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Startle Reaction Times in the Starling (Sturnus vulgaris)

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STARTLE REACTION TIMES IN THE **STARLING** {Sturnus vulgaris)

BY

HAROLD FREDERICK POMEROY

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

IN

ZOOLOGY

UNIVERSITY OF RHODE ISLAND 1973

MASTER OF SCIENCE THESIS OF

HAROLD FREDERICK POMEROY to and rore and wismal attack have been determined. Birds toring and regarding the activity of the birds was designed and qued for the coperigents. Display sodes of the recording

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UNIVERSITY OF RHODE ISLAND 1973

ABSTRACT

Startle response times of Starlings (Sturnus vulgaris) to auditory and visual stimuli have been determined. Birds were placed into an anechoic chamber and exposed to either a one msec flash of unfiltered white light, or a three msec pure tone burst. An electronic detection system for monitoring and recording the activity of the birds was designed and used for the experiments. Display modes of the recording apparatus allowed for an accuracy to 10^{-4} seconds in measuring reaction times. The mean reaction time of birds to light stimuli was 76.38 msec + 15.32 msec. The mean reaction time to sound stimuli was 80.64 msec + 14.40 msec.

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ACKNOWLEDMENTS

Many individuals have been of assistance and given useful advice throughout the preparation of this thesis. I thank the staff at the Manomett Bird Observatory for their assistance in obtaining birds. Wilson Lamb, of the Department of Ocean Engineering, and Dr. Hellmuth Etzold, of the Electrical Engineering Department, the University of Rhode Island, provided technical adivce and equipment. I am grateful to Dr. Etzold, and also Dr. Stanley Cobb, of the Department of Zoology, the University of Rhode Island, for reading this manuscript.

Dr. Frank Heppner, Department of Zoology, University of Rhode Island, deserves great thanks, for having patiently served as my major professor, committee chairman, mentor, and friend.

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INTRODUCTION

Recent analyses of flight flocking behavior in several species of birds have brought attention to the importance of reaction times of birds in determining the communication modes used to coordinate movements in flocks (Heppner and Haffner, 1973). The assumption of the use of auditory or visual signals to coordinate the apparently synchronous turning and wheeling movements of birds in flocks is contingent upon knowledge of the response times of the species involved.

Current data, and related hypotheses concerning reaction times (RTs) in birds are based upon speculations on the physiological and anatomical characteristics of the avian sensory systems (Pumphrey, 1961), or from observations of the temporal properties of vocalization of various species of birds (Thorpe, 1963; Grimes, 1965; Greenewalt, 1968).

Thorpe (1963) has noted that in species of tropical birds which live in dense scrub, where mutual recognition and the maintenance of pair contact by visual displays is ineffective, vocal displays may become very important. His suggestions on the speed of RTs are based on an investigation of the courtship calls of one such species of bird, the Black-headed Gonolek (Laniarius erythrogaster). These birds can not vary the pattern of their call. Pairs of these birds maintain the individual distinctiveness of their call through a precise and exactly maintained time interval between contributions of the two sexes. Thorpe suggested that the high degree of precision of time-keeping in the duets could render recordings of duetting pairs of birds useful in the establishment of auditory RT. Using spectographic analysis of recordings of duetting pairs of Black-headed Gonoleks as evidence for auditory RT, Thorpe (1963) reported a mean RT of

144 msec, with a standard deviation (SD) of 12.6 msec for the fastest single pair performance recorded. Grimes (1965), using similar techniques, found the mean RT for a pair of Shrikes (L. barbarus) to be 118 msec, with a SD of 30 msec.

The data analyzed in both instances is that of specialized vocal communication, where RTs are pair specific. Reliability of communication between members of a duetting pair is a function of constancy of RTs, rather than absolute speed of RT, so it is not probable that the fastest possible RTs in birds will be discovered by the stydy of duetting animals.

Greenewalt's (1968) sophisticated analysis of bird song indicates far greater powers of temporal discrimination than those suggested by Pumphrey (1961). However, results are still inferred from bird vocalizations, and to date no whole animal investigations involving RTs to known physical stimuli have been done with birds.

In September, 1971 I began a series of direct determinations of RTs in birds. Start le response times of the Starling (Sturnus vulgaris) to auditory and visual stimuli were electronically monitored and recorded under control led laboratory conditions.

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MATERIALS AND METHODS

The species chosen for testing, Sturnus vulgaris, was selected on the basis of demonstration of strong tendencies for flocking behavior, size limitations of the experimental apparatus, and availability. Subjects were caught with mist nets at the Manomett Bird Observatory, Manomett, Mass., and transferred to the university of Rhode Island facility. Here they were held in retaining cages while maintained on a 12/12 LD cycle. Birds were individually tested on several occasions.

