gain of the CRO input until the object no longer appeared to move. For the object to appear stationary immediately after 10 minutes' exposure, it had to undergo 12.0 percent of the motion experienced during exposure (S.E. = 0.9 percent). The aftereffect was also found to persist if a stationary luminous frame was placed around the luminous spot, thereby distinguishing it from the spontaneous movements luminous spots sometimes appear to undergo in wholly darkened rooms.

The next step in testing the theory was to see if this new perceptual adaptation required the recorrelation of eye and head movement. A second, stationary spot was added to the screen (by using the second channel of a dual-trace oscilloscope). During exposure the subject could now be told to keep his eyes trained on either the moving spot (condition 2, Fig. 1) or the stationary spot (condition 3, Fig. 1). An adaptation was found only in condition 2, where the correlation of eye and head movement had been rearranged. Ten of the 12 new subjects tested reported the aftereffect shown in row 2, Fig. 1. This aftereffect surprised the subjects, since the two spots moved together, rather than separately as in the exposure period. The exposure condition could not be compensated for by a rotation of the eyes; the aftereffect indicates that the adaptation was a rotation of the visual field, a compromise between what the exposure condition required and what eye movements could achieve. In condition 3 (tested in counterbalanced order with condition 2), where the correlation between eye movement and head movement had not been rearranged, only one of the 12 subjects reported an aftereffect, and that was of the form found in condition 2. The difference between the two conditions is significant at the .01 level ($\chi^2 = 7.13$).

The final tests of the theory were designed to determine whether diagonal eye movements, as occurred in conditions 1 and 2, were important in themselves for the adaptation. In condition 4 (Fig. 1) the subject's head was held stationary during the exposure period, and the spot on the screen was made to undergo the same diagonal movement relative to the head as in condition 1, by applying a ½-hz sine wave to both the horizontal and vertical amplifiers of the oscilloscope. None of the 12 subjects reported an aftereffect, after exposure for 7 minutes, when given the usual test of nodding their heads while gazing at the stationary spot.

The same group of 12 subjects was tested, in counterbalanced order, on condition 5 (Fig. 1), where the regular diagonal eye movement was eliminated, but the correlation between eye and head movement was preserved by moving the spot vertically on the screen asynchronously with the head movement, while allowing it to move horizontally in synchrony with the head. The spot moved in a varying Lissajou's pattern during head movement, and the tracking eye movements were correspondingly varied. However, the horizontal component of eye movement was still exactly correlated with vertical head movement. After 7 minutes' exposure, 11 of the 12 subjects reported the same aftereffect as in condition 1. The difference between conditions 4 and 5 is significant at the .005 level ($\chi^2 = 9.09$). Eight of the subjects showing an aftereffect reported not having been aware, during the exposure period, of the correlation between spot movement and head movement.

These results are consistent with recent findings on perceptual adaptation to a fixed displacement of optical directions from the head, which indicate that eye-positioning responses play an important role (*6*). The results offer a contrast to another type of visual-movement adaptation, the "waterfall aftereffect" that follows prolonged viewing of unidirectional movement. For the latter, movement of the image across the retina, rather than eye movement, seems to be the inducing factor (*7*).

JOHN C. HAY
Department of Psychology, Smith College, Northampton, Massachusetts

References and Notes

1. H. Wallach and J. H. Kravitz, *Psychonomic Sci.* **2**, 217 (1965).
2. I. Rock, *The Nature of Perceptual Adaptation* (Basic Books, New York, 1966), pp. 77-99.
3. J. C. Hay and H. L. Pick, Jr., *J. Exp. Psychol.* **72**, 640 (1966).
4. R. S. Woodworth and H. Schlosberg, *Experimental Psychology* (Holt, New York, 1954), pp. 492-527.
5. A mechanical technique for this purpose was introduced by H. Wallach and J. H. Kravitz, *Psychonomic Sci.* **3**, 165 (1965) and by I. Rock and R. L. Posin (*2*). The apparatus used here was derived from that of R. Held, A. Efstathiou, M. Greene, *J. Exp. Psychol.* **72**, 887 (1966).
6. R. E. Kalil and S. J. Freedman, *Percept. Mot. Skills*, **22**, 135 (1966); S. C. McLaughlin and R. G. Webster, *Percept. Psychophys.* **2**, 37 (1967).
7. S. M. Anstis and R. L. Gregory, *Quart. J. Exp. Psychol.* **17**, 173 (1965).
8. This research was performed at the Psychology Department of M.I.T. where I held NIH postdoctoral fellowship 1F3MH-6, 364-01 and NIH research grant MH97588. Dr. R. Held and his research group provided advice and support.

18 March 1968

Adaptation and Negative Aftereffect to Lateral Optical Displacement in Newly Hatched Chicks

Abstract. *Chicks wearing hoods containing 8.5-degree wedge prisms from the day of hatching showed both significant reduction in the average lateral displacement of pecking (adaptation) and significant pecking overcompensation in the direction opposite to the original displacement (negative aftereffect) when matched 0-degree plates were substituted for the prisms on the 8th day.*

Domestic fowl reportedly lack the capacity to adjust to altered visual input. Pfister (*1*) has reported that two adult hens were unable to adapt to monocular left-right reversal after a period of 3 months. Hess (*2*) reported that newly hatched Leghorn chicks were unable to adapt to 7° of lateral optical displacement during the first 4 days after hatching; but they did show a reduction of their pecking errors comparable to that of hooded chicks for which no displacement occurred.

