Eq. 10 does represent the temporal filtering effects of these visual cells on the signals they transmit.

D. H. KELLY

Visual Sciences Program, SRI International, Menlo Park, California 94025

H. R. WILSON

Department of Biophysics and Theoretical Biology, University of Chicago, Chicago, Illinois 60637

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10. Our results do not prove that the bipolar cells are the site of the second diffusion stage in primates, but this conclusion is implied by the process of elimination. We require a mechanism that (i) is proximal to the receptor cells, (ii) generates continuous, graded potentials, (iii) responds linearly, at least for small signals, and (iv) acts as a broadband, low-pass filter. Condition (i) eliminates the receptors themselves; (iv) would eliminate the horizontal cells; amacrine cells are also eliminated by (iv) and probably (iii); ganglion cells by (ii) and probably (iii). Condition (ii) would eliminate the spike-train signals of higher visual centers as well. (There may also be continuous, low-pass processes of some kind at the cortical level, but in view of the essential nonlinearities and other transformations that intervene, such higher processes could not play the role we assign to the bipolar cells.)
11. In the notation of (7), we set $k = p\tau$.
12. For example, S. Hecht and C. D. Verrijp, *J. Gen. Physiol.* **17**, 251 (1933); see figure 2.
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14. We thank R. M. Boynton, J. Pokorny, and V. C. Smith for helpful discussions. Supported by NIH grants EY 01128 (to D.H.K.), EY 02158, and research career development award EY 00062 (to H.R.W.).

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Cultural Transmission of Enemy Recognition: One Function of Mobbing

Abstract. *There are at least ten suggested hypotheses for the function of mobbing predators by fish, birds, and mammals. Experiments with captive European blackbirds support one of these—the "cultural transmission hypothesis." Perceiving a mobbing conspecific together with a novel, harmless bird induced blackbirds to mob the innocuous object. The mobbing response persisted during subsequent presentations of the novel bird alone, which was more effectively conditioned than an artificial control object. Enemy recognition could be culturally transmitted along a chain of at least six individuals.*

Ascribing a function to a particular trait of an organism implies that that trait enhances fitness. A given trait, however, may have more than one function (*1*), and it is likely that, of the selective forces molding that trait, only one or a few will select for its degree of adaptedness (*2*). Hence, when ascribing functions to a trait, fitness-enhancing properties of selection should be distinguished from those perfecting that trait.

The most serious drawback of the teleonomic approach, that is, the study of adaptations, is that one never knows when the list of functions suggested for a trait is exhausted (*1*). A self-checking procedure of detecting all functions of a given behavior by assessing its costs and benefits and relating these to fitness (*3*) may be a solution to this fundamental problem. The practical difficulties, however, are formidable.

Apart from notable exceptions [for example, (*4*)], the study of adaptation has remained largely guesswork, as evidenced, for example, by the numerous hypotheses regarding the function of mobbing predators. Although causal aspects of mobbing behavior have been frequently studied (*5–8*), little is known about its function or functions. There can be little doubt that mobbing has survival value, because it is potentially dangerous for the mobber (*9*) or its brood (*7*), is time-consuming, and is extremely widespread in vertebrates (*5, 8, 10, 11*). The type or degree of mobbing varies geographically as well as with the threat imposed by the respective predators (*7, 8*) and with the mobber's social organization (*12*). Yet the benefits of mobbing remain a matter of much speculation. The behavior has been suggested to confuse the predator (*13–15*), to discourage its presence through molestation (*5, 16*) or advertise the futility of further hunting (*12, 13*), to sensitize escape responses of other prey (*10, 17*), or to avoid the place where the encounter has previously occurred [(*10, 18*), but see also (*5*)]. The "cultural transmission hypothesis" suggests that perceiving other birds mob an object teaches an individual to fear that object and thus subsequently avoid it, mob it more strongly, or both (*14, 15, 17, 19*). Casual observations of jackdaws tend to support this suggestion (*20*). The benefits for the receiver are obvious, and while those for the transmitter are not so evident, the latter might benefit either immediately through confusing or molesting the predator, or at a future time from a larger number of knowledgeable warners it has engendered. However, these possible teacher benefits would be unnecessary if the receivers were relatives of the transmitter (*21*).