The latent period of startle response, this being the time from occurrance of stimulus to elicitation of response, was used as an index of RT. The criteria for a response did not require the birds to move from any prestartle position on the perch, as initial experiments demonstrated that birds' startle responses uniformly consisted of a rapid and virtually unnoticable sequence of flexor contractions such that the bird appeared to go into a semi-crouch position, resembling the startle pattern described for mammals by Landis and Hunt (1939).

A comparison of RT measurements in humans (Costa, Vaughan and Gilden, 1965) using both electromyographic and microswitch sensors noted a 7.5 msec difference in results, due to the lag time of the mechanical system. My efforts were thus focused on the design of a completely non-mechanical electronic system for the continuous monitoring of the activity of caged birds.

Experiments were conducted in an anechoic chamber (Fig. I). Calibrations of the ambient noise level in this chamber, and the intensities of the auditory and visual startle stimuli were done with a Bruel & Kjaer precision sound level meter, and the digital readout photometer of the Electrical Engineering laboratories at the University of Rhode Island. Auditory calibration was performed

in a manner similar to that described by Hoffman and Searle (1968). The experimental cage was placed in the anechoic chamber. The sound level meter was then placed inside this cage and a large number of measurements taken. The meter was moved after each measurement, until the entire area of the cage had been sampled. The intensity of the ambient noise in the cage was defined as the mean of the distribution of the measurements for ambient noise intensity. Sound pressure readings of the room in which the chamber was located for sounds in the 100 Hz to 20,000 Hz range were consistently 60 to 65 dB. This range was of crucial interest because the range of sounds audible to birds is approximately 200 Hz to 20,000 Hz (Sturkie, 1965). The noise level inside the chamber (28 to 32 dB) was 30 dB below that in the room. A fixed position measurement at the point in the chamber occupied by the birds was used to determine the SPL of the auditory stimulus. A reading of 120 dB + I dB was obtained. The mean of a series of trials was used as an index of the intensity of the light stimulus. The value obtained for 10 trials was 27 ft-Lamberts *±* 10%.

A trunk line of shielded wires leading into the bottom of the chamber connected outside apparatus to an internally mounted speaker, electronic flash unit, variable intensity inner lamp, and sensors. A front port, sealed by a clamp-on, double-paned glass door, allowed access to the inner area of the chamber, which contained the experimental cage. This box-like cage rested on a sliding base on the inner floor of the anechoic chamber. Thus the cage could be slid to the proximity of the front port where birds could be inserted or removed, and moved back to a position in the recess of the chamber where the experiments were run.

The cage itself (Fig. 2) was a 30X30X30 cm, clear Plexiglas cube with a 15 cm pyramidal bottom to discourage birds from sitting on its floor. A black cloth sleeve led to a hole of 12 cm diameter cut in one side of the cage. A rubber band placed around this sleeve prevented birds from escaping, yet allowed for easy removal of birds from the cage at the end of each trial.

Figure I. Anechoic chamber. The chamber was constructed of one half-inch plywood, which was glued together with three-eigth inch rubber strips between all wood to wood contacts. The outer surface of the chamber was coated with a one inch layer of foam rubber. The chamber rested on a platform which was suspended by springs from a wooden frame surrounding the lower part of the chamber.

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Figure 2. Experimental cage. $A = piezo-electric crystal$, B and $B' = high slope aluminum guides, C = hollow allow a luminum shaft which$ served as a perch, $D =$ screened portion of cage wall to allow sound pressure waves originating at the source of the acoustic startle stimuli (midrange speaker of 12.5 cm diameter, located directly outside this area of the cage) to enter the cage, $E = hole$ in cage wall to which black cloth sleeve was attached.

Visual Stimulus

A Honeywell Strobonar/400 electronic flash unit, mounted 12 cm above the cage, provided the visual startle stimuli. These consisted of a one msec flash of unfiltered white light (5500 K). The peak intensity of the light flash was 27 ft-Lamberts \pm 10%. The Plexiglas eliminated the small amount of heat generated by the flash. A controlled level of diffuse backround illumination was obtained from a variable intensity lamp which was mounted behind a gauze screen, and built into the ceiling of the inner area of the anechoic chamber. All experiments were conducted with a backround illumination of five ft-Lamberts + 15%.

