Observational learning of imprinting behavior in Japanese quail (*Coturnix coturnix japonica*)

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We investigated observational learning of imprinting behavior in Japanese quail. Restrained quail chicks observed a moving light or another chick following the moving light. Both kinds of experience led to following behavior in tests. Observer chicks followed better if they saw an imprinter chick following. However, imprinter chicks followed better in tests if no observer was present during training. Social contextual differences between training and testing viewed as interfering with a retrieval process could not account for the performance difference. Observational learning may compensate for individual differences in imprintability to promote clutch unity at exodus from the nest.

The conditions that prevail in nature in the nest of precocial birds after hatching may allow siblings to observe and imitate various attachment behaviors (Klopfer, 1959). Social experiences with conspecifics after imprinting training consolidate visual preferences for the familiar imprinting object (Lickliter & Gottlieb, 1987).

We were interested in using a traditional laboratory paradigm in imprinting to investigate whether Japanese quail observing imprinting behavior but not themselves following would show evidence in later tests of having learned following behavior or would become imprinted. It has been shown that Japanese quail are capable of observational learning at 40 days posthatch (Sanavio & Savardi, 1980). We were concerned with the following issues. (1) Is the motor experience of following necessary for imprinting to occur? (2) Are there innate preferences for stimuli that may be synergistic with or antagonistic to observational learning? (3) Is it necessary for the imprinting stimulus to move away from the subject during initial exposure to elicit later following behavior during testing?

We were also interested in comparing several dependent variables typically used to measure imprinting. We focused on the efficiency, convenience, and sensitivity of these various measures.

METHOD

Subjects

Japanese quail eggs (*Coturnix coturnix japonica*) were obtained from a commercial hatchery on either Day 1 or Day 14 of incubation. Eggs were placed in a forced-air incubator, and on Day 15 of the 17-day incubation period, they were put into individual cardboard cubes in which they hatched. The subjects were housed individually in aluminum cages 24 × 20.5 × 18.5 cm. The floor and front wall of each cage were made of .25- and .5-in. mesh hardware cloth, respectively. Masking tape covered the front screen and thus eliminated visual cues, but it was trans-

lucent enough to permit light to enter the cage. Food and water were not provided until experimentation was complete.

Apparatus

The imprinting apparatus consisted of an octagonal arena 91 cm in diameter with a plywood floor and foam-core board outer walls. Centered inside was a circular barrier of .5-in. mesh hardware cloth 9 cm high. The inner barrier created a runway 18 cm wide. This prevented the imprinter from approaching the observer but did not prevent visual contact. Centered inside the inner barrier was an observer booth of Plexiglas (7.6 × 7.6 × 6.4 cm). This confined the observer chick to the center of the arena, yet permitted visual access to the imprinting stimulus and/or the imprinting chick. The entire apparatus was painted flat gray. Pencil lines demarcated eight equal sectors in the runway, each of which was 25.4 cm long. Three 250-W infrared bulbs suspended above the apparatus maintained a temperature of 32° C on the arena floor. Illumination was provided by the room's fluorescent lights.

Imprinting stimuli were 6-V automobile bulbs painted white and green and mounted in the standard sockets. Stimuli hung 2.5 cm from the arena floor and were connected via the electrical wires to a rotating wooden arm suspended 38 cm from the floor. The arm, in turn, was attached to a 12-V motor, which was centered on an inverted U-shaped two by four structure that stood on the floor of the room. The stimulus moved at a rate of 7 cm/sec on an automated 15:15-sec motion:pause sequence.

Procedure

Eighty quail chicks were randomly assigned to four imprinting conditions and a no-exposure group. The experimental group consisted of an imprinter (I) chick who followed the imprinting stimulus and an observer (O) who was restrained in the Plexiglas booth but who could freely observe the imprinter. Three control groups were utilized to control for the effect of the observer on imprinter, imprinter on observer, and novelty effect of placement in the arena, respectively: the imprinter without observer (IWO) group, in which there was no observer in the booth; the observer without imprinter (OWI) group, which was composed of birds that saw only the moving light stimulus from the observer booth but no imprinter; and the no-exposure (NE) group, which was composed of birds that were restrained in the observer booth but that saw no moving stimuli or other chicks.

