*AUTOSHAPING THE PIGEON'S GAPE RESPONSE:
ACQUISITION AND TOPOGRAPHY AS A FUNCTION OF
REINFORCER TYPE AND MAGNITUDE*

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The pigeon's key-pecking response is experimentally dissociable into transport (head movement) and gape (jaw movement) components. During conditioning of the key-pecking response, both components come under the control of the conditioned stimulus. To study the acquisition of gape conditioned responses and to clarify the contribution of unconditioned stimulus (reinforcer) variables to the form of the response, gape and key-contact responses were recorded during an autoshaping procedure and reinforcer properties were systematically varied. One group of 8 pigeons was food deprived and subgroups of 2 birds each were exposed to four different pellet sizes as reinforcers, each reinforcer signaled by a keylight conditioned stimulus. A second group was water deprived and received water reinforcers paired with the conditioned stimulus. Water- or food-deprived control groups received appropriate water or food reinforcers that were randomly delivered with respect to the keylight stimulus. Acquisition of the conditioned gape response frequently preceded key-contact responses, and gape conditioned responses were generally elicited at higher rates than were key contacts. The form of the conditioned gape was similar to, but not identical with, the form of the unconditioned gape. The gape component is a critical topographical feature of the conditioned key peck, a sensitive measure of conditioning during autoshaping, and an important source of the observed similarities in the form of conditioned and consummatory responses.

Key words: autoshaping, respondent conditioning, response topography, response form, interresponse time, key peck, pigeons

Even in the absence of a response contingency and with little seeming utility, if a localizable stimulus (e.g., a keylight) signals food availability, pigeons will come to peck that stimulus (Hearst & Jenkins, 1974). This behavior is said to be "autoshaped," because explicit differential reinforcement contingencies are not necessary to the provenance of this behavior (Brown & Jenkins, 1968), although the possibility remains that adventitious contingencies may operate to sustain the response once it has been produced and is followed shortly thereafter by food. There are, to be sure, significant temporal conditions required to engender and maintain these pecking responses (Gibbon & Balsam, 1981), and researchers interested in this behavior have utilized, for the most part, as a dependent measure that part of the response which results in a closing of a microswitch. Indeed, the auto-

shaped key peck is typically operationally defined as a key closure.

Although this pecking response is usually treated as a unitary behavior, studies of pecking response form have shown that autoshaped (Jenkins & Moore, 1973) and operantly conditioned pecks (Wolin, 1968), as well as consummatory pecks at both food and water reinforcers (Zeigler, Levitt, & Levine, 1980), are decomposable into transport and gape components. The transport component may be defined as that part of the peck which moves the beak to the response key and which ultimately results in a switch closure; the gape component may be defined as beak opening and closing (Klein, Lamon & Zeigler, 1983; LaMon & Zeigler, 1984; Zeigler et al., 1980). The gape and transport components of pecking, although functionally related, may be affected differently by stimulus contingencies (respondent conditioning) and response contingencies (operant conditioning). For example, both force and duration of the transport component differ as a function of whether the pigeon pecks at a response key or at the reinforcer (LaMon & Zeigler, 1988).

Evidence also suggests, however, that the topographies of the gape to a response key and to the reinforcer are quite similar (Jenkins &

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Moore, 1973; LaMon & Zeigler, 1988; Wolin, 1968). When food deprived, pigeons' gapes at a response key as well as gape responses at food are both episodic, with the largest beak-opening values (peak gapes) varying with the size of the reinforcer. When pigeons are water deprived, gapes at a response key, like the gapes observed during drinking, are characterized by rhythmic jaw movements with small, relatively invariant peak gapes. It seems that among all of the components of pecking (e.g., force, duration, gape), the gape component unambiguously identifies responses supported by either food or water reinforcement conditions (LaMon & Zeigler, 1984). Such observations suggest that reinforcer properties are major determinants of the form of gapes directed at response keys. Indeed, the similarity of the gapes produced during key pecking and those produced during the ingestion of the reinforcer suggests that gape is a conditionable property of pecking behavior.

Direct evidence for this hypothesis is lacking. Because both autoshaped (respondent) and operant pecks are typically recorded as key contacts, which primarily reflect head movement, the study of pecking response form has focused largely on the transport component (e.g., differences in rate of responding observed by Spetch, Wilkie, & Skelton, 1981). Recent studies indicate that the gape component may also be brought under control using either operant or respondent conditioning procedures. Both the rate of jaw movement (Mallin & Delius, 1983; Remy & Emmerton, 1989) and its peak amplitude (Deich, Allan, & Zeigler, 1988) have been instrumentally conditioned using operant (response differentiation) procedures.

Evidence for respondent conditioning of gape also comes from the observed similarities in the topography of conditioned and unconditioned responses (Jenkins & Moore, 1973). Although Jenkins and Moore did not measure the gape responses of their birds, the photographic evidence is compelling—there appeared to be a difference between the gapes produced during key pecking when subjects were either food or water deprived (see Figure 2 from Jenkins & Moore, 1973). Further, although other studies have measured the gape responses of pigeons at the instant of key contact (LaMon & Zeigler, 1984, 1988), this work did not examine acquisition of the gape re-

sponse, and also lacked appropriate control conditions that would permit a clear separation of the effects of (a) deprivation state alone and (b) the stimulus-reinforcer contingency in the production of gape responses. It may be the case, for example, that only food or water deprivation is necessary to produce the characteristic large and small gape responses seen in birds deprived, respectively, of food and water. The case for the conditionability of the gape response would be enhanced if these gape responses to a response key were seen only when a stimulus-reinforcer contingency was arranged.