Auditory Stimulus

The acoustic stimuli originated from a modified Avid Pulser/Mixer-Variable Pitch Tone Burst Generator. This unit provided for control of tone frequency (0 Hz to 16,000 Hz) and duration (3 msec to 30 msec) of the burst of sound. A 2,000 Hz pure tone signal, duration three msec, traveled through a Heath 25 watt amplifier before reaching a midrange speaker of 12.5 cm diameter. The intensity of the sound burst was 123 dB. The attenuation of the burst traveling from the source to the bird inside the cage was two dB to three dB. Thus the actual burst arriving at the birds' heads was close to 120 dB $+$ \vert dB.

Following Hoffman and Fleshler's (1963) suggestion that a backround of steady noise facilitates acoustic startle by masking out random pulses of noise, white noise was added to the low level of ambient noise in the inner chamber. The white noise was generated by an Audiolab random noise generator, and fed through the Heath amplifier to a speaker mounted inside the chamber. This speaker also served as the acoustic stimulus transducer. The combined level of ambient noise and generated white noise inside the cage was 45 dB \pm 1dB.

Data Recording

A single-throw, double-pole visual stimulus switch permitted simultaneous closing of the flash circuit and a 12 volt DC trigger circuit wired to a double-throw, double-pole switch. The Avid

Pulser/Mixer was equiped with a built-in trigger circuit which was also wired to the double-throw, double-pole switch. The common poles of this switch were wired to the starter pickup of a digital timer, and one channel each of a Grass polygraph and Tektronic dual sweep oscilloscope. This design facilitated easy change from auditory to visual stimulus utilization within the system (Fig. 3).

A hollow aluminum shaft of one cm diameter extended along the bottom center of the experimental cage just above the pyramid area. The shaft served as a lightweight perch. It was coated with a sandpaper-like surface to allow perching stability. High slope aluminum guides were fixed to the cage walls over either end of the shaft to ensure that the birds perched only on the shaft's central portion. One end of the shaft was fixed to the cage to allow vertical pivoting freedom. A piezo-electric crystal (Astatic No 751d) was mounted under the free end of the shaft (Fig. 2). The alignment of the crystal was such that its vertical axis was perpendicular to a thin metal plate glued to the bottom of the free end of the perch. Disfiguration of the crystal along its vertical axis resulted in the production of a small ebectric potential. Because the output of the crystal was proportional to the rate at which disfiguration occurred, the device was highly sensitive to the sudden movements involved in startle, but was relatively insensitive to the slower movements involved in the general activity of the birds. The output of the crystal was fed through a fixed frequency filter section (General Radio, type 330: 2,000 Hz). Thus the 2,000 Hz audio startle stimuli were not picked up by the recording apparatus through those channels used to moniter the activity of the birds. The filter's output went to a No 741 operational amplifier (Fig. 3 and Appendix A). This amplified output was then sufficient to trigger ¹¹ stop11 in the digital timing device that had been started by the initiation of the startle stimulus. This design also provided for a visual record of the birds' responses when the crystal's amplified output was recorded on one channel of a Tektronic dual sweep oscil loscope, and one channel on a Grass polygraph. One channel of both recording units was wired to pick up the closing of the startle stimulus circuit, while the other channel received the amplified

crystal output. Thus the birds' activity before, during and after the response could be monitored and recorded, and the temporal position of the stimuli relative to responses unambiguously seen.

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Experimentally naive subjects were placed in the experimental cage and allowed three to five minutes to adapt to the apparatus. Each bird then received a series of auditory or visual stimuli at one to four minute irregular intervals. The auditory and visual tests were run independently, some birds receiving each test series first. Auditory and visual tests for each bird were separated by a period of at least three days. Birds seldom left the perch, but if they did extra adaptation time was allowed by the investigator so that the bird's return to a position on the perch did not initiate the next stimulus. Approximately 8 to 15 trials were made per run, with each run lasting between 30 and 45 minutes. Runs on 18 birds were conducted at various times of the day over a 30 day period.

To determine the effects of environmental influences on the data, three control experiments were performed. The first control experiment consisted of running a complete experimental trial, with no bird in the cage, and examining the polygraph, oscilloscope and timer records for electronic artifacts. The second control experiment included a bird in the cage, but the flash and/or speaker was disconnected so that the closing of the startle stimulus switch resulted in no visible or audible startle stimulus in the cage. The third control was directed to the visual tests. Heppner and Haffner (1973) have suggested the possibility of sensory reception of various electromagnetic stimuli by birds. Thus one possible artifact source might have been that the discharge of the capacitor in the strobelight was acting as a startle stimulus. For the third control experiment the strobe was left connected, but a black glass plate was placed between it and the top of the cage so the light flash did not penetrate to the bird. All control experiments failed to show artifacts on the records.