We examined the cultural transmission hypothesis directly by experimenting with captive blackbirds (*Turdus merula* L.) in the nonbreeding season. An "observer" bird was kept singly in an aviary (3 by 3 m) that was separated by a hallway 1 m wide from a second aviary (2 by 3 m) containing another blackbird that served as the "teacher" in all experiments, unless otherwise indicated. In the middle of the hallway a cardboard box with four radially and horizontally oriented chambers was rotated by a thread running to the experimenter behind a blind. By rotating the box 90°, an object in each of two opposite chambers was either exposed to the two birds on both sides of the hallway, or to only one of them. Two of the four chambers contained no object. A stuffed male noisy friarbird (*Philemon corniculatus*), an Australian honeyeater, was chosen as the conditioned object for the observer since it fulfilled the following necessary conditions: it is novel, resembles no genuine predator of blackbirds, yet is of a size similar to some actual predators. In order to effect the teacher's mobbing at the place of the honeyeater, a stuffed little owl (*Athene noctua*) was presented to it at the very moment rotation of the box exposed only the honeyeater to the observer. The stimulus objects occupied the two opposite chambers, 20 cm apart, that were hidden from view between trials. Juxtaposition of the two stimuli ensured, we think, that the observer associated the teacher's spatial orientation (if any) plus mobbing with the honeyeater alone. After presentation, the box was rotated back to its original position, revealing an empty chamber to each bird.

The first stimulus situation of an experiment, at 0930 hours, controlled for the stimulus effect of rotating an empty chamber back and forth. Rotation movements of a stimulus situation were spaced 5 minutes apart. The second situation, at 1000 hours, measured the stimulus effect of the novel honeyeater. The third situation, at 1200 hours, involved

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presenting the honeyeater paired with the teacher's mobbing at the little owl. The strength of this mobbing was surprisingly constant throughout all experiments (approximately 60 calls per minute, mostly "tix" calls, in addition to mobbing movements and locomotor behavior). The fourth situation, at 1400 hours, constituted the test of the observer's conditioning to the novel honeyeater. Except for the third situation, the teacher was visually shielded from the observer bird.

The strength of fear displayed by the observer was scored by summing all "duck" calls [low-threshold mobbing elements (*22*)], wing and tail flicks not accompanied by calls, and all flights exceeding 0.5 m. "Tix" calls [indicating high-threshold mobbing behavior (*22*)] did not occur. [For details of quantification, see (*23*).]

Experiment 1 demonstrated that mobbing the honeyeater significantly increased both during the response of the teacher (situation 3) and during the test for cultural transmission (situation 4) (Fig. 1). The drop in response strength from situation 3 to situation 4 appears to have been due to chance, that is, is not statistically significant.

In order to control for sensitization as a cause for the increase in response strength in experiment 1 the honeyeater was repeatedly presented to a fresh sample of blackbirds in succession (in experiment 2). Without reinforcement, that is, a teacher's mobbing, the observer habituated to the honeyeater after only one presentation. Hence, sensitization cannot account for the results of experiment 1.

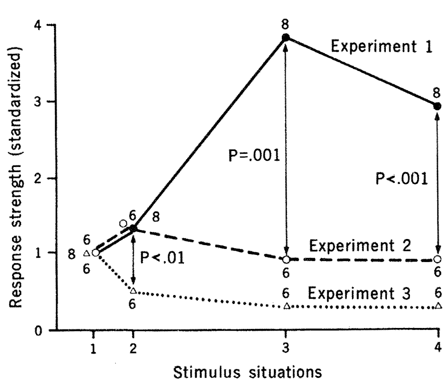

Fig. 1. Strength of mobbing a honeyeater by an observer blackbird. In experiment 1, the observer was shown a honeyeater while a conspecific mobbed a little owl in situation 3. In experiment 2, the honeyeater was shown without conspecific mobbing. In experiment 3, the honeyeater was removed from the box and the empty box was shown alone. Response strength was standardized with reference to the empty box control (situation 1). The significance of the response in situation 2 was calculated with a Mann-Whitney U test (two-tailed); in situations 3 and 4, a one-tailed test was used. The number of subjects is shown at curve points.