The aim of the present study was to compare the frequency, pattern, and topography of gape responses to a conditional stimulus (CS) in truly-random control and experimental subjects, and to clarify the contribution of unconditional stimulus (US) variables to the form of the conditioned gape response. In addition, because the transport and gape components may occur separately, the present study was designed to assess how frequently gape responses occurred in the absence of key contacts. If the birds gape with a relatively high frequency only during the CS, then perhaps gapes during the CS can serve as a sensitive measure of autoshaping. During the study, the US was varied along both qualitative and quantitative dimensions (food vs. water; pellet size). Both key contacts and gapes were recorded, but the focus of the present report is on the gape response, which appears to be a critical component of key-pecking topography.

Previous studies of gape responses during conditioning have used high-speed single-frame photography (LaMon & Zeigler, 1984, 1988). The technology employed in this study (Deich, Houben, Allan, & Zeigler, 1985) permitted continuous recording of the jaw movements during the acquisition and maintenance phases of conditioning. It was thus possible to compare the amplitudes and temporal distributions of gapes during CS and US intervals.

METHOD

Subjects

A total of 16 experimentally naive White Carneau pigeons served as subjects. They were individually housed under a 12:12 hr light/dark cycle, and food-deprived subjects were

maintained at between 75% and 85% of their free-feeding weights by restriction of daily food intake. For the food-deprived birds, water and grit were freely available in their home cages and all food was received in the test chamber. Water was removed from water-deprived subjects 2 days prior to the first hopper-training session; these subjects received all their water in the test chamber, with free access to food and grit in their home cages.

Subjects were assigned to random control food ($n = 2$) and random control water ($n = 2$) groups or to experimental food-US ($n = 8$; 2 subjects at each pellet size) or experimental water-US ($n = 4$) groups. Subjects in the random control food group were food deprived, and the US was a 4.9-mm diameter food pellet. The 8 food-US subjects were subdivided into four pellet-size subgroups (3.2-, 4.9-, 6.4-, and 8.7-mm diameter pellets) with 2 birds in each. During all experimental phases, these subjects received only the pellet size appropriate to their group.

Apparatus

Testing was carried out in an operant conditioning chamber (31.5 cm long, 34 cm wide, 35.5 cm high) with walls, ceiling, and floor made of clear acrylic. Modification of the ceiling allowed the insertion of a mercury commutator (Scientific Prototype). The front wall, which was painted gray, functioned as an intelligence panel. This panel was equipped with a set of three response keys (2.54 cm) positioned 23.5 cm above the chamber floor. Only the center key was used, and when activated, was transilluminated with red light. Pecks exceeding 0.17 N of force were counted as key contacts. To decrease the likelihood of damage to the beak-mounted transducers (see below), the key was modified with a 6-mm acrylic insert that raised its surface level with the chamber wall. A food aperture (9 cm wide, 10 cm high, and 5.5 cm above the chamber floor) allowed access to a custom-built feeder constructed to reduce the likelihood of damage to the beak-mounted transducers (see below). During reinforcement, a hopper light was turned on and a solenoid raised a watch glass (5 cm diameter) into a horizontal position flush with an aperture (4.8 cm diameter) cut into an acrylic block (18 mm thick). A Gerbrands feeder delivered pellets to the watch glass through a tube (12.7 mm) inserted into the

Fig. 1. (A) Diagram of the Hall-effect assembly illustrating the electrode wires, the Hall-effect integrated circuit on the upper beak, and a neodymium magnet on the lower beak. (B) A sample gape record over time, taken with the Hall-effect device during a bout of key pecking.

side of the block. Water was delivered through a tube (5 mm) inserted into the side of the block opposite the food-delivery aperture. Release of the solenoid lowered the watch glass into a receptacle to dispose of any remaining pellets or water. The test chamber was located within an acoustically shielded outer chamber illuminated by a 25-W houselight.

On-line monitoring of gape. Gape (i.e., interbeak distance) was transduced using a Hall-effect integrated circuit chip (Panasonic IC No. DN6835), which outputs a voltage monotonically related to the strength of an applied magnetic field. This chip was glued (with cyano-acrylate) to the top beak, and voltages were induced by a cylindrical neodymium magnet (3.3 mm diameter; Permag, Inc.) glued to the bottom beak (Figure 1A). The electrode wires soldered to the Hall-effect chip were connected to the mercury commutator installed in the ceiling of the chamber. The changing voltage values that were a function of beak movements were continuously monitored at 250 Hz (see

Figure 1B). These values were amplified and digitized by an A/D interface (the electronics of the transducing system have been described elsewhere; Deich et al., 1985).

At the start of each session, the monitoring system was calibrated by recording the digital readouts produced, first when the jaws were fully closed, and then with the jaws opened to varying degrees by the insertion of a series of six different spherical stimuli (3.2, 4.9, 6.4, 8.7, 11.1, and 20 mm in diameter). The obtained digital values corresponding to each of these millimeter values were entered into a computer program that generated a continuous calibration curve used subsequently to interpolate the millimeter value of digital values falling between those actually measured. This calibration process was carried out again at the end of each session to monitor the stability of the transducing system. Both calibration curves were stored for later analysis. Data acquisition (gape values and key-closure times) and storage, as well as control of all schedule events, were carried out by a personal computer.

