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11. The delayed synaptic activation presumably does not appear with the stronger stimuli because of the powerful postsynaptic inhibition following antidromic invasion (*8, 15*).
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13. Although an interneuron cannot be entirely ruled out for the excitations of longer latency, the major interneuron of the olfactory bulb is the granule cell and this has been shown to be inhibitory (*15*).
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30 September 1970

Illness-Induced Aversions in Rat and Quail: Relative Salience of Visual and Gustatory Cues

Abstract. *Bobwhite quail, like the rat, learn in one trial to avoid flavored water when illness is induced by a drug ½ hour after drinking. In contrast to the rat, quail also learn to avoid water that is merely darkened by vegetable dye. The visual cue is even more salient than the taste cue in quail.*

Earlier work on illness-induced aversions to eating and drinking shows rather clearly that the rat, at least, must have either a gustatory or an olfactory cue in order to learn to avoid ingesting a substance if the illness that follows ingestion is delayed by ½ hour or more. Visual, auditory, and tactual cues, even though conspicuously present at the time of ingestion, do not become danger signals for the rat in such circumstances (*1, 2*). On the other hand, blue jays (*Cyanocitta cristata bromia* Oberholser, Corvidae) easily learn to reject toxic monarch butterflies (*Danaus plexippus* L., subfamily Danainae) on sight, although the model suggested for this learning gives emetic reinstatement of taste during illness a prominent, mediating role (*3*).

Impetus for our experiments came from the general view that the behavior of an organism, including what it can and cannot readily learn, is largely a product of its evolutionary history. In view of the rat's highly developed chemical senses, nocturnal feeding habits, and relatively poor vision, its ability to learn to avoid toxic substances on the basis of their taste or smell, rather than their appearance, is not surprising. But how general is this phenomenon across species? Might we not expect a diurnal bird, with its superior visual equipment and greater reliance upon vision in foraging for food and drink, to show a different pattern? Perhaps such birds, even in situations involving long delay between the time of ingestion of some food and the onset of illness, can learn to avoid ingesting substances that are distinctive in appearance only.

We report here two experiments which show that bobwhite quail (*Colinus virginianus*) can associate a purely visual cue with a long-delayed, illness consequence. In the first experiment we investigated the relative salience of a visual cue and a gustatory cue in both rats and quail. In the second experiment, in which we used quail only, we controlled for two variables which, unless accounted for, would not have allowed clear-cut interpretation of the first experiment.

Forty 90-day-old male Sprague-Dawley rats and 40 adult male bobwhite quail were subjects (*4*) in the first experiment. All were caged individually and had free access to food throughout the experiment. At the start, both species were trained over a period of several days to drink all of their daily water from 30-ml glass Richter tubes. Water was presented at the same time each day, and the time allowed for drinking was gradually reduced to a 10-minute period. Baseline drinking was then measured for 1 week, after which experimental treatments were imposed.

On treatment day, subgroups of each species received an initial 10-minute exposure to water that was either dark blue ($N = 8$), sour ($N = 8$), or both blue and sour ($N = 24$). Water was made blue by the addition of three drops of vegetable food coloring to 100 ml of water. Sour water consisted of a weak hydrochloric acid solution (0.5 ml per liter). One-half hour after removal of the distinctive fluid all subjects were injected intraperitoneally with the illness-inducing drug, cyclophosphamide. The dosage for the rats was 66 mg/kg, a dosage known to be effective for establishing one-trial aversions to distinctive tastes in the rat. We used a larger dose (132 mg/kg) for the quail, however, because exploratory use of the drug with the birds showed that the larger dose was necessary in order to produce the primary symptom of illness that rats exhibit, namely, extensive diarrhea.

For 2 days after treatment all subjects drank plain water at the regular 10-minute daily drinking period. This allowed them time to recover from the illness, as evidenced by remission of diarrhea and a return to baseline amounts of water consumption. Extinction tests were then begun to determine whether aversive conditioning had been established to the cues present in the water on treatment day. Five 10-minute tests were conducted, one every third day, with 2 days intervening between tests during which subjects were allowed to drink plain water to reestablish the baseline.

Animals that drank sour water on treatment day were tested with sour water (S : S); those that drank blue water on treatment day received blue water in the extinction tests (B : B). However, the 24 animals of each species that had drunk blue-sour water on treatment day were divided into three subgroups for testing. One group of each species was tested on blue-sour water (BS : BS), another on sour water (BS : S), and the third on blue water (BS : B).