Figure 3. Schematic of experimental apparatus. $A = \text{variable}$ pitch tone burst generator, $B =$ random noise generator, $C =$ amplifier, $D =$ double-throw, double-pole switch, $E =$ digital readout timer, $F = polygraph$, $G = oscilloscope$, $H = visual stimulus control switch$, $I =$ control switch for variable intensity lamp, $J =$ on/off switch for circuit K, $K = No$ 741 operational amplifier, $L = fixed$ frequency filter sectopn (2000 Hz), $M = piezo$ -electric crystal, $N = electronic$ flash unit, $0 = \text{variable intensity }$ lamp, $P = \text{midrange }$ speaker.

RESULTS

Results of auditory and visual trials for all birds tested are shown in Table |. The unequal number of observations for each bird was the result of the observation that not all birds reacted in a similar manner to confinement in the chamber. Some birds habituated to the stimuli, and others became hyperactive after varying lengths of confinement. The standardized frequency distributions of RTs to 1 ight and to auditory stimuli are shown in Figures 4 and 5 respectively.

Startle reaction times to light flash stimuli for 18 Starlings are shown in Figure 6. The mean of the means and mean standard deviation (SD) for the latencies for all birds were 76.65 msec (range 66 .93 msec to 85.37 msec) and 13.23 msec (range 6.65 msec to 21.54 msec) respectively. The grand mean was 76.38 msec, with a SD of 15.32 msec. The variance within individual birds' performances on different trials was greater than the variance between mean RTs of different birds (F.025 (17,198) = .15; F.025 critical = .48). No significant difference between mean RTs of birds to light stimuli was found $(F.95 (17.198) = 1.69)$.

Reaction times to auditory stimuli for 12 Starlings are shown in Figure 7. The absence of auditory trials for six birds is a result of the deaths of four individuals before tests could be performed, and the dismissal due to high irregularity in results of two birds. The mean of the means and SD of the latencies for all birds were 80.76 msec {range 68.59 msec to 88.97 msec) and 14.02 msec (range (0.28 msec to 22.55 msec) respectively. The grand mean was 80.64 msec, with a SD of 14.48 msec. The variance within individual birds' performances was again greater than the variance between mean RTs of different birds $(F.025 (11.132) = .21$; $F.025$ critical = .43). A significant difference between mean RTs

of birds was found $(F.95 (11,132) = 2.3)$. This difference was not significant at the .01 level however.

Type of stimulus had a small but significant effect on **RT** (t.95 (360) = 2.6; t.95 critical = 1.65). Mean **RT** to visua l stimuli was 4.3 msec faster than to auditory stimuli.

TABLE I

Startle reaction times, in msec, of birds A through R to auditory and visual stimuli. The mean (upper) and standard deviation (lower) of the trial values in each collum are listed slightly below that collum.

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TABLE I (CONT'D)

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Figure 4. Frequency distribution of reaction times of 18 Starlings (Sturnus vulgaris) to light flash stimuli. Frequency of occurrance (ordinate) is plotted against RTs falling within five msec intervals (abscissa).

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Figure 5. Frequency distribution of reaction times of 12 Starlings (Sturnus vulgaris) to sound burst stimuli. Frequency of occurrance (ordinate) is plotted against RTs falling within five msec intervals (abscissa).

Figure 6. Distribution of mean reaction times of 18 Starlings (Sturnus vulgaris) to light flash stimuli. Individual birds are represented by the letters A through R. The number below the letter code for bird is the number of trials for that bird. The vertical line represents the range of RT values. The rectang le extends over one standard deviation from the mean RT value, which is represented by the hash mark across each vertical line.

RT IN MSEC

Figure 7. Distribution of mean reaction times of 12 Starlings {Sturnus vulgaris) to sound burst stimuli. Individual birds are represented by the letters A through L. The number below the letter code for bird is the number of trials for that bird. The vertical line represents the range of RT values. The rectangle extends over one standard deviation from the mean RT value, which is represented by the hash mark across each vertical 1 ine.

DISCUSSION

The frequency distributions of RTs to both auditory and visual stimuli are skewed to the left (Fig. 4 and Fig. 5). Inspection of Figures 6 and 7 confirms that no particular bird, or birds are responsible for the slower RTs resulting in this pattern of distribution. Rather, the data for each bird yields skewed distributions of RTs. Learning, or any trial dependent effect on RT was not demonstrated by regression analyses performed with RTs of each bird dependent on trials. A probable explanation for the skewed distributions is the observation that the left most part of the distribution represents the physiological limit for minimum RT. The large within bird variance can then be interpreted as a result of birds not always responding at this minimum limit, with many responses slower, and some responses considerably slower than minimum.