Procedure

Pretraining. Subjects in both the experimental and control groups were exposed to the test chamber and were hopper trained with two 25-trial sessions, during which the hopper was raised for 6 s on a variable-time (VT) 30-s schedule. Each of the experimental food-US subjects was hopper trained with the pellet size to be used as the US during autoshaping (diameters and weights were 3.2 mm, 20 mg; 4.9 mm, 94 mg; 6.4 mm, 190 mg; or 8.7 mm, 500 mg). The control food-US subjects were hopper trained with 4.9-mm pellets. For the 6 experimental water-US and control subjects, 1 cc of water was released onto the surface of the watch glass. For all subjects in all groups, the houselight was continuously present before, during, and after all sessions.

Experimental groups. Autoshaping was carried out over three daily sessions consisting of 25 trials. Each trial included three components: (a) a VT 60-s intertrial interval (ITI), (b) a 6-s CS period, and (c) a 6-s US delivery period. The duration of each ITI was determined at the beginning of the trial. The computer program randomly selected one of five ITI values: 30, 45, 60, 75, or 90 s. Each of the 8 animals in the food-US groups was au-

toshaped using the pellet size employed during hopper training. Because a single small pellet (3.2 or 4.9 mm) was often not taken by the subjects, the number of pellets offered during the 6-s US period was varied as a function of pellet size: five 3.2 mm, three 4.9 mm, two 6.4 mm, and one 8.7 mm. Key pecks and jaw movements were recorded by the computer during the last 6 s of the ITI (pre-CS period), during the 6 s of keylight presentation (CS period), and during the 6 s of hopper presentation (US period).

Random control group. Control subjects underwent an identical regimen during three 25-trial test sessions, with each trial divided into three 6-s segments that were equivalent to the pre-CS, CS and US (post-CS) periods for the experimental groups. For the control subjects, however, deprivation-appropriate reinforcers were delivered on the same VT 60-s schedule but occurred randomly with respect to CS occurrence. Thus, the only difference between the two groups was the absence, for the control groups, of a contingency between the occurrence of the CS and the presentation of the US. Because there were no constraints on the timing of reinforcer delivery, instances of CS-US contiguity and overlap did occur, but most food or water presentations occurred during the ITI.

For all subjects, the data (gapes and key contacts) recorded during each of the 6-s periods (pre-CS, CS, and US, or post-CS for the controls) were displayed on the computer monitor at the conclusion of each trial. During the initial 5 s of the ITI, the data were stored to disk for later analysis.

Data analysis. Two data arrays were stored; one containing key-contact data (stored as a string of 0s and 1s), the other containing a string of digital values converted from the original analog Hall-effect input. An analysis program read the two arrays, transforming the Hall-effect data into millimeter values and relating them to the temporal position of the key contacts.

Determination of peak gapes required the development of an algorithm that would exclude fluctuations reflecting system "noise" but that would still include small jaw movements made during pre-CS, CS, and US (or post-CS) intervals. Consequently, the peak gape was determined by scanning the converted A/D data and identifying the highest value that oc-

curred after a minimum of five increasing values, without a reversal. The use of this algorithm made possible the detection of a wide range of gape values. When at least two peak gape responses were detected during pre-CS, CS, or US intervals, an interresponse time (IRT) was calculated for those gape pairs. Key-contact IRTs were also calculated.

RESULTS

Figure 2 presents records obtained during one food autoshaping trial (Bird 66, Session 3) and one water autoshaping trial (Bird 12, Session 3). These records were chosen because they contain examples of response forms observed for all birds in the study. The gape records are divided into the three 6-s periods—pre-CS, CS, and US. During the pre-CS interval, for the food-US subject, there were no key contacts, and the gapes were of low frequency and amplitude and possessed similar forms (Figure 2, pre-CS, *a*). The CS intervals for both birds contained both gapes (waveforms) and key contacts (vertical lines). For the food subject, most key contacts occurred at approximately the peak of the gape, but gapes also occurred without key contacts. The sample of gape responses includes three distinct response forms (Figure 2, CS, *a*, *b*, *c*), one of which resembles a pre-CS form (*a*) and is so labeled. The gape labeled *b* is characteristic of the peak opening observed prior to or simultaneous with key closure, and the gape labeled *c* represents a reopening after the beaks have begun to close. These three forms of gape movement were observed in all subjects and on most of the trials in which gape responding occurred.

The first half of the food-US interval included response forms similar to those made during the pre-CS and CS intervals and are similarly labeled (Figure 2, US, *a*, *b*, *c*); the last half of the interval contained three records with more complex waveforms (Figure 2, US, *d*, *e*). Previous studies suggest that each of these waveforms represents an ingestive response to one of the three food pellets. The waveform includes an initial (opening-grasping; gape *d*) component, followed by a series of opening and closing movements (mandibulations; gape *e*) probably reflecting transport of the pellet within the oral cavity (Bermejo et al., 1989, Figure 1; Zeigler et al., 1980).

For the water-US subject (Figure 2) there were no key contacts in the pre-CS period, but there was a distinct bout of low-amplitude gape responses. The CS period contained both key-contact and gape responses, but key contacts and gapes often occurred without each other. The US period was characterized by a rhythmic series of jaw movements, with approximately constant amplitude. This is the characteristic pattern of responding seen during drinking (Klein, LaMon, & Zeigler, 1983). Two distinct response forms are labeled (Figure 2, US, *a*, *b*); the *a* form resembles responses seen in the pre-CS and CS periods, and the *b* form represents actual drinking (during which the beaks remain briefly open at a relatively constant gape value).