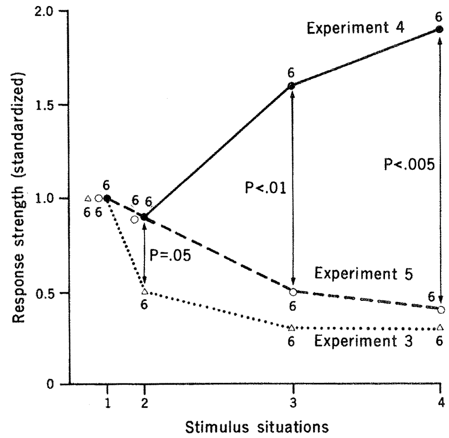

Fig. 2. Strength of mobbing a multicolored bottle by an observer blackbird. Experiments 4 and 5 parallel experiments 1 and 2, respectively.

Despite the apparently innocuous nature of the honeyeater stimulus, it elicited a definite although small amount of mobbing (situation 2 in experiments 1 and 2) (Fig. 1). Hence, there was some fear of a novel bird in the absence of reinforcement [see also (*7*)]. The question of whether every novel object elicits fear can be indirectly answered. The presentation box when rotated constitutes a novel moving stimulus. Repeated presentations of this novel stimulus alone in situations 1 through 4 of experiment 3 (empty box control) caused a more rapid decrease in the response (from situation 1 to situation 2) than occurred to the honeyeater (situation 2 to situation 3) in experiment 2 (Fig. 1). The difference is aggravated by the fact that the box necessarily accompanied each stimulus object shown to the birds and had been seen once before the honeyeater was presented in experiment 2 (situation 2). The difference in the rate of habituation to the box versus the box plus the honeyeater suggests that more than mere novelty caused the blackbirds to respond to the honeyeater more strongly than to the box.

In a further series of experiments we examined whether blackbirds could be conditioned to an artificial, unnatural object. In this series (experiment 4) a multicolored plastic bottle similar in overall length to the honeyeater (26 cm) was presented to new blackbirds as the honeyeater had been in experiment 1. The response to the bottle was also reinforced by the teacher's mobbing (situation 4) (Fig. 2). Moreover, the birds responded during conditioning significantly more strongly than they did without reinforcement (compare situation 3 of experiments 4 and 5). The further increase after situation 3 is apparently a chance effect. The bottle elicited mobbing prior to any cultural transmission (situation 2) although less so than the honeyeater did in the same situation (compare Figs. 1 and 2); but the bottle elicited more mobbing than the empty box did.

To depict the extent to which responses to the honeyeater differed from those to the bottle, we juxtaposed the data (Fig. 3). The honeyeater elicited an initially stronger response than the bottle did, and it was more strongly mobbed during reinforcement (despite nearly constant mobbing by the teacher). The test of learning revealed a difference in the same direction ($P < .05$). There appear to be constraints on learning in that transmission of information about different stimulus objects was not equally effective.

It is tempting to speculate that the effectiveness of transmission is related to the decoding of stimulus attributes during the nonreinforced initial encounter, as measured by the novelty response in situation 2. The honeyeater would release, then, more fear than the bottle, and thus information about the former would be more effectively conveyed.

To determine whether the final test re-

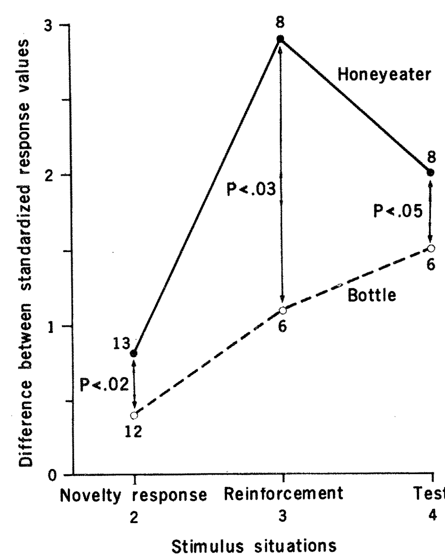

Fig. 3. Comparison of cultural transmission by mobbing between recognition of a honeyeater and a multicolored bottle. Response values were standardized with reference to the empty box control values from Figs. 1 and 2. Significance according to the Mann-Whitney U test was calculated with a one-tailed test in situations 3 (transmission) and 4 (test) because the response to the honeyeater as a novel stimulus (situation 2) was significantly stronger than that to the bottle according to a two-tailed test.

sponse to the honeyeater reflects fear of a frightening stimulus comparable to that of a real predator, we conducted another experiment. Six blackbirds that had been habituated and then conditioned to the honeyeater were presented the stuffed little owl between 1 day and several days after the last honeyeater test. Responses to the two stuffed birds did not differ significantly (Wilcoxon matched-pairs signed-ranks two-tailed test). Hence, at least under the conditions of testing, cultural transmission of honeyeater recognition leads to a response resembling that to a genuine predator. Whether transmission can lead to still higher response levels when associated with more dangerous predators than little owls needs investigation.