For all groups, training occurred 12–16 h posthatch. Training sessions lasted for 20 min. Testing occurred 24 h posthatch and consisted of a following test and a choice-discrimination test. The birds were trained on either the white or the green light. It should be noted that the subjects in the experimental (IO) group were trained together but tested separately.

Following behavior during testing was assessed during a 10-min exposure to the imprinting stimulus and a 10-min exposure to the nonim-

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printing stimulus presented in a counterbalanced order in the runway. The three dependent measures were (1) the number of seconds spent following within 1 ft of the light; (2) the number of sector lines crossed while following occurred; and (3) the gross number of sector lines crossed whether following occurred or not. The latter two measures were assumed to reflect specific and general activity, respectively.

The choice test consisted of a simultaneous presentation in the arena of two stationary lights—an imprinting and a nonimprinting color—for 2 min. The stimuli were approximately 40 cm from the subject, and a choice was defined as the subject's approach to within 12 cm of one of the lights and remaining there for at least 10 sec. The testing sequence of whether the choice or following test was administered first was counterbalanced across subjects.

RESULTS

An analysis of variance was performed on all three dependent measures that were applicable during either the training or the testing sessions. Obviously, only two groups could show scores during training, IO or IWO. During testing sessions, both imprinters and observers with and without another chick provided analyzable data on all three measures. Responses to the white and green stimulus lights during training as well as during testing were analyzed separately.

Training

The mean training scores for the two imprinter groups with and without an observer are shown in Table 1. There were no significant group differences in following time and specific activity, but there was a group effect in general activity. The IWO group scored higher than the IO group [$F(1,16) = 5.01, p < .05$].

Testing

The choice test involving stationary lights showed no significant main effects or interactions. In the following test, each subject was given a 10-min exposure to the imprinting stimulus and the 10-min exposure to the nonimprinting stimulus. The green-trained subjects followed the white, nonimprinting stimulus but showed no group differences ($F < 1.0$). It should be noted that all chicks showed a strong preference for the white light over the green, regardless of training. The following scores with imprinting stimuli are shown in Tables 2 and 3. The green-trained subjects showed a main effect due to differences from the NE group [$F(4,8) = 9.59, p < .01$], but no

Table 2
Mean Group Testing Scores With Imprinting Stimuli for White-Trained Subjects

Group	Dependent Measure		
	Following Time (Seconds)	Specific Activity	General Activity
Imprinter with observer	360	39	52
Imprinter without observer	417	49	81
Observer with imprinter	229	22	45
Observer without imprinter	150	15	53
No exposure	58	12	1

Note— $N = 8$ for each group.

Table 3
Mean Group Testing Scores With Imprinting Stimuli for Green-Trained Subjects

Group	Dependent Measure		
	Following Time (Seconds)	Specific Activity	General Activity
Imprinter with observer	167	17	52
Imprinter without observer	178	27	91
Observer with imprinter	171	19	76
Observer without imprinter	180	24	95
No exposure	35	16	1

Note— $N = 8$ for each group.

other group differences (Table 3). For white-trained subjects, a significant group main effect was found for following behavior [$F(4,8) = 8.13, p < .01$], number of sector lines crossed (specific activity) [$F(4,8) = 4.04, p < .05$], and overall number of sector lines crossed whether following occurred or not (general activity) [$F(4,8) = 6.54, p < .05$]. Tukey post hoc tests showed that the main effect for general activity was due to the lower scores of the NE group. If the total number of crossings is used as an index of general arousal, these findings offer only very weak support for a general arousal theory of imprinting. On the other hand, post hoc tests on following time and specific activity led to the following ordering of groups: IWO > IO > OI > OWI > NE. These results suggest that observation of a conspecific performing an imprinting response significantly enhances imprinting behavior in Japanese quail.

In addition to the main group effects, a significant stimulus presentation order effect was found on two of the dependent measures. For both following [$F(1,40) = 8.29, p < .01$] and specific activity [$F(1,40) = 5.72, p < .05$], scores were always lower for the white stimulus when it was presented first. This suggests the possibility of a warm-up effect.