Response Acquisition

Figure 3 illustrates, with two representative plots, an entire session (25 trials) of gape responding across all three data-collection periods for a food-US subject (Bird 73, Session 2) and a water-US subject (Bird 12, Session 3). The delay between the last gape responses during the CS and the first gape responses during the US period reflects the latency to respond to the US. It is during this delay that the pigeon's head moves from the key to the hopper. Note the relatively high frequency of gape responses during the CS but not the pre-CS interval. Within birds, there are also some striking similarities between the shape of gape responses during the CS and US intervals. This similarity across CS and US intervals was observed for all experimental subjects, under both food or water deprivation.

Figure 4 presents similar plots for representative food (Bird 58, Session 3) and water (Bird 51, Session 3) control subjects. In this condition the US could occur in any of the three 6-s intervals, as can be seen in the food control plot, that contains a presumably ingestive bout of gapes during the pre-CS interval and two bouts extending from the CS interval into the post-CS period. If examined carefully, individual ingestive responses can be discerned (compare with Figure 2, food-US, *d*). In contrast to the data in Figure 3, there was no systematic relation between CS presentation and the occurrence of gape responses.

Food-US. Figure 5 plots, across all three sessions (75 trials) and for all birds (experimental and control), food-US cumulative fre-

Fig. 2. Complete gape records collected during one food (Bird 66, 6.4-mm pellet, Session 3) and one water (Bird 47, Session 3) autoshaping trial. The pre-CS period represents gape changes during the ITI; CS data were collected while the response key was illuminated; and the US data were recorded while the food or water was presented. Solid vertical lines indicate the temporal positions of actual key contacts. The letters *a* through *e* label five types of gape frequently seen in these three intervals (see text for complete description of these response forms).

quency curves for key contacts (labeled *Key*) during the CS interval and gape responses during the pre-CS, CS, and US intervals (as labeled; note that data for Session 3, Bird 73, were not stored). In other words, when the data were analyzed, key-contact and gape re-

sponses were accumulated during pre-CS, CS, and US 6-s periods, and the cumulative record for that particular trial was incremented by that accumulated amount.

In almost all cases (however, see Birds 44 and 66) the pre-CS gape rates were fairly low

Fig. 3. Trial-by-trial plots of all gape data collected in single food (Bird 73, Session 2) and water (Bird 12, Session 3) sessions for individual subjects. Perturbations along the z axis (vertical) represent changes in gape over time. Trials are presented along the y axis and time changes along the x axis. Pre-CS, CS, and US intervals are indicated. Each increment on the z -axis scale represents 2 mm of gape.

and constant. For evidence of autoshaping of the gape response, two factors should be examined: (a) divergence of the CS trace from the pre-CS rates and (b) a sustained increase in the slope of the CS curve as compared with the pre-CS curve. For all 8 experimental birds, there is a clear divergence of CS and pre-CS curves, demonstrating an increase in the rate of gape responding in the presence of the CS. For several of the birds (43, 18, 66, and 44) during the last 20 to 30 trials, the rate of CS gape production is very similar to the rates produced in the presence of the US. Indeed, for Subjects 68 and 41, the rates of CS gape

responding during these trials were just lower than their US rates, and for Birds 73 and 72, the CS gape rates were higher than comparable US gape rates.

The conditioned character of CS gaping is dramatically revealed when the experimental birds' cumulative CS gape records are compared with those produced by the random control subjects (Birds 57 and 58). Although comparable US gape records are not available, the control subjects' pre-CS, CS, and post-CS cumulative curves show little difference in slope, suggesting a lack of control by the CS. In fact, the control birds simply did not produce very

Fig. 4. Trial-by-trial plots of all gape data collected for a pair of control subjects (Birds 58 [food] and 51 [water], Session 3) during pre-CS, CS, and post-CS intervals. Other details are as indicated in Figure 3.

many gapes during the intervals between feedings. In this respect, the rates produced during these intervals are similar to the pre-CS rates produced by the experimental subjects.

All of the experimental birds pecked during the CS period, albeit at very low rates. Because none of the experimental birds pecked during either the pre-CS or the US periods (although there were occasional pecks that terminated the CS), the autoshaped character of these CS key pecks is fairly clear. However, the evidence supporting the autoshaped character of gape responding during the CS is even more dramatic (see Figure 5). Although these birds never pecked without simultaneously gaping at the key, there were many recorded instances of

gape responses without any key contact. Indeed, none of the food-US birds' rates of key pecking were higher than their comparable rates of gaping during the CS. In addition, several of the CS gape functions began to increase, and even stabilize, well before the first key peck. For example, Bird 73's CS gaping increased within the first five trials of the first session, whereas key pecking did not begin until Trial 17. Several other subjects showed a similar difference in CS gape and key-peck provenance (Birds 68, 73, 18, 72, and 44). The data seem to provide clear evidence of the autoshaped character of the gape response under conditions of food deprivation and food delivery (during the US period).

Fig. 5. Food-US cumulative frequency curves for key pecks during the CS interval, and gape responses during the pre-CS, CS, and US intervals (as indicated to the right of each cumulative trace), as a function of conditioning trials. For the truly-random controls, data are provided from pre-CS, CS, and post-CS intervals. Because these curves overlap, no labels are provided. Except for Bird 73 the plotted data come from all three sessions or 75 trials of training, as indicated along the x axis. Bird numbers are indicated at the upper left of each plot, and pellet sizes are shown at the right of each row of plots.

