*INCOMPATIBILITY BETWEEN THE PIGEONS'
UNCONDITIONED RESPONSE TO SHOCK AND THE
CONDITIONED KEY-PECK RESPONSE¹*

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High-speed photography was used to compare the pigeon's response to unsignalled shock with the pigeon's key-peck response. During shock, pigeons flex their neck (*i.e.*, the distance between their eyes and shoulders decreases). Following shock, the neck is extended. During key pecking, the neck remains extended and the head moves toward the key in a slight arc as though attached to a fixed fulcrum. Response topography during pecking and shock appear to be incompatible, and it is concluded that the difficulty in key-peck training pigeons to escape electric shock is due to interference from the unconditioned flexion response. This conclusion supports the species-specific defense theory of escape and avoidance behavior.

Several investigators (Hoffman and Fleshler, 1959; Rachlin and Hine, 1967; Hine and Rachlin, 1969; Macphail, 1968) have reported failure, or great difficulty, in training pigeons to escape electric shock when escape is made contingent on the key-peck response. However, successful avoidance and escape behaviors in pigeons have been conditioned when responses other than key pecking have been selected. Hoffman and Fleshler (1959) obtained conditioning when a head-lifting response was used; Macphail (1968) and Bedford and Anger (1968) reported successful conditioning using a shuttle response; Smith and Keller (1970) and Foree and LoLordo (1970) obtained conditioning using a treadle response, and Graf and Bitterman (1963) successfully used general activity as an avoidance response.

In reviewing these findings, Smith and Keller suggested that the difficulty in training avoidance and escape stems from inappropriate response selection, rather than inappropriate species selection. These authors theorized that successful conditioning depends on the selection of a conditioned response topographically similar to the unconditioned response elicited by shock. Thus, key pecking is easily

conditioned with food as the reinforcer because food elicits topographically similar pecking behavior. Similarly, shock elicits general escape activity that is compatible with shuttle responses, treadle pressing, and general activity. The Smith and Keller interpretation suggests that the immediate unconditioned response to shock is incompatible with the key-peck response.

The present study employed high-speed photography of food-reinforced key pecking and unconditioned responses (UCRs) to shock in order to determine whether the topography of the key-peck response would oppose the topography of the UCR to shock.

METHOD

Subjects

Four experimentally naive, male, Carneaux pigeons, 1 to 3 yr old at the beginning of the study, were used. During the key pecking phase of the experiment the birds were maintained at 80% of their free-feeding weights; during the shock phase, the birds were permitted free access to food and water in their home cages.

Apparatus

The apparatus consisted of an L-shaped conditioning chamber designed to contain the bird within the focal field of the camera. The chamber was equipped with a pecking key (Lehigh Valley, 1348) and food hopper as

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Fig. 1. Diagram of the L-shaped experimental chamber. Placement of the key and hopper opening are shown as the circle and rectangle behind the open gridwork. The birds were photographed through the gridwork.

shown in Figure 1. The key was located 9.75 in. (24 cm) above the floor of the chamber and was set to operate with a force of 14 g (0.14 N).

The technique used to photograph responding (Smith, 1968) involved a 35-mm kymographic camera (Grass, C4). Tri-X film was moved past the continuously open shutter of the camera at a rate of one meter per second. Individual frames were exposed by strobing the subject at a rate of 100 flashes per second with a General Radio (1531) stroboscope (flash off-time = 9.85 msec, on-time = 0.15 msec). The flashing strobe remained on throughout each session, and, since its rate exceeded the experimenters' critical flicker frequency, it was assumed that the strobe provided general illumination for the birds as well. In addition to photographing the subject, one edge of the film was continuously exposed to the beam of a textonix oscilloscope. This beam monitored shock onset and offset or key-switch closure, depending on the experimental conditions in effect. Thus, the film strips were composed of 10-msec frames; each frame contained the position of the subject and the state of stimulus or response events.²

Conventional electromagnetic equipment located in an adjacent room was used for contingency scheduling, camera control, and data

collection. Shock was delivered through stainless steel wire electrodes chronically implanted through the pubic arch as described by Azrin (1959). Shock was produced with a constant voltage source set at 6.3 v ac, and shock duration was set at 80 msec (range 70 to 90 msec).