DISCUSSION

Among the dependent variables we chose, following time and number of sector lines crossed during following (specific activity) were the most sensitive. General activity scores showed no correlation with imprinting effectiveness, nor with any of the other dependent measures. Also, choice tests did not prove to be significant across any of the experimental groups.

Tolman (1963) suggested that arousal levels revealed in general activity scores of neonatal precocial birds may underlie the onset of the critical period. Therefore, general activity should correlate positively

Table 1
Mean Group Training Scores for Two Imprinting Stimulus Colors

Group	Dependent Measure		
	Following Time (Seconds)	Specific Activity	General Activity
Imprinter With Observer			
White	489	46	90
Green	307	26	79
Imprinter Without Observer			
White	511	53	121*
Green	279	28	120*

Note— $N = 16$ in all groups; 8 subjects were trained with white and 8 were trained with green stimuli. * $p < .05$.

with imprinting performance during training and with imprinting strength during testing. The present results do not support this suggestion.

The lack of significance of the choice test may be ascribed to two possible factors. One is that the experimental context of the choice test was different from that of the training situation. The other is that the stimuli in the test lacked an essential characteristic of the training stimulus—movement. The latter suggestion is supported by the fact that tests involving moving stimuli did in fact demonstrate that the subjects were able to discriminate the stimuli, as is shown by the difference in following performance with white versus green light.

The absence of group differences in green-trained subjects and their greater following of a white stimulus may be due to the inability of training to overcome an innate preference. However, the training experience may have been enough to exert a priming effect so that some following would occur in all but the NE group. Klopfer (1964) reported that once the following response is primed in the training situation, innate or perceptual preferences may cause a subject to choose a novel stimulus over an imprinting stimulus. Green (1982) has also made reference to other reports of this type of response and has advanced a spatial memory process in which the chick continuously updates the memory of the location of its mother. This would then form the focal point of approach behavior of the chick if threatened by danger. His view is that the spatial location with respect to the chick, rather than the stimulus properties of imprinting objects, is updated in memory.

The hypothesis that observational learning may play an important role in the imprinting process was supported by the present results. The observer chicks exposed to the imprinting stimulus in the presence of an imprinter scored higher than observers exposed to the stimulus with no imprinter present. This could be viewed as an observational learning process, since practice effects or proximity to the stimulus were not permitted for the observers during training. On the other hand, imprinters trained alone scored higher during testing than imprinters trained with an observer, and this may indicate that social inhibition is operating during active imprinting training. The imprinter may be distracted by the observer and not attend to the stimulus as well as imprinters without an observer. It should be noted that in preliminary training, we found it necessary to provide a mesh barrier to keep imprinter chicks from approaching the observer booth. A comparison of groups during training showed greater following without an observer, but the difference was not statistically significant.

The social contextual difference between training and testing for IO groups as an explanation for their lower performance than that of IWO groups can be evaluated through consideration of the observer groups. The OI group scored higher than the OWI groups, suggesting that observational learning of a moving stimulus in a social context can augment attachment responses. This is in spite of the fact that the change in context between training and testing occurred in the OI group and not the OWI group. Thus, even if a negative influence of a change in social context from training to testing exists, it was ineffective in reducing the positive influence of the imprinter on the observer during observational training. It seems more likely that imprinters are distracted by observers while observers are learning something by watching the im-

printers. The behavior of chicks inside the booth suggested that they were orienting to stimuli outside the booth and were in fact observing even though they were not allowed to imitate following. The social context remained the same in both the OWI group and the NE group. The former group scored higher, thus showing that some degree of imprinting can occur merely through observation of the stimulus without the motor practice of following or of watching a conspecific following. The performance level was inferior to that of the chicks that could observe following, however. These results concur with those of Sherry and Galef (1990), who showed that observational learning can occur in a social context without imitation or practice effects in black-capped chickadees. The hypothesis of Hess (1959) that overt motor responses are required for imprinting stimuli to be effective is not supported.

It has been noted that considerable variation in imprintability exists in precocial birds, which suggests some degree of behavioral polymorphism (Klopfer, 1978; Klopfer & Gottlieb, 1962; Kovach, 1978). Any interaction among conspecifics in the nest that leads to the initiation and maintenance of the following response would then ensure that all members of the clutch would respond properly at the time of exodus and in subsequent social situations during early stages of neonatal life.

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