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CONDITIONED SUPPRESSION TO ODOROUS STIMULI IN PIGEONS[1,2]

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The conditioned suppression technique was employed to establish criterion discrimination of an amyl acetate concentration of 3% of vapor saturation, and to generate differential response rates in the presence of equal concentrations of amyl acetate and butyl acetate. The magnitude of suppression was also recorded as a function of amyl acetate concentration, with the concentrations presented in descending, ascending, and irregular series. The three stimulus presentation procedures generated approximately equivalent suppression *versus* concentration functions. Amyl acetate suppression thresholds were 0.16%, 0.50%, and 0.73% of vapor saturation for three subjects. Amyl acetate, butyl acetate, and butyric acid thresholds for two additional subjects were approximately 0.10% of vapor saturation. No suppression was recorded during control trials.

Anatomical descriptions of the olfactory organs of birds indicate that all birds have an olfactory epithelium and an olfactory bulb (Marshall, 1960). Electrophysiological data on the responses of small peripheral twigs of olfactory nerves indicate that the olfactory receptors of birds are functional (Tucker, 1965). Although the necessary anatomical and neurophysiological characteristics are present, most previous data indicated that birds have no behavioral olfactory sensitivity. In separate series of experiments, Walters (1943) and Neuhaus (1963) investigated odor discrimination in various species of birds, and reported no change in the frequency of instrumental responses when odor was paired with food, contaminated food, contaminated water, or electric shock. Calvin, Williams, and Westmoreland (1957) conditioned an avoidance response to the simultaneous presentation of light and perfume. Subsequent trials with perfume alone failed to elicit the response.

Two recent studies, however, indicated that pigeons can respond in a discriminative manner to odorous stimuli. In a three-key operant experiment, Michelsen (1959) reinforced the responding of two pigeons on one key with odor present and on a second key with odor absent. Sessions with unspecified concentrations of sec-butyl acetate and iso-octane yielded a mean of approximately 45 correct trials out of 50, as against a mean of 25 to 30 correct trials during control sessions. Henton, Smith, and Tucker (1966) trained pigeons to criterion conditioned suppression using amyl acetate concentrations of either 5% or 6% of vapor saturation as the suppression stimulus. In the further training of one subject, an amyl acetate concentration of 0.2% of vapor saturation reliably evoked suppression. Sectioning the olfactory nerves eliminated the selective suppression to the low amyl acetate concentrations in all subjects. However, the suppression was again conditioned when the concentration was increased to 15% of vapor saturation.

These two experiments, using a total of five subjects, suggest that pigeons can discriminate the presence and absence of a single odor. The purpose of the present experiment was to determine if pigeons can discriminate between two physically similar odors. Amyl acetate

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and butyl acetate, which have been described as the two most similar odorants (Moncrieff, 1956) were employed as the discriminative stimuli. An additional purpose of this study was to examine odor discrimination thresholds in pigeons to amyl acetate, butyl acetate, and butyric acid. These odorants embrace a 10-fold range in vapor pressure, and have been employed in electrophysiological (Tucker, 1963) and human threshold (Mullins, 1955) studies. The conditioned suppression procedure has been employed as a technique for threshold determinations in vision (Hendricks, 1966; Powell, 1966), audition (Dalton, 1966), olfaction (Henton *et al.*, 1966) and X-ray detection (Morris, 1966). All of these investigations have used a descending series of stimulus intensities and a modified method of limits. The present experiment was designed to compare the reliability of the suppression threshold, and the general suppression *versus* intensity function, as determined by a descending, an ascending, and an irregular stimulus presentation procedure.

METHOD

Subjects

Four White Carneaux pigeons and one homing pigeon were used. Three of the White Carneaux, approximately six weeks of age at the start of the experiment, and the homing pigeon, #608, of unknown age, were experimentally naive. The other Carneaux, #01, was approximately 2 yr of age and had been previously employed in a visual flicker fusion suppression threshold study. The subjects were independently housed and maintained at approximately 70% of their free-feeding body weights. Water and grit were freely available.

Apparatus

The odorant delivery system was a modification of that designed by Tucker (1963). Laboratory compressed air was passed through a pressure-reduction valve maintained at about 2.5 lb/in.^{2}. The air was then diverted into three channels, cleaned with silica gel and activated cocoanut shell charcoal, and saturated with either distilled water, amyl acetate, butyl acetate, or butyric acid. All gas washing bottles containing the materials were immersed in a constant temperature water bath maintained at approximately 25° C. The flow volume of the vapor-saturated air from each channel was measured by a bank of Fischer-Porter Tri-Flat Flowmeters and controlled by a series of Teflon needle-valve stopcocks. A series of manually operated stopcocks and converging joints subsequent to the flow meters permitted the mixing of air from the odor channels with that of the continuously flowing wash channel. A monitor channel was used to set the needle-valve stopcocks before each trial.

A standard Foringer pigeon box was modified to house the glass breathing chamber (Henton *et al.*, 1966). This chamber was a truncated cylinder 8-in. long and 3.5 in. to the rear wall, with funnel-shaped intake and exhaust ports at either end. Perforated discs within the ports dispersed the air more uniformly within the chamber. On the face of the chamber, a 4-in. by 2.5-in. opening permitted the subject access to the pigeon key and grain hopper mounted behind openings in the glass rear wall. A plywood box, 4.5 ft by 2 ft by 2.5 ft, was lined with acoustical tile and housed the unit. A "white" masking noise was presented through a 4-in. speaker mounted 9 in. above the subject. All scheduling was done with a conventional system of electrical switching circuits. Chronic stainless steel electrodes were implanted around the pubis bones of each subject to deliver the electric shock (Azrin, 1959).