It has been shown in studies involving humans that reaction time to light flash stimuli is determined by exposure to an extremely brief burst of luminous energy, and that for luminances over 300 ft-Lamberts, reaction time is unrelated to duration of the flash (Rabb and Fehrer. 1962). For very low levels of luminance (three ft-Lamberts), duration has a marked effect on RT, with RT being a function of flash briefness. Rabb and Fehrer (1962) found only a 5% increase in RT when flash duration was reduced from five msec to one half msec if they used a moderately intense flash stimulus (30 ft-Lamberts). Because of the medium intensity of the flash utilized in the present experiments (27 ft-Lamberts), it is possible that the one msec light flash stimulus was not of sufficient duration to obtain absolute minimum RTs from the birds. As there was no significant difference between the mean RTs of different birds to light stimuli, the mean of the means (76.6 msec) is assumed as a representative figure $(+5\%)$ for the mean RT of Starlings to light flash stimuli.

Thorpe (1963) recorded duetting bird songs in the field. He assumed that the birds were equidistant from the microphone, and estimated this distance to be between 10 and 20 meters. Incorporating the speed of sound with possible distance errors encountered, Thorpe predicted the true mean RT of the birds recorded to be between 90 msec and 135 msec (minimum RTs between 70 msec and 116 msec), with a SD of 12.6 msec. The results reported here for auditory RTs are in close agreement with the estimates of avian auditory RT proposed by Thorpe.

Fleshler (1965) concluded that startle reaction in the rat is invariant over a wide range of stimulus durations. The time at which the stimulus reaches and remains at peak intensity is critical only in that it occurs in an initial critical period, 12 msec in the rat. This initial period is equal to, or less than, the RT minus the time for neural transmission involved in the perception of stimulus and evocation of response. In the rat, the initial period is about 75% of the total RT (Fleshier, 1965). The RT values obtained in the present experiments wou ld yield an initial period of over 75% of the total RT. Theref6re, the acoustic bursts of three msec duration reached peak intensity well within the probable limits necessary to elicit minimum or near minimum startle reaction times.

Startle response latency for rats as determined by Fleshler (1965), Hoffman and Searle (1963), and Landis and Hunt (1939), is approximately four to five times faster than that obtained for birds in this investigation. Fleshier (1965) makes a conservative estimate that 25% of the total RT to acoustic startle stimuli in the rat is involved in the time required for neural transmission. Investigations of neural transmission rates of nerve fibers in mammals (Prosser and Brown, 1966) has shown that mylinated fibers transmit impulses at 100 to 120 m/sec (large diameter fibers), and 25 to 50 m/sec (small diameter fibers). Birren and Wall (1956) reported a conduction velocity of 60 m/sec in the rat. One would seemingly have to assume a slower rate of transmission, or a proportionally longer distance of travel, or a combination of both in birds, to account for the longer latency of response. Graf (1956), investigating representative sections of the peripheral nervous system in the Rock Dove (Columba livia), reported an absence of larger

diameter fibers. Sturkie (1965) concludes from this observation that the conduction velocities of nerve fibers should be less in birds than in mammals. Investigations of conduction velocity of nerve impulses in chickens would support this hypothesis (Carpenter and Bergland, 1957). No data on conduction velocity of impulses in Starlings is presently available. However, using Carpenter's measure of 40 m/sec, and assuming an approximately equal distance of impulse travel as that estimated by Fleshier (1965) for in the rat, a time of six msec ut ilized for nerve transmission is calculated. This represents only 8% of the total startle response time of Starlings to auditory stimuli. This suggests that differences in nerve conduction velocity and distance of impulse travel may account for as little as 12% of the observed increase in RT seen in birds.

Hoffman and Searle (1963) suggested that the organization of startle occurs in some specific brain center, and it is the level of activity of this center that determines the elicitation of startle by the individual, and the brevity of response time. Differences in the functioning of a center such as this could account for the increase in RT noted. Circumstantial evidence {Pomeroy, unpublished) has indicated that birds may be able to maintain two discrete functioning levels of this center, and thus respond to the same stimuli at very different rates.

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The closed loop gain for an operational ampplifier with sufficiently high open loop gain is equal to R_1/R_2 . For the described bird stimulus detector, a No 741 operational amplifier was used. The open loop gain condition is fulfilled with this unit. The following values for R₁ and R₂ were chosen for the experiment: $R_1 = 500 K$, $R_2 = 5 K$. The gain is therefore 100. This is adequate to register the signal from the crystal at the noninverting input·

APPENDIX B

ANOV for reaction times of 18 Starlings to light flash stimuli.

ANOV for reaction times of 12 Starlings to sound burst stimuli.