Figure 1 shows a comparison of the amount of water drunk by rats and quail over five extinction trials for each of the five treatment : test conditions. Differences between mean drinking scores on treatment day and the first extinction trial (E_1) were assessed for statistical significance by the *t*-test. Results in the S : S condition show that the sour taste by itself was an effective cue for avoidance in both rat ($P < .02$) and quail ($P < .05$). Only the quail, however, showed reduced drinking ($P < .01$) of water that was colored blue on treatment and test days (B : B). In the BS : BS condition, both species again showed significantly reduced drinking in the tests ($P < .001$).

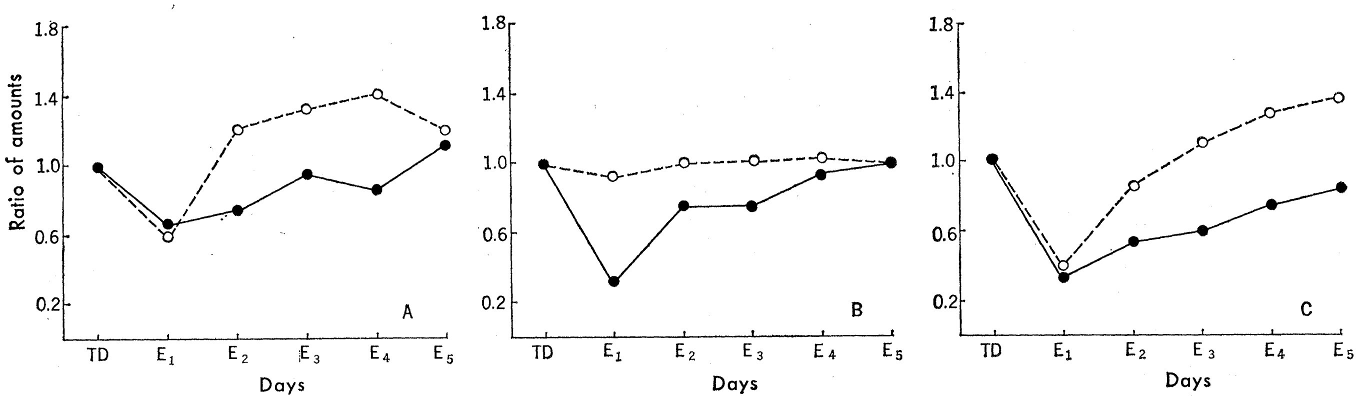
Perhaps the most striking results

Table 1. Means and standard deviations (S.D.) of drinking scores in all groups of both experiments from the last baseline day through the first extinction test (E_1). Probabilities (P) of differences between means of the treatment day (TD) and E_1 were calculated by the t-test for repeated measures.

Group	N	Last baseline day		TD		First recovery day		Second recovery day		E_1		P
		Mean (ml)	S.D.	Mean (ml)	S.D.	Mean (ml)	S.D.	Mean (ml)	S.D.	Mean (ml)	S.D.	
						Experiment 1						
S : S quail	8	12.9	3.16	9.1	3.24	9.8	4.49	12.6	3.75	6.0	3.77	$<.05$
S : S rat	8	17.8	4.60	10.6	2.31	17.6	2.04	19.0	3.16	6.2	3.99	$<.02$
B : B quail	8	12.4	2.52	14.1	2.83	9.5	4.50	11.4	1.90	5.1	3.66	$<.01$
B : B rat	8	17.4	2.71	19.6	3.70	13.1	2.60	17.6	2.27	18.1	3.71	
BS : BS quail	8	13.0	1.80	6.8	2.49	12.2	3.03	13.0	2.35	2.2	2.68	$<.001$
BS : BS rat	8	20.4	2.30	13.1	2.29	15.9	3.38	19.4	3.09	5.0	2.92	$<.001$
BS : S quail	8	13.2	3.07	6.6	3.03	13.2	4.81	12.2	2.59	7.1	3.61	
BS : S rat	8	17.9	2.90	12.0	2.24	17.6	2.53	17.8	2.17	4.5	2.96	$<.001$
BS : B quail	8	11.5	2.55	8.8	3.19	11.8	3.70	11.9	2.06	2.2	3.19	$<.001$
BS : B rat	8	18.5	3.08	12.2	3.73	15.9	1.93	17.5	2.96	12.2	4.35	
						Experiment 2, quail only (tinted tube)						
Drug-treated	20	14.1	2.61	13.2	3.58	9.5	3.24	11.4	3.44	7.0	3.63	$<.001$
Saline-treated	20	13.3	2.86	13.5	3.98	13.0	3.87	13.5	3.30	12.5	3.10	