Procedure

In the presence of a flow rate of 97 cm^3/sec of air saturated with distilled water, each subject was trained to place its head inside the breathing chamber and peck the key. Reinforcement was the presentation of the grain hopper for 3.0 sec. The schedule of reinforcement was advanced from continuous reinforcement through a series of increasing variable-ratio schedules (Ferster and Skinner, 1957) over successive 1-hr sessions. After a high rate of responding was exhibited on variable-ratio 40, the schedule was changed to a variable-interval 1 min. The variable-interval schedule was increased in 10-sec increments over each succeeding session, terminating in a Fleshler-Hoffman 16-term variable-interval 2-min schedule (Fleshler and Hoffman, 1962). This geometric schedule was employed to generate stable baseline response rates, and provided reinforcement of responses on the average of once every 2 min.

After baseline responding had stabilized, as determined by the formula given by Schoenfeld, Cumming, and Hearst (1956), suppression training was begun. During each session, 10 suppression trials, 10 zero-concentration control trials, and five baseline control trials were randomly interspersed. Trials were initiated during interreinforcement intervals greater than 60 sec, with the initiation of a trial at least 15 sec after reinforcement and the termination of a trial at least 20 sec before reinforcement. Thus, reinforcement was unavailable during all trials, and the intertrial interval varied from 35 to 300 sec. All trials were 18 sec in duration. A suppression trial consisted of introducing 3 cm^3/sec of air saturated with amyl acetate to the continuously flowing air stream for the 18-sec period. All suppression trials were terminated by an 85 msec, 100-v, ac shock delivered through 10 K ohms resistance to the subject. Zero-concentration control trials (air control trials) consisted of the addition of 3 cm^3/sec of air saturated with distilled water to the continuously flowing air stream. Baseline control trials consisted of recording the number of responses emitted in an 18-sec interval. The response rate during each trial was compared to the response rate in the immediately preceding 18-sec interval by using the suppression ratio of

$$\frac{\text{(Pre-trial responses)} - \text{(Trial responses)}}{\text{(Pre-trial responses)}}$$

(Hoffman *et al.*, 1963). Using this ratio, equal response rates in the two periods, which should be approximated during zero-concentration control trials and baseline control trials, would produce a suppression ratio of 0.00. Complete absence of responding during a trial would produce a ratio of 1.00. All subjects were trained to a criterion of suppression stability of three consecutive sessions with a mean suppression ratio of 0.90 or greater to the odorous stimuli.

Discrimination of Amyl Acetate and Butyl Acetate

For three subjects, five nonshock trials with a butyl acetate concentration of 3% of vapor saturation were randomly presented each session, in addition to the 10 amyl acetate suppression trials, 10 zero-concentration control trials, and five baseline control trials. Training was continued until the mean suppression ratio during amyl acetate trials was 0.90 or greater, while the mean suppression ratio during butyl acetate trials was less than 0.10, for two consecutive sessions.

Amyl Acetate Suppression Thresholds

As preliminary training, 12 suppression trials, 10 zero-concentration control trials, and five baseline control trials were randomly presented each session. An amyl acetate concentration of 3% of vapor saturation was used as the suppression stimulus. To examine the effects of shock omission on one trial upon subsequent suppression trials, eight of the 12 suppression trials were terminated by shock for Subjects #01, 9, and 12, and 11 of the 12 suppression trials were terminated by shock for Subjects #3 and 608. Each subject was trained to criterion stabilization of the suppression ratio on the intermittent shock schedule. Stabilization was defined as three consecutive sessions with a mean suppression ratio of 0.90 or greater to the amyl acetate stimulus. Subjects #01, 9, and 12 were then employed in the descending and ascending training series, and Subjects #3, 9, and 608 were subsequently employed in the irregular stimulus presentation series.

Descending Series

Four amyl acetate concentrations were each presented in a block of three trials per session, with the concentrations presented in a descending sequence. Stimulus increments of 0.2% of vapor saturation were employed throughout training. Stimulus concentrations were reduced over sessions in non-overlapping sets of four concentrations until an odorant concentration was presented which yielded a mean suppression ratio of less than 0.50.

Ascending Series

Within each session, one block of three trials at each of four stimulus concentrations were presented, with the stimuli presented in an ascending order. The concentration for the first block of trials was that found to elicit suppression less than 0.50 during the descending series. The concentration was then increased by 0.2% of vapor saturation for each of the three remaining blocks of trials per session.

During the descending and ascending training series, any two of the three trials per concentration were terminated by shock, independent of the degree of suppression.

Irregular Series

Subject #9 was returned to the preliminary threshold training schedule and again trained to criterion suppression to an amyl acetate concentration of 3% of vapor saturation. For Subjects #3, 9, and 608 each of four odorant intensities in increments of 0.2% of vapor saturation were then randomly presented within each session. Each stimulus intensity was presented three times per session. For Subject #9, any two of the three trials per concentration were terminated by shock, independent of the degree of suppression. For Subjects #3 and 608, 11 of the 12 suppression trials per session were terminated by shock, with the one nonshock trial randomly assigned to stimulus concentrations over sessions. A lower set of four concentrations were presented over each succeeding session, until a reduced concentration was presented which evoked a mean suppression ratio of less than 0.50.

