1.

Males received 1 female in one of the goal boxes and 8 females in the other goal box. The assignment of the reward magnitude was counterbalanced with respect to the goal boxes to minimize possible spatial biases. The order of forced election trials was also counterbalanced.

In the election phase, the subjects were placed in central start compartment during 30 s. Then both doors of this compartment as well as the doors of the goal boxes were elevated simultaneously. The assignment of the reinforcement was the same as in the previous phase. Twenty-five election trials were administered at a rate of 4 trials per day, 90-min apart. The frequency of election of each reinforcement magnitude and goal box were registered.

## Results

Subjects consistently chose 8 females over 1, in a proportion of 0.71 to 0.29. These differences are statistically supported by the results of a test of proportions differences,  $z = -5.94$ ,  $p < 0.05$ . Subjects preferred the side of the alley that was always associated with the larger reward. An analysis of side preferences for the group as a whole showed that subjects were not spatially biased toward a specific goal box. The proportion of choices for each of the two goal boxes was 0.47 and 0.53,  $z = 2.456$ ,  $p > 0.05$ . This means that the between-subject elections did not result from the subjects' preference for a specific place of the experimental apparatus, but from the value of reinforcement.

## Discussion

The results obtained in Experiment 2 demonstrated that male quail discriminate between the two reinforcement values used in Experiment 1; sexual access to 8 females was preferred over access to a single female. Therefore, the overlapping of acquisition curves of two experimental groups and the reversed MREE in male quail's performance observed in Experiment 1 cannot be attributed to a failure to discriminate the reward magnitude.

There are different dimensions of magnitude of reinforcement such as quantity, density, or time of access to reinforcers; the manipulation of each one of these parameters could produce results different from those reported here. In addition, time exposure to the reinforcer may interact with other parameters of reinforcement to produce different results. This requires a redefinition of the concept of reward magnitude that specifies multiple effects produced by each parameter not only mentioned in the field of paradoxical reinforcement effects but in other areas such as incentive contrast (Pellegrini, Ruetti, Mustaca, & Muzio, 2004). In the case of this experiment, although males consistently chose 8 females over 1, it is not possible to isolate the effect of reinforcer magnitude from the effect of exposure time to the goal box. For example, a single female, available during 8 min, may have the same value as eight females available at a rate of one per minute.

## General Discussion

The results of Experiment 1 demonstrated a reversed MREE in the runway in sexually reinforced quail. The acquisition curves for groups L and S overlapped and did not show any effect of reward magnitude on the speed of acquisition. This was surprising because in previous studies an inferior performance level has generally been observed in the small reward group compared to the large reward group, which shows a faster response acquisition. It was not possible to determine whether this overlap was the result of differences of sexual reinforcement with regard to other types of reinforcement, or the result of a difficulty to discriminate between the two reward magnitudes. Experiment 2 provided clear evidence for the discrimination of magnitude designed to discriminate between these possibilities in terms of performance.

Taking into account the results of both experiments, acquisition in Experiment 1 may be explained in two ways. First, the observed pattern of responses may reflect some property of the straight runway. It is possible that the length of the alley was too short and it did not allow the observation of differences in acquisition rate. In several studies on incentive contrast, very long (610 cm) or inclined straight alleys were used to avoid ceiling or floor effects (Flaherty, 1996).

Second, although quail discriminated between two reinforcement magnitudes, the motivation level generated by copulatory access to a single female may have been too high and subjects may have not exhibited differential performance toward the preferred reinforcement magnitude. In fact, the high level of sexual motivation was one reason for the use of this species as a laboratory

model for sexual conditioning. It may be argued that the manipulation of other reinforcement parameters (e.g., a longer time of exposure to a single female) would produce results different from those reported here.

As several studies with sexual reinforcement suggest, some properties displayed by these reinforcers are different from those of other appetitive reinforcers. For example, Domjan (1997) pointed out that contrary to what happens with other behavior systems in which only appetitive components are modifiable by learning, in the sexual behavior system both, appetitive components and consummatory components, are susceptible to modification by conditioning procedures.

At a methodological level, opposing patterns of acquisition could result from procedures used to provide reinforcement. For example, noise generated by the manual introduction of mates may have affected the reinforcing effect from exposure to female quail. Domjan and Crawford (1998) pointed out an inherent difficulty with the delivery of sexual reinforcers, especially in nonrestricted procedures. In this sense, the development of automation of such procedures offers a challenge for researchers of sexual behavior. Nevertheless, the fact that the choice test showed a significant tendency toward a large reinforcement demonstrates that this procedural manipulation preserves the reinforcement value.

During extinction, there is an effect of magnitude of sexual reinforcement on the instrumental response. Subjects showed a nonparadoxical performance, in agreement with Thorndike's Law of Effect. These discoveries resemble results with pigeons using different magnitudes of food reinforcement. Accordingly, it could be argued that the reproductive behavior system has a similar functioning to the foraging system. Papini (1998, 2002b) pointed out a tendency to conservation in learning mechanisms, at least in vertebrates. Such a conservation or generality is related to the fact that ecological niches and problems faced by organisms that inhabit them share a variety of common dimensions. Learning mechanisms evolved so that individuals faced basic survival challenges, such as searching for and obtaining energy and nutrition sources. Behavior then would have been organized in fundamental modules of information storage and used to solve basic individual tasks. When a new basic task arises, since there is a preexistent modular organization, this tends to be coupled to previous organization and, in this way, similar mechanisms of information gathering and use will evolve. Such cooption of learning mechanisms could explain similarities among foraging and sexual behavior systems across different species and lead to predict a dissociation between MREE and PREE with sexual reinforcement analogous to that found with food reinforcement (Thomas & Papini, 2003).

It is necessary to design similar studies with two objectives. First, applying the principle of systematic variation (Bitterman, 1975), establish the role of contextual factors (variables other than reward magnitude) on performance during the acquisition and extinction of sexual behavior. Second, to determine if the dissociation between paradoxical effects is also observed in the sexual behavior system. Once the basic parameters of sexual reinforcement manipulation and the functional regularities have been established for a group of closely related species, it would be possible to design studies aimed at uncovering underlying mechanisms

at levels of analysis (Papini, 2006). In addition, generalizing research to other reinforcers in the same species would help determine the similarities and properties of different behavior systems and of their possible evolutionary history.

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