Water *Truly-Random Controls*

Fig. 6. Water-US cumulative frequency curves for key pecks during the CS interval, and gape responses during the pre-CS, CS, and US intervals (as indicated to the right of each cumulative trace), as a function of conditioning trials. Except for Bird 47 the plotted data come from all three sessions or 75 trials of training. Other details are as indicated in Figure 5.

Water-US. Figure 6 depicts similar cumulative key contact and gape records for the water-US subjects in the experimental and random control groups (note that data for Bird 47, Session 3, were not stored). As with the food-US subjects, the pre-CS gape slopes for the water-US subjects are relatively shallow and unchanging. By Trial 30, all CS slopes produced by the experimental subjects diverged from the pre-CS functions. Unlike the food-deprived subjects, 3 of the 4 water-US subjects produced high rates of key pecking. In addition, unlike the food-US subjects, the

key-pecking functions for water-deprived birds diverged shortly after the CS gape functions increased. In fact, Birds 12, 38, and 47 produced key-peck and CS gape functions whose slopes were almost identical. Bird 32 was the only experimental subject who failed to peck at a relatively high rate.

The consistent rates of gaping during the US period are a function of the regularity and speed of the gapes produced during the ingestion of water. For 2 of the subjects (Birds 32 and 38), the CS gape slopes were not as steep as their comparable US gape functions, but

for all birds, both CS and US rates of gaping were much greater than the rates produced during the pre-CS periods.

The water-US control subjects, as in the food-deprivation conditions, showed almost no difference between pre-CS, CS, or post-CS cumulative slopes, although the absolute rates of gape production seemed to be somewhat higher than those produced by food-deprived control subjects (cf. Figure 6; truly-random controls).

Response Topography: Food-US Gapes

The three-dimensional plots in Figure 3 highlight the two most obvious characteristics of jaw-movement topography during conditioning of the pigeon's key pecking: (a) the marked differences between the food-US and water-US conditions and (b) the obvious similarities in the form of the conditioned and unconditioned gape responses. These topographic impressions, though compelling, are purely qualitative. Quantitative data were obtained by examining (a) the distributions of gape amplitudes during pre-CS, CS, and US (or, in the case of the control birds, post-CS) intervals, (b) the distributions of gapes measured at the moment of key contact during the CS period, (c) the distribution of peak-gape IRTs during the pre-CS, CS, and US (or, in the case of the control birds, post-CS) periods, and (d) the distribution of key-contact IRTs during the CS period (cf. LaMon & Zeigler, 1984, 1988).

Figures 7a and 7b present distributions of peak-gape amplitudes taken from the third session (for Bird 73, Session 2) for the 8 food-US subjects, each of whose responses were autoshaped using a different pellet size (as indicated above each subject's column of plots; pre-CS, CS, US, and gape at the moment of key contact [key gapes] are labeled along the right border of the figure). Although pre-CS responding was very low for all subjects, there are few other distribution similarities across subjects. The gape distributions of individual subjects seem to be somewhat idiosyncratic; however, within subjects the ranges of gapes produced during corresponding CS and US intervals were strikingly similar, and in several cases the shapes of the distributions were quite similar as well (although see data from Bird 68).

During the pre-CS period, distributions of

peak gapes were roughly unimodal and the frequencies were quite low. For the most part, the key-gape (gape at the moment of key contact) distributions were also unimodal, with the mode always lower than at least one of the modes observed during the CS and US periods, and sometimes higher than the pre-CS modes. This finding suggests that, at the moment of key contact, the pigeons were still opening or closing their beaks; either that, or the only pecks that resulted in key contact were those with relatively small accompanying gapes. When the individual traces of gapes associated with key contact were examined, the peak gapes for 87.6% of these responses occurred after key contact, confirming the former notion.

During both the CS and US intervals, there was a tendency for some distributions towards bimodality, especially at the larger pellet sizes (Bird 66, 6.4 mm; Bird 72, 8.7 mm; and Bird 44, 8.7 mm). For these 3 subjects, the first mode seems to represent a collection of relatively small gapes (generally less than 5 mm), much like those labeled *a* or *c* in the food-US panel of Figure 2. Indeed, this collection of small gapes during the US period would be ineffective grasping responses, because the pellets being delivered to these birds exceeded 5 mm in diameter. The second mode seems to represent the more functional responses that would permit a successful grasp of the pellet.

Birds 41 (3.2 mm), 43 (4.9 mm), and 73 (4.9 mm) showed selected gape distributions that were bimodal. Bird 41 produced a bimodal US gape distribution although most of the responses, regardless of the modal group from which they were drawn, would probably have been effective grasp responses. Oddly, Bird 43 produced a strongly bimodal gape distribution during the CS but not during the US interval. The accompanying key-gape distribution (gapes at the moment of key contact), which was also bimodal, suggests that the CS literally supported two different yet characteristic gape sizes (compare with Bird 41, whose key gapes were all very small, with the CS gapes covering a much wider gape range). Finally, Bird 73 produced a US gape distribution that seems to be somewhat bimodal, with the second, higher modal group representing potentially effective grasping responses.

The final 2 birds (68 and 18) produced CS and US gape distributions that were unimodal but that certainly covered a range sufficient to

Fig. 7a. Peak-gape frequency histograms derived from Session 3 (Session 2 for Bird 73) for each of 4 food-US experimental birds. For each bird, pre-CS, CS, US, and key-gape (as indicated to the right) histograms are presented. Bird numbers are indicated at the upper left, with pellet sizes presented above each column of plots. Gape bins are 0.5 mm wide and range over 20 mm.