Butyl Acetate and Butyric Acid Thresholds

Subjects #3 and 608 were returned to the preliminary threshold training schedule, with a butyl acetate concentration of 3% of vapor saturation employed as the suppression stimulus. After criterion stabilization of the suppression, the butyl acetate threshold was determined by the irregular stimulus presentation procedure. The subjects were returned to the preliminary threshold training schedule and trained to criterion suppression to a butyric acid concentration of 3% of vapor saturation. The butyric acid threshold was also determined by the irregular stimulus presentation procedure.

During training with all procedures and odorants, if a subject had a mean suppression ratio of 0.50 or greater to the 0.2% of vapor saturation stimulus, the concentration was subsequently reduced to 0.1%, and, if necessary, to 0.05% of vapor saturation, until a concentration was presented which yielded a mean suppression ratio of less than 0.50. After initial determination of the threshold, the threshold suppression *versus* concentration function under each procedure was replicated over three additional sessions for each subject. The same terminal set of four odorant intensities was presented in each threshold replication session.

RESULTS

The suppression to the 3% amyl acetate concentration generally increased over sessions, though not monotonically, for each subject. The number of trials to criterion suppression for Subjects #01, 3, 9, 12, and 608 were 40, 190, 90, 220, and 110, respectively. The acquisition of the suppression was found to be most rapid in Subject #01, which had previously been trained to suppress to a flickering light.

Discrimination of Amyl Acetate and Butyl Acetate

Figure 1 presents the mean suppression ratio per session during the acquisition of the discrimination of amyl acetate and butyl acetate for each subject. Subject #01 showed immediate discrimination of amyl acetate and butyl acetate, as demonstrated by the different suppression ratios elicited by the amyl acetate and butyl acetate stimuli. The suppression elicited by the amyl acetate was initially diminished, dropping to a mean suppression ratio of 0.82 during the first session. Over subsequent sessions, the suppression of key pecking increased during amyl acetate presentations and decreased during butyl acetate presentations, with criterion discrimination recorded after five sessions. The introduction of the five nonshock trials with the 3% butyl acetate concentration also decreased the suppression to the amyl acetate stimulus by Subject #12 during the second through fourth sessions. Concurrently, the suppression behavior generalized to the butyl acetate stimulus throughout the first two sessions. The effect of the differential shock contingency was clearly established by the third session, with the mean suppression ratio elicited by the butyl acetate dropping to less than 0.10 by the fifth session. For Subject #9, the suppression behavior generalized to the butyl acetate stimulus through eight sessions, with no concurrent decrease in the mean suppression elicited by the amyl acetate stimulus until the fifth session. Not until the ninth session was

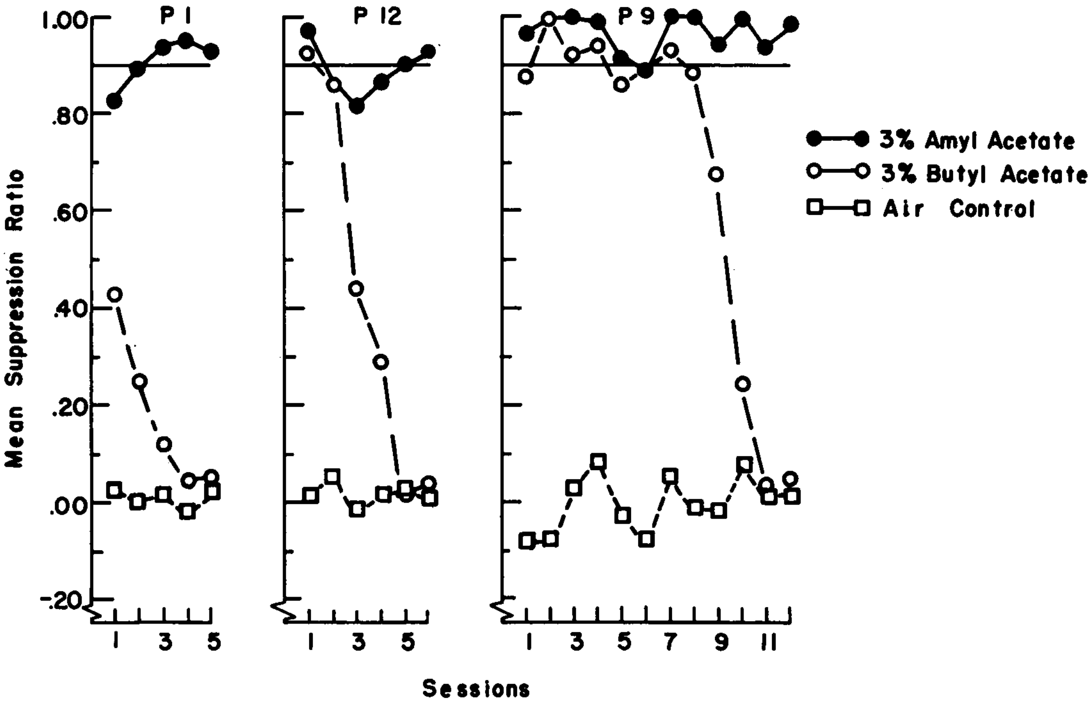

Fig. 1. Performance of three subjects during discrimination training with amyl acetate and butyl acetate concentrations of 3% of vapor saturation at 25° C. All subjects were trained to the discrimination criterion, with 10 amyl acetate suppression trials, five butyl acetate trials, 10 zero-concentration (air control) trials, and five baseline control trials (not shown) per session.

differential responding recorded during the presentation of the two stimuli.