Procedure

During a 1-hr hand-shaping session, two pigeons (P3 and P4) were trained to key peck for occasional 5-sec periods of access to mixed grain. After shaping, the birds were given 24 daily 30-min sessions on a variable-interval 30-sec schedule of reinforcement. Key pecking was photographed during the twenty-fifth and twenty-sixth sessions. Two days after photography of key pecking, these birds received 20 shocks presented intermittently at an average inter-shock interval of 3 min during a single 60-min photographic session. The reinforcement schedule was discontinued during the shock session. The procedure was identical for the other two birds (P5 and P6), except that the shock series preceded food reinforcement.

RESULTS

Close visual inspection of the film strips obtained during the shock sessions revealed changes in the curvature of the neck as the most distinctive component of the UCR to shock. The extent of curvature was quantified by measuring the distance between a bird's eye and shoulder at shock onset, 80 msec after onset (approximately shock offset), and 210 msec after shock onset. The frame exposed 210 msec after shock onset was chosen on the basis of other data that indicated that the post-shock response was complete by this time (Gustavson, Smith, and Gregor, 1971). In Figure 2, decreases of at least 0.25 in. (0.5 cm) in the distance between eye and shoulder were tallied as "flexion" cases; increases of at least 0.5 cm were tallied as "extension" cases. A total of 70 film strips, which represented the four birds about equally, were judged suitable for the analysis. Measurements from these strips constitute the "cases" referred to in the figure. The left panel of the figure shows the percentage of cases in which no change or neck flexion occurred during shock (no cases of extension were observed). The right panel shows the post-shock distribution of no change, flexion, and extension responses.

²Additional questions regarding the photographic procedure should be addressed to the senior author.

Fig. 2. Bar graph showing changes in the eye-shoulder distance in the presence of shock (left panel) and after shock (right panel). The figure is based on a total of 70 cases (*i.e.*, 70 film strips) representing responses from all four birds.

The left panel of Figure 2 reveals that the neck was flexed in 73% of the cases. No change was observed in the remaining cases; however, in 70% of these cases, maximum neck flexion happened to coincide with shock onset (*i.e.*, the distance between the eye and shoulder was 2 in. (5 cm) or less). Thus, in 96% of the total cases, the birds either flexed after shock onset or had already flexed their necks at shock onset. The right panel of Figure 2 reveals that the neck was extended after shock offset in 91% of the cases and, with one exception, the remaining cases produced less than 0.5-cm change. The average eye-shoulder distances at shock onset, offset, and 210 msec after onset were 6.5, 5.5, and 7.5 cm respectively.

The analyses summarized in Figure 2 were possible because the distance between the pupil of the eye and an anchor point on the shoulder could be measured accurately from projected film strips. The anchor point on the shoulder was provided by the contrasting shock packs worn by the birds (see Figure 5). Use of the anchor point was not anticipated in the

Fig. 3. Bar graph showing changes in the pupil height during the key peck (left panel) and after the key peck (right panel). The figure is based on a total of 64 cases (*i.e.*, 64 film strips) representing responses from all four birds.

experimental design. Consequently, the shock-packs were not worn by birds run on positive reinforcement schedules and determination of the anchor point in photos of key pecking was impossible. Nevertheless, an alternative measure of topography was obtained that permits a reasonable comparison of the key peck and response to shock. The distance from the floor of the chamber to the pupil of the eye was measured at 40 msec before key-switch closure, at switch closure, and 80 msec after switch closure. These data, plotted in Figure 3, are presented in a fashion similar to the eye-shoulder data shown in Figure 2. That is, decreases of at least 0.5 cm in the height of the pupil were tallied as "down" cases; increases of at least 0.5 cm were tallied as "up" cases. A total of 64 film strips, which represent the four birds about equally, were used to provide data for the figure. The left panel of Figure 3 shows the percentage of cases in which no change, downward movement, or upward movement occurred during the 40-msec interval before switch closure. The right

panel shows the post-response distribution of no change, downward, and upward movements.

In general, little vertical movement characterizes the pre-closure response. The average pupil height at response initiation was 24.5 cm, the average height at switch closure was 24.5 cm, and the average height at 80 msec after closure was also 24.5 cm. When movement did occur it was generally in the downward direction; however, the magnitude of the movement was small. That is, only six cases of downward movement exceeded 0.5 cm. Upward, downward, and no change characterize the post-closure response about equally often.