Fig. 7b. Peak-gape frequency histograms for the remaining 4 food-US experimental birds. Data are from the third session. Details as in Figure 7a.

include gapes that served as pellet grasping responses. Bird 18, who received 6.4-mm pellets, produced a CS gape distribution that was almost entirely below 5 mm. However, this subject's US gape distribution contained many responses exceeding the 6.4-mm level.

For all birds, at least one of the modes in the US gape distributions was well correlated

with pellet size. Although for most birds this correlation was also visible during the CS gape and key-gape distributions, there are a few exceptions (Bird 68, key; Bird 41, key; Bird 18, CS and key). Two of these subjects (68 and 41) received smaller food pellets (3.2 and 4.9 mm), with the 3rd (Bird 18) receiving a 6.4-mm pellet.

Response Topography: Water-US Gapes

In contrast with the food-US subjects, both the absolute values (modal values of 1 to 3 mm) and the range of gape amplitudes were small in the water-US subjects (Figure 8; data taken from Session 3 for Birds 12, 32, and 38 and Session 2 for Bird 47). The distributions of CS gapes overlapped those of the US, but tended to cover a wider range. In 3 of the 4 subjects (Birds 12, 32, and 47) the modal CS gape value exceeded the modal US gape value by approximately 1 mm. Gapes at the moment of key contact were clustered at the low end of the amplitude distribution, indicating that the pigeon's beak was almost closed at the moment of key closure (for Bird 32, key pecking was infrequent, confirming what is observed in the cumulative records of Figure 6). Indeed, when the traces of gapes associated with key contact were examined individually, the peak gapes for only 32.8% of those responses occurred after key contact. Indeed, for over 61% of the responses, birds were closing their beaks at the moment of key contact.

It appears, from Figure 8, that the CS gape functions (compared to the pre-CS functions) for Birds 32 and 38 fail to provide dramatic evidence of autoshaping of the gape response. However, it is simply the case that gape responses are spread out across the gape continuum. Review of these subjects' cumulative data (Figure 6) confirms the autoshaped character of these CS gapes. Additional evidence may be drawn from a comparison of the CS and pre-CS gape distributions.

Response Topography: Food-US IRTs

For food-US subjects, IRT distributions for gapes and key contacts are plotted in Figures 9a and 9b (IRTs were calculated from Session 3 for all birds except Bird 73, for whom Session 2 was analyzed). In all cases, the IRT distributions were calculated independently; that is, the times of each peak gape, whether associated with a key contact or not, were included in the CS gape IRT distribution. Similarly, the times of each key contact, regardless of the associated gape value, were included in the calculation of the key-contact IRT distribution.

The IRT distributions for the CS and US intervals overlapped, and did not seem to vary with the size of the food pellet. The subjects producing bimodal CS and US gape distributions (Birds 66, 72, and 44) also produced

some bimodal IRT distributions, especially during the CS interval. This provides suggestive evidence that both the gapes and IRTs plotted for these subjects have, as one of their putative sources, the large-small gape response sequence seen in Figure 2 (food-US, at *b* and *c*). Although the IRTs between the largest gapes are probably best represented by the second (longest interval) mode, the shorter IRT mode was probably generated by the small reopenings so characteristic of these food-deprived subjects.

The key-contact IRTs (labeled key IRTs) generally follow the trend of the CS and US distributions (modal values less than 0.5 s), although they only maintain one mode, often similar to the second mode of the CS and US distribution (approximately 0.25 to 0.4 s; see Blough, 1963; Palya, 1992).

Response Topography: Water-US IRTs

Figure 10 presents IRT distributions of the water-US subjects (IRTs were calculated from Session 3 for all subjects except Bird 47, for whom Session 2 was analyzed). Although the water-US IRT distributions were similar to those recorded for food-deprived subjects, water-US distributions generally had smaller modal values (between 0.15 and 0.3 s). Three of the 4 water-US birds (Birds 12, 38, and 47) pecked at relatively high rates and produced IRT key-peck distributions with very small modal values (approximately 0.1 s). As others have reported (Jenkins & Moore, 1973), the water-deprived subjects generally made a single initial contact with the key and then engaged in "mumbling" motions against the key, thereby operating the key very rapidly with key-peck rates of up to 10 per second. In contrast, none of the food-US subjects maintained IRT distributions whose modes were much below 0.4 s.

Response Topography: Random Control Food-US and Water-US

Figure 11 presents gape distributions and Figure 12 presents the corresponding IRT distributions for the food-US and water-US random control subjects (for all subjects in both food-US and water-US groups, Session 3 was analyzed). The most striking aspect of these distributions is the similarity of pre-CS, CS, and post-CS distributions within subjects. In fact, the control subjects' gaping during all intervals resembled the gaping produced by the

Fig. 8. Peak-gape frequency histograms derived from Session 3 (Session 2 for Bird 47) for each of the 4 water-US experimental birds. Bird numbers are indicated at the upper left of each set of plots. Because water-deprived birds produced gapes over a restricted gape range, gape bins are 0.1 mm wide, ranging over 4 mm. Other details are as indicated in Figure 7a.

Fig. 9a. IRT frequency histograms derived from Session 3 (Session 2 for Bird 73) for 4 of the 8 food-US experimental birds. For each bird, pre-CS gape, CS gape, US gape, and key-contact IRT histograms are presented (as indicated to the right). Bird numbers are indicated at the upper left, with pellet sizes presented above each column of plots. Although there were occasional IRTs longer than 2 s, the plotted data represent 97% of all recorded IRTs.