Amyl Acetate Suppression Thresholds

Figure 2 presents the suppression performance of Subject #12 as the amyl acetate concentration was reduced over sessions during the descending stimulus presentation procedure. Suppression ratios of approximately 0.90 were reliably elicited by all amyl acetate concentrations down to 0.4% of vapor saturation. The transition from high suppression ratios to suppression ratios less than 0.50 covered an odorant intensity range of 0.4% to 0.1% of vapor saturation, with the 0.2% concentration eliciting suppression ratios ranging from 0.65 to 0.75. The transition from high to low suppression ratios in the remaining subjects occurred at higher amyl acetate concentrations, covering a range of 1.0% to 0.6% and 0.8% to 0.4% of vapor saturation for Subjects #01 and 9, respectively.

Table I presents the suppression ratios recorded on each of the three trials per concentration during the last four descending training sessions, the four subsequent ascending training sessions, and, lastly, the last four irregular training sessions for Subject #9. For all subjects, the suppression at each amyl acetate concentration was approximately equivalent and quantitatively reproducible both within and across the descending training sessions. The range in the suppression ratios increased with decreasing stimulus intensity, with the greatest range recorded for the lowest amyl acetate concentrations. In spite of this increasing variability with decreasing amyl acetate concentration, the suppression ratios elicited by the subthreshold concentrations was always less than that elicited by any of the higher concentrations. To determine the odor threshold, the three suppression ratios for each concentration were averaged and the threshold estimated by linear interpolation for the 0.50 suppression ratio. The amyl acetate suppression thresholds for Subject #9 were 0.53%, 0.48%, 0.52%, and 0.48% of vapor saturation for the first through the fourth descending threshold sessions respectively.

Table II presents the mean amyl acetate threshold over the four sessions, the range in threshold over the four sessions, and the range

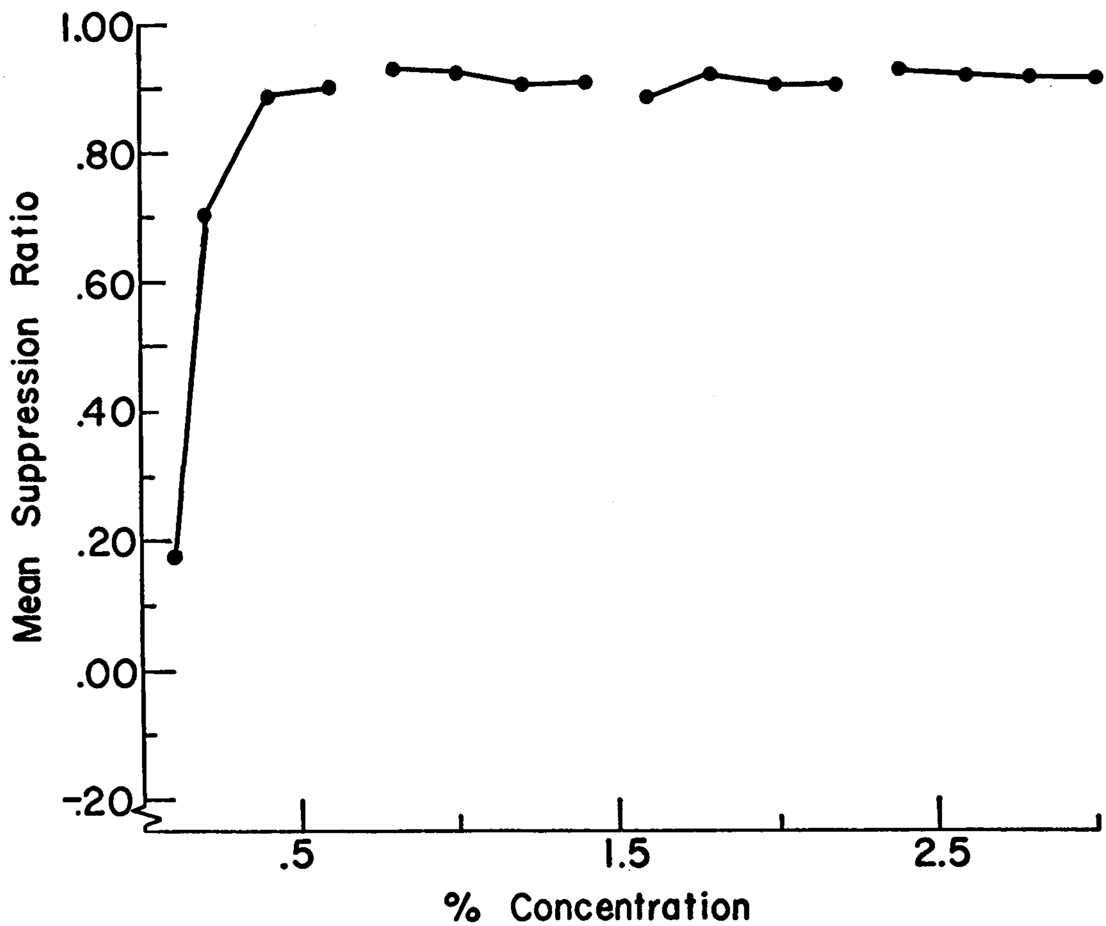

Fig. 2. Initial determination of the amyl acetate suppression threshold–with descending stimulus presentation for Subject 12. Concentration is in terms of vapor saturation at 25° C. Each data point represents the mean of three suppression trials. Zero-concentration control trials and baseline control trials are not shown.