Cultural transmission embodies a type of nongenetic transfer of information that probably protects the observer in a dangerous situation in one or more of the ways mentioned. The transfer would be even more effective if there were no appreciable loss of information when passed on in chainlike fashion. The length of such a chain would depend on several constraints, notably the decrement of transmission due both to the information lost in each single learning act and to forgetting. We tested this hypothesis by making the observer bird in one trial the teacher in the next trial and so on. From the second trial on, the honeyeater was presented at the end of the hallway in a way such that it could be seen by both the new teacher and the observer. There was no discernible decrement of information transfer through a total of six presentations, involving six observers that were subsequently teachers. Response strength in all six cases was less during conditioning than in the subsequent test ($P = .05$, Wilcoxon matched-pairs signed-ranks one-tailed test).

Our demonstration of cultural transmission of enemy recognition has probably revealed only one function of mobbing, namely, enhanced fitness of the observer. The benefits accruing to the teacher remain to be investigated. Since blackbird dispersal is viscous (*24*), kinship effects or other more immediate benefits seem possible. Although we have established one function of mobbing, we are far from understanding which selection pressures have molded the adaptedness of this behavior (*23*).

E. CURIO, U. ERNST, W. VIETH
Arbeitsgruppe für Verhaltensforschung, Ruhr-Universität Bochum, Postfach 10 21 48, 4630 Bochum 1, German Federal Republic

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Light Stimulates Tyrosine Hydroxylase Activity and Dopamine Synthesis in Retinal Amacrine Neurons

Abstract. *Retinal dopamine-containing amacrine neurons are rapidly activated by light, as shown by an increase in the rate of dopamine formation in vivo and a concomitant increase in the activity of tyrosine hydroxylase, measured in vitro with a subsaturating concentration of pteridine cofactor. Activation of tyrosine hydroxylase also occurs when isolated eyes from rats killed in the dark are exposed to a strobe light. Studies of amacrine neurons should provide basic data about the biochemical processing of visual information, as well as the physiological presynaptic regulatory mechanisms of dopamine-containing neurons.*

In the retina, the neurotransmitter dopamine is found in some amacrine neurons (*1*) that play an important role in local circuit processing of visual information. We found that in amacrine cells of the rat, the activity of tyrosine hydroxylase (E.C. 1.14.16.2), the rate-limiting enzyme for dopamine formation, is modulated by environmental lighting. The enzyme is rapidly activated when either the whole animal, or the isolated eye of dark-adapted rats, is exposed to light. When the light is removed, enzyme activity decreases. Activation is apparently the result of a decrease in the Michaelis constant of tyrosine hydroxylase for its pteridine cofactor. Concomitant with enzyme activation is a fourfold increase in the rate of formation of dopamine by amacrine neurons. To our knowledge, the retinal dopamine-containing amacrine neurons are the only dopamine-containing neurons that can be experimentally activated and inactivated by a physiological stimulus. The retinal amacrine neuronal system should provide valuable data about the biochemical processing of visual information, the molecular mechanisms of tyrosine hydroxylase activation, and the regulation of dopamine synthesis.

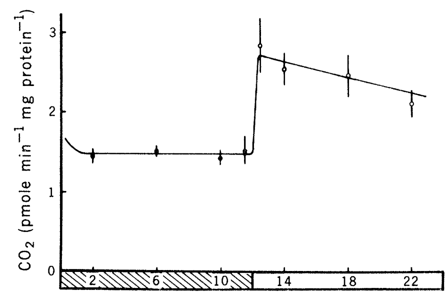

Fig. 1. Circadian rhythm of retinal tyrosine hydroxylase activity. Lights were off from 0 to 12 hours. Solid circles represent samples taken in the dark and open circles represent samples taken in the light. Data are expressed as mean ± standard error for five duplicate determinations.

Male Sprague-Dawley rats (Zivic-Miller, 190 to 210 g) were exposed to 12 hours of light per day for 3 days before