Fig. 9b. IRT frequency histograms for the other 4 food-US experimental birds. Data are from the third session. Other details as in Figure 9a.

experimental birds during the pre-CS intervals (food-US, amplitudes 2 to 4 mm, IRTs < 0.5 s; water-US, amplitudes 1 to 3 mm, IRTs < 0.5 s).

DISCUSSION

Analysis of Gape Response Forms

The gapes recorded in this study include a variety of response forms that differ in their context, their potential stimulus determinants,

and their functional significance. For example, small (2 to 5 mm) gapes were recorded from both food-US and water-US subjects. In the food-US subjects these gapes occurred in the absence of other response forms, prior to the start of a larger opening response, or following a reclosure; in the water-US group these small gapes also occurred in all three intervals (pre-CS, CS, and US). Two of the food-US responses (Figure 2, *d, e*) are components of the ingestive response. A large response (Figure

Fig. 10. IRT frequency histograms derived from Session 3 (Session 2 for Bird 47) for each of the 4 water-US experimental birds. Other details are as indicated in Figure 9a.

Fig. 11. Gape distributions for both food-US and water-US (as indicated above each column of plots) truly-random control subjects. The data were derived from Session 3 for all birds. Bird numbers are indicated at the upper left of each set of plots. The plots depict pre-CS, CS, and post-CS gapes (as indicated to the right) in 0.5- or 0.1-mm bins.

2, food, b) was present in both the CS and US intervals. During the CS interval it frequently terminated in a key contact; during the US interval it probably indicates an unsuccessful ingestive response (see Bermejo, Allan, Houben, Deich, & Zeigler, 1989, Figure 1).

Although we are not ignoring such qualitative distinctions, the present quantitative analysis treats all jaw-opening movements as equivalent members of a sample of responses that occur during a conditioning trial. A computer algorithm was used to distinguish jaw movements from "noise" (i.e., random baseline fluctuations), and the movements were classified solely in terms of their amplitudes and IRT times. This strategy may be criticized for treating functionally distinct response forms as equivalent. However, it does provide an unbiased record of the different response forms that occurred during the pre-CS, CS, and US intervals.

Acquisition of the Conditioned Gape Response

Response probability. It is clear that during autoshaping of the pigeon's key peck, the gape,

as well as the transport component of pecking behavior, came under the control of the key-light CS. Evidence for the conditioned nature of this control comes from two sources. First, in the random control conditions (i.e., in the absence of a CS-US contingency), jaw-movement frequencies during the pre-CS and CS intervals did not differ (moreover, the control data provide no evidence for an alpha response, i.e., an increase in baseline activity in response to CS presentation; see Gormezano & Kehoe, 1975). This evidence also suggests that the large and small gapes seen in food- and water-deprived subjects, respectively, are probably not due simply to the type of deprivation; rather, these differences in gape are more likely due to the pairing of the CS and US. It is fairly clear, then, that the unconditioned gapes directed at food affected the form of gapes produced during the CS. Second, for both food-US and water-US birds, the asymptotic rates of gape responding during the CS intervals were much higher than in the pre-CS interval, which served as a comparative control period.

Dissociation of pecking response components. An assumption underlying this study is that

Fig. 12. IRT distributions for both food-US and water-US truly-random control subjects. The data were derived from Session 3 for all birds. The plots show IRT distributions (in 25-ms bins) extracted from pre-CS, CS, and post-CS intervals.

the transport and gape components of key pecking may easily be dissociated, because key contacts reflect only the transport component. This assumption holds true for the food-US subjects, whose gapes were initiated at some distance from the key. However, many of the key contacts recorded in the water-US subjects may not all reflect head transport but may have been the result of repetitive jaw opening-closing movements ("mumbling") made while the beak was in contact with the key (see also Wolin, 1968). Indeed, the acquisition functions for key contact and gape responses had similar slopes in the water-US birds. Conversely, because only transport responses terminating in key contacts were recorded, these results may underestimate the relative frequency of head transport during the CS in the food-US group. Nevertheless, the time course of conditioning differed for the gape and transport components; the first increase in gape responding generally preceded the first key contacts, often by many trials and sometimes by more than one session.

The pigeon's conditioned key-pecking be-

havior involves a sequence of discrete response components (locomotion, gape, head transport) whose acquisition may have different time courses (Deich et al., 1988; LaMon & Zeigler, 1988). Informal observations (see also Brown & Jenkins, 1968) indicate that the first behavior to come under the control of the CS is general orientation, then locomotion, followed by jaw movements and then by small transport movements that do not initially terminate in key contact. The gape response appears to be a sensitive measure of the autoshaping process for several reasons: (a) It appears to be acquired prior to the emergence of CS key contacts, (b) it is produced at equal or higher rates than key-contact responses, and (c) it reflects critical features of unconditioned response topography. Indeed, the observation of CS gapes may provide a very sensitive measure of the effect of autoshaping (respondent) procedures.

Response Topography

The present design and procedures made it possible to specify the topographic features common to the unconditioned gape responses

(URs) and conditioned gape responses (CRs), to determine whether variations in reinforcer properties are reflected in common topographic changes, and to identify some of the potential sources of the differences between unconditioned and conditioned response forms.