divided by the mean threshold, for each subject and each stimulus presentation procedure. During the ascending stimulus presentation procedure, the stability of the suppression behavior at each stimulus concentration replicated that found during the descending series for each subject. The variability in the suppression ratio was again found to be inversely related to stimulus concentration, with the suppression elicited by a given concentration quantitatively reproducible within and across ascending training sessions. As described in Table I, the reliability of the suppression ratio, and the general suppression *versus* concentration function, was approximately identical under both stimulus presentation procedures. The difference between the mean descending and ascending amyl acetate thresholds was less than 0.004% of vapor saturation for each subject. The range in the session threshold values over the four ascending threshold sessions was, however, slightly greater than over the four descending sessions for Subjects #01 and 12.

The performance of Subjects #3, 9, and 608 during the irregular stimulus presentation procedure was similar to that found when the stimulus concentration was reduced during the descending training series with Subjects #01, 9, and 12. As the stimulus concentration was reduced from 3.0% of vapor saturation, the suppression remained at approximately 0.90 for all subjects until a concentration of 0.6% of vapor saturation was presented to Subject #9, and 0.2% was presented to Subjects #3 and 608. At these values the suppression decreased and became more variable, ranging from 0.59 to 0.80. Further decrease in the amyl acetate concentration elicited more variable suppression of less than

Table I

Suppression ratios recorded for Subject #9 on each suppression trial during training with descending, ascending, and irregular stimuli procedures.

Per Cent of Vapor Saturation	*Descending Session*				*Ascending Session*				*Irregular Stimuli Session*			
	1	*2*	*3*	*4*	*1*	*2*	*3*	*4*	*1*	*2*	*3*	*4*
1.0	0.90	0.90	0.87	0.94	1.00	1.00	0.93	0.91	1.00	0.97	0.90	0.98
	0.90	0.86	0.88	0.87	0.88	0.91	0.97	0.90	1.00	1.00	0.95	1.00
	0.89	0.88	0.86	0.84	0.91	0.89	0.92	0.94	1.00	1.00	0.91	0.88
0.8	0.86	0.79	0.79	0.82	0.78	0.86	0.90	0.89	0.97	0.94	0.85	0.84
	0.83	0.82	0.79	0.92	0.90	0.88	0.86	0.84	0.94	0.85	0.87	0.89
	0.81	0.87	0.88	0.64	0.75	0.81	0.89	0.89	0.89	0.90	0.71	0.90
0.6	0.64	0.59	0.62	0.60	0.86	0.71	0.74	0.71	0.67	0.67	0.74	0.62
	0.78	0.88	0.76	0.60	0.64	0.69	0.67	0.71	0.78	0.70	0.73	0.79
	0.58	0.60	0.56	0.72	0.80	0.77	0.71	0.73	0.79	0.73	0.64	0.74
0.4	0.29	0.48	0.44	0.42	0.06	0.00	0.42	0.21	0.19	0.45	0.38	0.35
	0.24	0.49	−0.09	0.47	0.32	0.00	0.33	0.20	0.38	0.43	0.35	0.42
	0.04	0.19	0.47	0.29	0.36	0.35	0.35	0.43	0.32	0.28	0.39	0.32
0.0	−0.24	0.00	0.06	0.05	0.06	0.08	0.04	0.11	0.00	−0.12	0.00	−0.02
(Control)	−0.06	0.18	−0.09	−0.14	−0.05	0.11	0.21	−0.03	−0.05	−0.19	−0.07	0.13
	0.10	−0.10	0.06	0.07	0.09	0.11	−0.08	−0.09	−0.21	0.15	−0.02	0.00
	0.03	0.06	−0.24	0.17	−0.24	−0.15	−0.17	0.00	0.06	−0.15	0.13	0.05
	0.07	0.15	0.12	0.00	−0.10	0.06	−0.12	0.09	−0.05	0.12	0.00	−0.08

0.50. As seen in Table I, the suppression ratios recorded at a given amyl acetate concentration during the irregular stimulus presentation procedure were relatively equivalent in magnitude and reliability to the suppression during the descending and ascending stimulus presentation procedures.

Table III compares the response rate of each subject during each of the 18-sec pre-trial periods and the 18-sec trial periods during the last amyl acetate threshold training session under each stimulus presentation procedure. As the suppression ratios decreased with decreasing stimulus concentration, the baseline response rate remained relatively unchanged, as shown by the similar response rates during the 18-sec pre-trial periods throughout the session. Thus, pairing of shock with stimuli which did not elicit high suppression ratios did not disrupt the baseline response rates of any subject under any procedure. Subjects #3 and 608 were trained with a less intermittent shock schedule which resulted in a greater frequency of shock pairings with stimuli eliciting low suppression ratios. The baseline response rates of Subjects #3 and 608 were similarly undisrupted by shock presentation in the absence of a stimulus eliciting high suppression ratios.