were shown by the last two subgroups for which the compound cue (BS) of the treatment day conditioning trial was split for separate testing of each component. In the latter two conditions (BS : S and BS : B) rats and quail showed a remarkable difference with respect to the salience of gustatory and visual cues. When the sour element of the compound conditioning stimulus was the test cue (BS : S), rats avoided it ($P < .001$) but quail did not. On the other hand, when the blue color was the element tested (BS : B), quail avoided it ($P < .01$) but rats did not. The behavior of the quail in these split-cue tests is especially informative. Although the quail learned the aversion to taste alone (S : S condition), removal of the visual element from the compound conditioning stimulus (BS : S condition) apparently constituted such a radical change in stimulus for them that it rendered the remaining taste element ineffective. The results demonstrate, therefore, not only that quail can associate a visual cue with long-delayed illness, but also that a visual cue can be so salient as to overshadow taste when the two cues are compounded.

The most important result of this experiment is that quail were somehow able to associate blue water with a subsequent illness which we induced arbitrarily ½ hour after removal of the drinking tube. Failure of the rats used in our experiments to do so does not, of course, constitute a powerful argument that this species cannot associate a visual cue over a long delay. It is conceivable, although we think it unlikely, that rats see no difference between plain and dark blue water. In any event, Garcia and his co-workers (*1*) have reported much more convincing evidence than ours that rats do not utilize a visual cue in delayed-



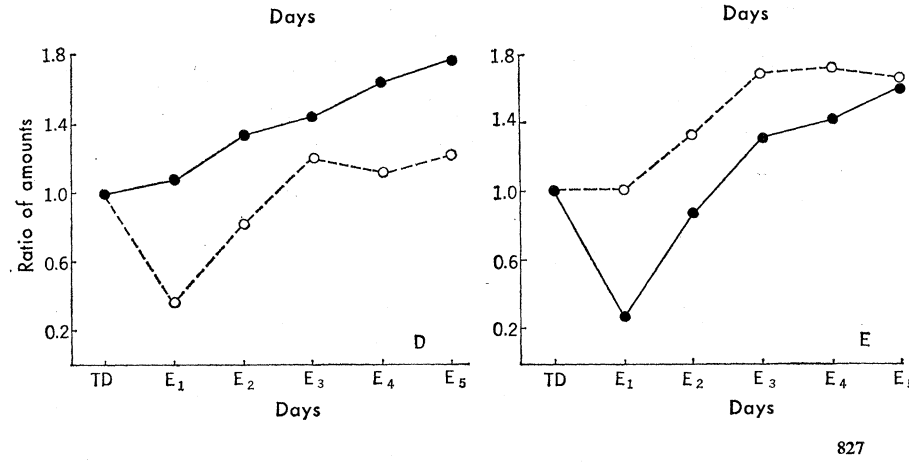


Fig. 1. Comparison of the amount of water consumed by quail (solid lines) and rats (dashed lines) expressed as a ratio of the amount consumed on a given day to the amount consumed on treatment day (TD); E_1 through E_5 are the five extinction trials given at 3-day intervals after the single conditioning trial on TD. (A) Group S : S; (B) group B : B; (C) group BS : BS; (D) group BS : S; (E) group BS : B.

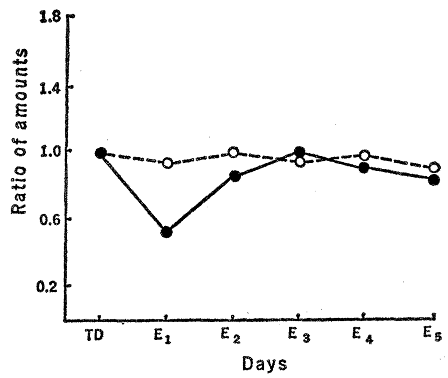


Fig. 2. A comparison of the amount of plain water drunk from tinted tubes by drug-treated quail (solid line) and saline-treated quail (dashed line). The amount drunk is expressed as a ratio of the amount ingested on a given day to the amount consumed on treatment day (TD).

illness avoidance learning. Thus, our main concern after the first experiment was whether the results for quail were unequivocal, rather than whether rats could actually see our visual cue.