It should be noted that upward and downward movements could result from neck extension or flexion; they may also result from the arc described as the head moves with respect to the key, from body angle, or from height adjustments produced by leg extension or flexion. Evidence from two sources suggests that neck extension and flexion contribute little upward and downward movement during pecking. Five observers reviewed the film strips of key pecking. They agreed that there was no evidence for the occurrence of either extension or flexion during the 40 msec before closure nor during the 80 msec after closure. Perhaps the more persuasive evidence comes from a study of the vertebral structure of the neck. The pigeon's neck is composed of 14 vertebrae; beginning at the head, the first two (atlas and axis) provide for head rotation. The remaining 12 vertebrae are grouped around three points, which provide for neck extension and flexion. According to Stresemann quoted by Bellairs and Jenkin (1960): "The joint surfaces of the neck vertebrae are arranged in such a way that the front part moves freely forward, middle backward and posterior part forward again [p. 249]." We plucked the neck of one of our birds and manipulated the three points of flexion. Our conclusions concur with Stresemann's, and they suggest the following descriptions of neck movement during pecking. Before pecking, the middle section of the neck seems to be used to adjust the height of the head with respect to the target. This flexion point does not seem to be used during the actual peck. Instead, the posterior flexion point is used as a fulcrum about which the head is thrust toward the key. The anterior flexion point appears to be used to make minor

adjustments in the angle at which the beak strikes the target. Thus, decreases in pupil height probably result most commonly from the arc described about the posterior flexion point. The flexion points are used quite differently during the UCR to shock. During shock, the head is moved toward or onto the breast; a response that requires near maximum flexion of each of the three points.

A typical orientation of the head and neck during three phases of a key peck is shown in Figure 4. The figure was produced by projecting and tracing film images obtained at 40 msec before key switch closure, at key switch closure, and at 80 msec after key switch closure. The "X" in each frame shows the location of the pupil of the eye at 40 msec before switch closure and gives the reader a reference point for judging the extent and direction of head movement in the succeeding frames.

Figure 4 should be compared with Figure 5, which shows similar line tracings of a typical response during and following shock. It should be noted that while a forward and downward movement of the head occurs with respect to the starting position in the second frame of each figure, the two sequences differ considerably in their topography. In Figure 4, the forward-downward movement is produced with the neck fully extended. In Figure 5, the forward-downward movement results from increased neck flexion. The change in orientation from the second to the third frames in each figure can be described as an upward and backward motion. However, after switch closure, the motion seems to result from an arc described around a rather fixed fulcrum; after shock, the motion seems to result from neck extension.

To compare the two responses shown in Figures 4 and 5 it was necessary to establish a time before switch closure at which the pecking response was initiated, just as the UCR to shock was initiated at shock onset. The frame taken 40 msec before closure was chosen on the basis of a temporal analysis of the probability of forward head movement. Figure 6 shows the average probability of forward head movement in 10-msec units before and after switch closure. Movement was defined as a change of at least 0.5 cm per 10 msec in the location of the eye. The analysis was based on photographs of 64 key pecks produced by all four birds.

Fig. 4. Line tracings of projected film strips taken during three phases of a single key peck. The "X" in frames 2 and 3 marks the location of the pupil in the first frame.

This figure reveals a sudden increase in the probability of movement at 30 msec before switch closure. It was, therefore, decided to accept the posture obtained in the 10-msec frame preceding the change in probability as typical of the birds' positions at the time of response initiation. There are at least two reasons why the function fails to approach unity at or about the time of switch closure: (1) If the bird approached the key slowly (*i.e.*,

Fig. 5. Line tracings of projected film strips taken during three phases of a UCR to shock. The "X" nearest the eye in frames 2 and 3 marks the location of the pupil in the first frame. The anchor points used to measure eye-shoulder distance are also shown in the first frame. Note that the shoulder is visible against the contrasting shock pack.

Fig. 6. The probability of forward movement at times before and after key-switch closure. Data from all four birds were averaged in order to produce the function. The zero abscissa value marks switch closure.

at a rate less than 0.5 cm per 10 msec), the approach was not tallied as movement. (2) Smith (1968) discussed switch-closure that results from an arc described by the upper bill as birds close their beaks while in contact with the key. These responses, which Smith found accounted for as many as one-third of the total switch closures per session, do not result in significant movement of the eye. The figure also reveals a high probability of forward movement at 10 and 20 msec after switch closure. Since the key could be moved only 0.5 cm beyond the point of switch closure, a high probability of movement after closure indicates that the key was usually displaced to its maximum.