Butyl Acetate and Butyric Acid Thresholds

In Fig. 3, the mean suppression ratios elicited by each concentration of butyl acetate and butyric acid are compared to the mean

Table II

Mean threshold, range in threshold, and per cent mean threshold of range in threshold, expressed in per cent of vapor saturation.

Subject No.	*Descending Series*			*Ascending Series*			*Irregular Stimuli Series*		
	Mean	*Range*	*% Range*	*Mean*	*Range*	*% Range*	*Mean*	*Range*	*% Range*
12	0.16	0.01	7.3	0.16	0.05	32.0			
9	0.50	0.05	10.0	0.50	0.05	10.0	0.47	0.02	4.9
01	0.73	0.01	0.96	0.73	0.10	13.7			
3							0.16	0.03	16.6
608							0.16	0.04	24.5

Table III

Comparison of response rates during each 18-sec trial with response rates in the immediately preceding 18-sec period for the last session of descending, ascending, and irregular stimulus presentation for each subject.

Per Cent of Vapor Saturation	Subject #01		Subject #9			Subject #12	
	Descending	Ascending	Descending	Ascending	Irregular	Descending	Ascending
1.2	36/3	33/3					
	*34/6	34/6					
	36/4	*33/6					
1.0	30/4	*30/4	34/2	35/2	44/1		
	35/6	30/8	37/5	*30/3	40/0		
	*37/3	32/4	*32/5	36/13	*33/4		
.8	33/10	34/17	34/6	*36/4	43/7		
	36/10	*31/14	*36/3	31/5	36/4		
	*34/10	28/11	36/13	36/4	*39/4		
.6	30/28	*32/31	35/14	30/8	42/16	24/1	34/2
	*31/26	25/21	43/17	*31/9	*43/9	*26/1	*30/2
	37/33	33/35	*43/12	38/30	37/24	32/3	26/3
.4			36/21	28/16	43/28	27/2	33/3
			*38/20	*35/28	48/28	28/2	*29/2
			34/24	38/30	*37/24	*32/3	26/3
.2						28/11	*25/4
						*28/10	29/8
						33/8	*32/10
.1						33/30	32/25
						32/25	26/23
						*24/21	28/22
0.0	29/30	28/30	43/41	28/25	43/44	34/31	36/30
	32/29	33/27	37/42	33/32	46/40	26/29	30/30
	27/24	32/27	41/38	34/37	36/36	27/28	32/36
	30/32	28/27	41/34	35/35	39/37	29/30	28/29
	28/25	36/39	30/30	34/31	36/33	32/30	32/28

*Denotes trials which followed non-shock suppression trials.

suppression ratios elicited by similar concentrations of amyl acetate for Subject #608. For both subjects, the suppression behavior recorded during the butyl acetate and butyric acid threshold training sessions was similar to that described in Table I. That is, a given odorant concentration reliably elicited quantitatively similar suppression ratios within and across sessions, with increasing variability in the suppression ratios with decreasing stimulus intensity. The mean discrimination thresholds for butyl acetate and butyric acid, in terms of vapor saturation, were 0.09% and 0.09%, respectively, for Subject #3, and 0.16% and 0.15%, respectively for Subject #608. The range in the butyl acetate and butyric acid threshold values over the four threshold training sessions were 0.08% to 0.11% and 0.08% to 0.11% of vapor saturation respectively for Subject #3, and 0.15% to 0.17%, and 0.12% to 0.18% of vapor saturation, respectively, for Subject #608.

For all subjects, the mean suppression recorded during zero-concentration control trials and baseline control trials remained at approximately 0.00 throughout the experiment.

DISCUSSION

The suppression of food-reinforced behavior during odor stimulation periods, and the absence of differential responding during the baseline control trials and the zero-concentration control trials, indicated that each subject was discriminating the presentation of the odor stimuli. Additional artifact controls consisted of replacing and interchanging components within the olfactometer and of presenting the odor stimuli through either or both of