Comparison of URs and CRs. It is already known that the topography of ingestive jaw movements in the pigeon is quite distinctive and highly stereotyped. Drinking is characterized by relatively constant peak gape values (range, 1 to 3 mm) and rates (range, four to seven per second) (Klein et al., 1983). During eating, pecks are generally produced at the rate of about three per second, and peak gapes are often observed to be proportional to the size of the food object (Bermejo et al., 1989; Zeigler et al., 1980).

The sample of gape responses recorded in the food-US interval includes at least three different gape types: the small openings exemplified in Figure 2 (a), the potential grasping responses depicted in Figure 2 (d), and the mandibulation responses of Figure 2 (e). The US interval also maintains gape forms (Figure 2, b, c) that are not functional with respect to pellet grasping (Bermejo et al., 1989, Figure 1). Because of the construction of the food hopper and the fact that the pellets were moving when they came into the food dish, some of these responses may have been directed at moving pellets before they came to rest. This would help to explain the rather large number of gape responses during the US interval that did not contain a mandibulation response (Figure 2, e). In contrast, the great majority of gape responses recorded during the water-US interval had the form of the consummatory response.

A quantitative analysis of gape response distributions during the CS and US intervals reveals both similarities and differences in unconditioned and conditioned gape form. For the food-US subjects, distributions of CS and US gapes were strikingly similar (but see Figure 7, Bird 43), suggesting that the gape amplitudes controlled by the CS are very similar to those controlled by the US. The similarity of the individual-bird CS-US IRT distributions (Figure 9) indicates a pattern of response production common to both CS and US intervals.

For the water-US birds, it is unclear why there was a shift in the modal gape amplitude in both CS and key-contact distributions, even though the gape responses fell into a restricted

range (0 to 4 mm). Three of the 4 subjects produced gapes to the key that were roughly 1 mm larger than those produced when the beaks were inserted into the water and drinking began. Perhaps when birds pushed against the key their beaks were forced apart; however, the key-gape distributions provide evidence against this explanation, because most gapes at key contact were smaller than those produced during the US interval. Comparison of the CS and key-contact distributions suggests that water-deprived subjects were probably producing their largest gapes either off the key or while the microswitch was not activated. In combination with the overlapping water-US IRT distributions, it is clear that CS gape, US gape, and key responses were very rapid, sustaining very small beak openings.

Effects of US manipulations. Qualitative and quantitative variations in US properties that modified the form of the US gapes also affected the form of the CS gape responses in a predictable manner. A water US produced CS gapes whose form paralleled that of the rhythmic, low-amplitude gapes produced during the US (when the birds were drinking); a food US produced CS gapes resembling jaw movements observed during the US interval (when the birds were eating). Increasing the diameter of the food US across groups produced a corresponding increase in the amplitude of gapes that was maintained during both the CS and US periods. This relation between US size and the amplitude of the CS gape was also seen when gape was measured at the moment of key contact. In the present study, however, pellet size may be confounded with pellet number (magnitude of reinforcement), so that it is impossible to specify the effective US variable. However, the relationship between pellet size and jaw-opening amplitude has been demonstrated, for both CS and US gapes, in previous experiments in which such confounding effects were absent (e.g., Bermejo et al., 1989; LaMon & Zeigler, 1988; Zeigler et al., 1980). Clearly, a within-subject study might better resolve the contribution of US size to the control of CS gape amplitude.

The present results indicate that the form of the CS gapes, although not necessarily identical with the form of the consummatory response, may be a reflection of topographic elements that are present and presumably elicited during the US interval. This finding suggests that all response forms present during the US

interval are potential candidates for association with the CS and may contribute to the topography of any resulting CR. The data from the random control subjects also imply that the inclusion of an element of UR topography in the CS gape is dependent upon the temporal relations between the CS and responses that occur in the US interval. These conclusions are consistent with previous studies of conditioned response form (Holland, 1984, pp. 141–144) and may account for some differences between the UR and the CR seen in the present study. For example, although the IRT distributions for CS and US gapes (in the food-US group) were very similar, with several well-defined bimodal distributions, during the US interval there was an additional potential source of high-frequency gapes—the mandibulation phase of the consummatory response (as depicted in Figure 2, *e*). During the CS interval, the only source for short IRTs is the *c* response shown in Figure 2. Perhaps there are other instances in which only a subset of US-elicited topographical components may come to be elicited by the CS.

Conditioned gape responses and the form of the key-pecking response. Previous studies of conditioned key pecking suggest that the CS elicits and directs the transport component (for a comprehensive review, see Locurto, Terrace, & Gibbon, 1981), but few have collected data on the accompanying gape component of that response. LaMon and Zeigler (1984) found that neither variations in the size of the CS (over a range from 2 to 14 mm in diameter) nor in CS contrast (white on black, black on white) affected the form of gape responses made during key pecking. Moreover, the size of the CS gape was very sensitive to the manipulation of US properties. The present results confirm and extend that conclusion and suggest that the form of the CS gape component is determined primarily by US variables. This suggests that the observed similarities in the form of conditioned and ingestive pecking that have figured so prominently in the autoshaping literature may reflect, in large part, respondent conditioning of the gape response.

In conclusion, it is fairly clear that the form of the US gape response has an effect on the topography of CS gapes for both food- and water-deprived pigeons. The similarities in gape and pattern of response production are striking. In addition, because gape responses

accompany most, if not all, transport responses, and because these gape responses may occur in the absence of a key closure (i.e., the transport response does not terminate in key contact), the gape response may serve as one of the most sensitive measures of conditioning in an autoshaping experiment.

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