DISCUSSION

The pigeons' response to shock differs markedly from the key-peck response. In fact, the response to shock appears to be topographically incompatible with key pecking. In order to produce a key peck during shock, the bird would have to overcome neck flexion and perform the opposing response of neck extension before striking the key. Since the response to shock is reliable both within and between birds, we view the behavior as a respondent that directly interferes with the operant conditioning of the key-peck escape response.

This conclusion seems justified even though the present study offers a limited comparison between the key peck and the UCR to shock. The limitations stem from two sources. First, the key peck was handshaped on only one type of key, at a single height, and photographs were obtained while birds were run on a single schedule. Different shaping procedures, equipment, or reinforcement schedules could modify the topography of the key-peck response. However, any effective topography would require movement of the head toward the key. Since the UCR to shock involves near maximum flexion of the neck, with the head coming to rest against the breast, any movement toward a key would require some ("incompatible") neck extension. The second limitation involves the use of different measures for describing the UCR to shock (eye-shoulder distance) and the key peck (height of the pupil). While the height of the pupil fails to provide an index of neck curvature, which would be desirable for a complete description, the data do suggest

that the neck was extended during all phases of the key-peck response (*i.e.*, the neck was extended at switch closure and pupil height failed to differ reliably before and after closure).

The headlifting escape response used successfully by Hoffman and Fleshler (1959) may appear to be incompatible with the UCR to shock. However, these authors used a pulsing aversive stimulus composed of brief shocks presented at a rate of one per second. We have shown that birds begin to extend their necks at shock offset and complete this response within 130 msec. It is assumed that neck extension occurred during Hoffman and Fleshler's brief inter-shock interval. Presumably, the neck-extension response was strengthened and used to interrupt the train of shocks. It is also possible that the UCR reported in the present study was specific to the shock parameters used. Pilot data obtained with higher shock intensities (but about the same duration) failed to influence the flexion component of the response. However, it seems possible that neck extension might begin before shock offset if long shock durations were used.

The topographical data presented here suggest an explanation of the problem of training key-peck escape in pigeons. At a more general level, the data lend support to the species-specific defense interpretation of escape and avoidance behavior (Bolles, 1970). Bolles' position differs from other theories of avoidance behavior (*e.g.*, Mowrer and Keehn, 1958; Dinsmoor, 1954; Anger, 1963) in at least three ways: (1) Little or no conditioning is postulated, (2) the most important determinant of successful avoidance is the response selected, and (3) the theory originates from considerations of natural avoidance behavior.

In each of the other theories, an experimenter-determined response is assumed to terminate or reduce a hypothetical aversive stimulus (*i.e.*, Mowrer's "fear", Dinsmoor's "dependent stimuli", or Anger's "conditioned aversive temporal stimuli"). The hypothetical stimulus (which may be external, postural, or temporal) is said to acquire aversive properties through classical pairings with the primary aversive event. Once the stimulus has acquired aversive properties, an operant can be reinforced by contingent reduction or termination of the stimulus. Bolles postulates neither classical nor operant processes. Instead, he says

that any sudden, novel, or painful stimulus will elicit a "species-specific defense reaction" (SSDR). Freezing, flight, and aggression are common SSDRs for the rat (Bolles, 1970; Azrin and Holz, 1966). If one of these SSDRs also satisfies the experimenter's definition of the avoidance or escape response, then learning will occur; if the SSDRs do not satisfy the response definition, learning will not occur. "Learning" in this situation appears to be similar to the punishment process discussed by Dinsmoor (1954). That is, the ineffective SSDRs are suppressed, and the rat retains only the effective SSDR. Bolles based his theory on a review of the literature involving rats. The evidence presented in this paper as well as by Smith and Keller (1970), Gustavson, *et al.*, (1971), Stein, Hoffman, and Stitt (1971) and others suggest the point is equally well taken with pigeons.

Both Bolles (1970) and Gustavson, *et al.*, (1971) discussed the unlikelihood that conditioned aversive stimulus theories can be applied to natural avoidance situations. Their arguments can be summarized by the question: "How many times must a pigeon be bitten by a fox before the pigeon learns to avoid stimuli associated with the approach of the fox?" Perhaps we should not expect the laboratory pigeon to behave differently from the wild pigeon. In the presence of an aversive stimulus, both birds are expected to emit SSDRs. The laboratory pigeon will only learn to avoid or escape the stimulus successfully if the escape or avoidance response is compatible with a natural defense respondent.

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