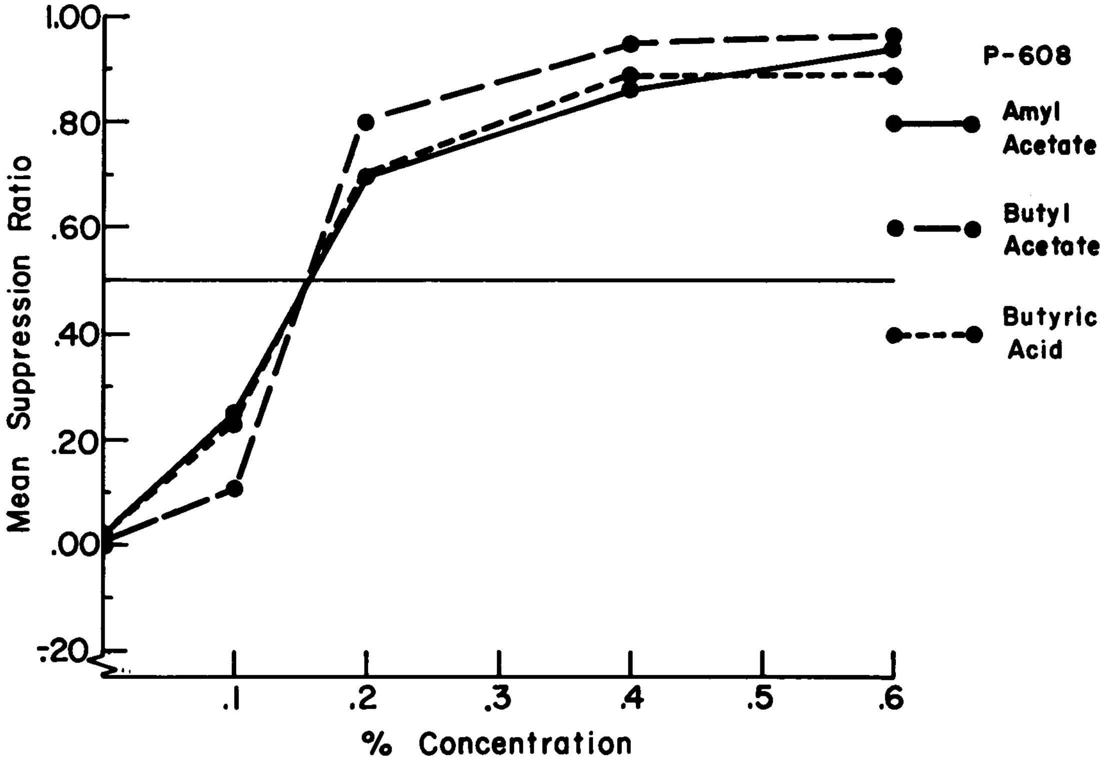

Fig. 3. Comparison of mean suppression ratios elicited by equivalent concentrations, in terms of per cent of vapor saturation at 25° C, for amyl acetate, butyl acetate, and butyric acid in Subject #608. Each data point represents the mean of 12 suppression ratios, except the data plotted at zero concentration which represents the mean of 20 zero-concentration control trials.

the odor channels. In all cases, the presentation of odor elicited the suppression while the presentation of an equivalent volume of air saturated with distilled water failed to elicit the suppression. Henton *et al.* (1966) trained pigeons to suppress ongoing food-reinforced behavior during the presentation of an amyl acetate concentration of 5% or 6% of vapor saturation. The present results indicate that an amyl acetate concentration of 3% of vapor saturation is an effective stimulus for the acquisition of the behavioral discrimination.

At the outset of differentiation training, some initial generalization of the suppression behavior to the butyl acetate stimulus occurred during the first few sessions. However, this lack of discrimination was gradually replaced over trials by differential responding in the presence of the two stimuli. With the performance at the criterion level, the suppression ratios elicited by the butyl acetate stimulus were less than 0.10 and equal to the suppression ratios elicited during zero-concentration control trials. Thus, with training, the subjects were discriminating between the suppression stimulus and the differential stimulus as readily as they were discriminating between the presence and absence of the suppression stimulus. With reference to the development of the olfactory organs of birds, Bang (1960) described the pigeon as being "feebly equipped". The present behavioral data suggest that the pigeon is able to perform in a discriminatory manner while in the presence of two similar odors of equal partial vapor pressures, as well as discriminating between the presence and absence of a single odor. That the subjects were able to discriminate between two neighboring members of the acetate ester series suggest that the pigeon is capable of making more subtle behavioral odor discriminations than previously described. Whether this discrimination of amyl acetate and butyl acetate is a quality or an apparent intensity discrimination is yet to be determined. However, subsequent data (Shumake, in press) indicated that odor intensity discrimination is relatively poor in pigeons. Using a conditioned suppression technique, pigeons were trained to discriminate between the presentation of amyl acetate concentrations of 7% and 1% of vapor saturation. The subjects continued to discriminate between the amyl acetate concentrations as the lower concentration was increased to 2% of vapor saturation. However, no differential responding was recorded during the presentation of the two stimuli when the concentrations were 7% and 3% of vapor saturation. These data would then suggest that the discrimination of equal fractions of vapor saturation of amyl acetate and butyl acetate may be a quality odor discrimination rather than an apparent intensity odor discrimination.

The amyl acetate threshold data evidenced considerable intersubject differences, ranging from 0.16% to 0.73% of vapor saturation. However, the intrasubject variability in suppression thresholds was quite low for all subjects within and across training procedures, as shown in Table II. The wide intersubject threshold differences may reflect inequities in the behavioral control across subjects in spite of the apparent similarity and low variability in the behavioral thresholds. However, the uncontrolled factors affecting odor discrimination may be more basic to the observed differences. The magnitude of neural activity recorded from primary olfactory nerves is dependent upon nasal flow rate as well as odorant concentration and odorant species (Tucker, 1963). The rate of respiration effectively controls the presentation of the odorous stimuli to the olfactory receptors, with the rate of respiration varying from approximately 30 to 50 respirations per minute in pigeons. Additionally, nasal constriction and nasal dilation, affecting the accessibility of the olfactory receptors to the odorous stimuli, are both under the control of the autonomic nervous system (Tucker, 1963). An equally reasonable speculation, therefore, is that the observed differences in the amyl acetate thresholds are dependent upon individual differences in nasal flow rate, respiration rate, and receptor accessibility.