In the second experiment we attempted to answer two questions: (i) Could the quail have been relying on some subtle taste of the dyed water rather than solely upon its appearance?; and (ii) Was the effective consequence that produced aversion to blue water really the drug-induced illness, or was it the considerable trauma of being caught, handled, and injected?

Birds from each of the five earlier subgroups were assigned to one of two groups, assignment being random except for the restriction that the groups be balanced with respect to prior treatment and test conditions. Procedural details were the same as in the first experiment. On treatment day, however, both groups drank from tinted blue tubes filled with the same plain water to which they were accustomed. One group ($N = 20$) was then injected with cyclophosphamide ½ hour after drinking, whereas the other group ($N = 20$) was injected with normal saline.

Figure 2 shows the result. Birds that received the illness-inducing drug drank less from the tinted tube when they next encountered it ($P < .001$), whereas those injected with saline did not.

Although Figs. 1 and 2 give a clear picture of the relative changes in drinking occasioned by treatment-day and test conditions, they give no information on the absolute amounts ingested or the degree of variability. Accordingly, means and standard deviations are shown in Table 1 for all groups each day from the last baseline day through the first extinction test. Comparison of baseline scores with those of treatment day shows that sour water, whether blue or not, was somewhat aversive to both species at first encounter, that is, before induction of illness; blue water alone was not. The amount of plain water drunk on the two recovery days after treatment shows a return to baseline levels. Effects of the delayed-illness conditioning trial are seen best by comparing scores of treatment day with those of the first extinction test.

Despite the controls introduced in the second experiment, it could be argued that the results represent not true associative learning but only the birds' increased wariness of strange-looking fluids as a result of recent illness. However, studies now completed in our laboratory (*5*) show that, although such sensitization or heightened neophobia contributes to the effect, there is a significant associative learning component as well. We are confident, therefore, that at least one avian species can associate a purely visual cue with a delayed illness without mediation by means of peripheral mechanisms such as reinstated taste.

It seems reasonable to expect that this capacity will be widespread among animals whose visual systems are highly developed and whose niches demand great reliance upon vision in foraging. If so, the implications for ecology, behavior theory, and evolutionary theory are of considerable importance.

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5. H. C. Wilcoxon, W. B. Dragoin, P. A. Kral, in preparation.
6. This research is part of the program of the John F. Kennedy Center for Research on Education and Human Development, George Peabody College for Teachers, Nashville, Tennessee, under a Biomedical Sciences Support grant from the National Institutes of Health.
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2 November 1970; revised 3 December 1970

Atmospheric Aerosol Background Level

In their report Porch *et al.* (*1*) consider the existence of a background level of atmospheric aerosol, in which they derived a "scattering component of the extinction coefficient of air (b_{scat})" from atmospheric turbidity measurements made with a Volz sunphotometer at McMurdo Station, Antarctica (*2*). They compare b_{scat} values with the "component due to air with no aerosol (b_{Rayleigh})." The November–December 1966 value of this ratio at McMurdo Station, Antarctica, is 1.36, whereas the value for Mount Olympus, Washington, in February–March 1968 is 1.5 and for Point Barrow, Alaska, in March 1970 is 1.95 (*1*). Porch *et al.* speculate that the increase from 1968 to 1970 may "represent the cumulative effect of 2 years of aerosol production," but discard this hypothesis in favor of one invoking a difference in altitude between the last two stations.

In my report I stated that four stations in Antarctica showed turbidity values lower than those measured at McMurdo Station (*2*). The ratio $b_{\text{scat}}/b_{\text{Rayleigh}}$ for these four stations [(*2*), group 1 stations] is $1.24\,^{+0.05}_{-0.06}$, which is lower than the value for Antarctica used by Porch *et al.* and, in fact, is lower than any value in their table 1. If the Antarctic value of 1.24 and the Mount Olympus and Point Barrow values of 1.5 and 1.95, respectively, are plotted against the time of determination, they fall very nearly on a straight line; this result tends to support the idea that the differences are indeed due to the increase of atmospheric aerosols with time. The value for McMurdo Station of 1.36 lies noticeably above the time trend line. During the austral summer there is quite a bit of activity and fuel consumption at McMurdo Station; hence the station itself undoubtedly contrib-