Mullins (1955) reported that the olfactory thresholds in humans to odorants of various vapor pressures, including amyl acetate and butyric acid, were commonly 10^{-3}, or 0.1% of vapor saturation. Tucker (1963) described the threshold response of peripheral olfactory nerves as being approximately 0.1% of vapor saturation for amyl acetate in the gopher tortoise. Similarly, the amyl acetate, butyl acetate, and butyric acid thresholds of Subjects #3 and 608 were approximately 0.1% of vapor saturation. For Subject #3, the amyl acetate thresholds were higher than either the butyl acetate or the butyric acid thresholds, whereas for Subject #608 the amyl acetate threshold was equal to the butyl acetate and butyric acid thresholds. For both subjects, the butyl acetate and butyric acid thresholds were equivalent. The present data suggest that pigeons may exhibit behavioral odor discrimination thresholds equivalent to threshold measures reported in other species for similar odorants.

In previous psychophysical studies in which the conditioned suppression technique was used as the training procedure, shock has not been delivered whenever a stimulus intensity was presented which elicited suppression below a defined threshold. This schedule prevented the disruption in baseline responding due to delivery of shock in the absence of a discriminable stimulus. This procedure is essentially a generalization procedure in which the contingency associated with training stimuli is eliminated during the first presentation of a test stimulus. If the test stimulus elicited suppression above 0.50, it then became a training stimulus, and the next intensity in the series became a test stimulus. Unpublished data indicated that this procedure resulted in a loss of behavioral control when the stimuli were presented in an ascending sequence, with greatly increased variability and decreased suppression at all odorant concentrations. This differential shock contingency was eliminated in the present study, and a uniform shock procedure was employed in which the methodological procedures were equivalent for all stimuli independent of the degree of behavioral discrimination. Intermittent shock schedules of 67% were employed with three subjects and 92% with two subjects, with no observable disruption in baseline responding produced by shock presentation with stimuli eliciting subthreshold suppression. Intrasession and intersession stimulus control was maintained in all stimulus presentation procedures. The magnitude and stability of the suppression evoked by a given stimulus intensity was relatively independent of the direction and order of stimulus progression. As Subjects #3 and 608 were not used in the descending and ascending series, their data suggest that the maintenance of stimulus control during the irregular presentation of intensities did not depend upon a previous history of threshold training.

REFERENCES

Azrin, N. H. A technique for delivering shock to pigeons. *Journal of the Experimental Analysis of Behavior*, 1959, **2**, 161-163.

Bang, B. G. Anatomical evidence for olfaction in some species of birds. *Nature*, 1960, **188**, 547-549.

Calvin, A. D., Williams, C. N., and Westmoreland, N. Olfactory sensitivity in the domestic pigeon. *American Journal of Psychology*, 1957, **188**, 255-256.

Dalton, L. W. *Conditioned suppression as a technique for the determination of auditory sensitivity in pigeons*. Master's thesis, Florida State University, 1966.

Estes, W. K. and Skinner, B. F. Some quantitative properties of anxiety. *Journal of Experimental Psychology*, 1941, **29**, 390-400.

Ferster, C. B. and Skinner, B. F. *Schedules of reinforcement*. New York: Appleton-Century-Crofts, 1957.

Fleshler, M. and Hoffman, H. S. A progression for generating variable interval schedules. *Journal of Experimental Analysis of Behavior*, 1962, **5**, 529-530.

Hendricks, Jean. Flicker thresholds as determined by a modified conditioned suppression procedure. *Journal of the Experimental Analysis of Behavior*, 1966, **9**, 501-506.

Henton, W. W., Smith, J. C., and Tucker, D. Odor discrimination in pigeons. *Science*, 1966, **153**, 1138-1139.

Hoffman, H. S., Fleshler, M., and Jensen, P. Stimulus aspects of aversive controls: the retention of conditioned suppression. *Journal of the Experimental Analysis of Behavior*, 1963, **6**, 575-583.

Marshall, A. J. *The biology and physiology of birds*. New York: Academic Press, 1960.

Michelsen, W. J. Procedure for studying olfactory discrimination in the pigeon. *Science*, 1959, **130**, 630-631.

Morris, D. D. Threshold for conditioned suppression using X-rays as the pre-aversive stimulus. *Journal of the Experimental Analysis of Behavior*, 1966, **9**, 29-34.

Moncrieff, R. W. Olfactory adaptation and odor likeness. *Journal of Physiology*, 1956, **133**, 301-316.

Mullins, L. J. Olfaction. *Annals New York Academy of Science*, 1955, **62**, 249-276.

Neuhaus, W. On the olfactory sense of birds. In Y. Zotterman (Ed.), *Olfaction and taste*. Oxford: Pergamon Press, 1963. Pp. 111-124.

Powell, R. W. *The pulse-to-cycle fraction as a determinant of critical flicker fusion in the pigeon*. Doctoral dissertation, Florida State University, 1966.

Schoenfeld, W. N., Cumming, W. W., and Hearst, E. On the classification of reinforcement schedules. *Proceedings of the National Academy of Science*, 1956, **42**, 563-570.

Shumake, S. Odor intensity discrimination in pigeons. *Journal of Comparative and Physiological Psychology*, in press.

Tucker, D. Electrophysiological evidence for olfactory function in birds. *Nature*, 1965, **207**, 34-36.

Tucker, D. Olfactory, vomeronasal and trigeminal receptor responses to odorants. In Y. Zotterman (Ed.), *Olfaction and taste*. Oxford: Pergamon Press, 1963. Pp. 45-69.

Walters, W. G. Some experiments on the sense of smell in birds. *Archives neerlandaises de physiologie de l'homme et des animaux*, 1943, **27**, 1-73.

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