The negative results reported in these two studies have been used as support for the position that the ability to adapt to displaced visual direction is limited to the higher primates (*3*) or at least to mammals (*4*). Hess (*2*) predicts that no negative aftereffects would occur after removal of the prism displacement since this would involve performing a response which is antagonistic to an instinctive one.

I have tried to determine whether chicks could adapt after more extended exposure to displacement, and, if they can, to demonstrate a negative aftereffect to lateral optical displacement. Positive results would require reexamination of the prevailing current theory concerning the phylogenetic limitations of adaptation to altered visual input.

Twenty-eight newly hatched White Leghorn cockerels were fitted with latex hoods with 8.5° (15 diopter) prisms mounted binocularly in the hoods (Fig. 1). Half of the chicks had base-right oriented prisms; half had base-left oriented prisms. All chicks were double-banded with pigeon identification leg bands. Each chick was then assigned to one of four cages (61 by 91 by 35.5 cm), seven chicks per cage. Each cage was further subdivided so that it contained three chicks with base-right prisms and four with base-left prisms (or vice versa). One 8-day-old ("starter") chick without a hood was placed in each cage to facilitate the establishment of normal pecking responses in the hooded subjects. The use of the "starter chick" decreased the mortality rates and general inactivity which occurs in hooded subjects during the first week after hatching. The floor of each living cage was filled with Libby-Owens white silica sand to a depth of 19 mm. Parakeet seeds were placed on the sand, and the sand and parakeet seeds were raked together so that the seeds were distributed equally throughout the sand. Sufficient additional seeds were added to this mixture so that the surface distribution of the parakeet seeds after raking averaged two to three seeds per 6.5 cm^2 of surface area. The ratio of sand to seed and the surface seed distribution (*5*) were monitered and adjusted to this standard at least once a day.

On the first day of hatching (0 days of age), approximately 33 cm^3 of commercial chick starter mash was placed in a small mound directly beneath the light bulb (60 watt) in each cage. This was the only time that starter mash was used. Water was supplied by means of a 25-mm-wide (narrow mouth size), 3.78-liter-capacity watering trough device. The room temperature was maintained at an average of 27.5°C, whereas temperatures near the 60-watt bulb in each cage ranged from 29.5° to 32.2°C.

The prisms were cleaned once every 2 days. During the cleaning, the chicks were wrapped in a double paper towel, to restrain them and occlude their vision.

All chicks were tested for pecking accuracy after 4 and 8 days exposure to prismatic displacement. Each day's test consisted of the chicks' pecking response elicited by the presence of each of five consecutive test targets described below. At the conclusion of the day-8 testing period, each chick was tested for his initial pecking error on a single target when first exposed to 0° displacement (that is, tested with a control hood containing clear blank plates). The targets were pieces of cardboard (25 by 25 mm) covered with brown-colored Plast-i-clay 3 mm deep. A pencil-point indentation was placed in the center of each test square, and a single parakeet seed was placed on top of this depression. After the chick had responded, each square also was marked with his identifying number and his standing position (precise left-right body orientation) with respect to the seed. Each square was examined under a stereoscopic microscope with a reticle pattern divided into tenths of a millimeter. The lateral distance in millimeters between the center of the seed and the center of the pecking distribution was recorded. If the subject removed the seed from the clay, it was scored as 0 mm displacement. Obviously, only pecks which were heavy enough to deform the clay could be recorded. Three independent observers agreed, however, that any pecking response that resulted in direct contact of the chick's beak with the clay left a visible depression, usually a double (open mouth) mark. Examination revealed an average of 2.71 peck marks per target (with a standard deviation of ± .997). The data were collected and scored under a "double-blind" procedure to minimize the possibility of experimenter bias. A more detailed description of the test targets and the standardized shaping procedure to elicit high response rates in all chicks is found in Rossi (*6*).

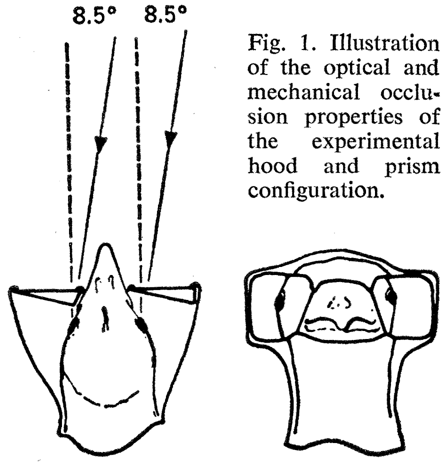

Fig. 1. Illustration of the optical and mechanical occlusion properties of the experimental hood and prism configuration.

Of the 28 chicks which began the experiment, only 11 (five base-right and six base-left) survived and responded on both day 4 and day 8 of the test period. Animals that failed to respond at either day 4 or day 8 were eliminated so as to satisfy an experimental design and analysis which required that the same subject respond on both test occasions. The five chicks with base-right prisms missed the seed targets by an average of 3.04 mm to the left on day 4 and 2.00 mm to the left on day 8. The six with base-left prisms missed the seed targets by an average of 2.40 mm to the right on day 4 and 1.40 mm to the right on day 8 (Fig. 2).

An analysis of variance using unequal size groups and one variable correlated and one variable independent (*7*) was performed on the absolute size of the

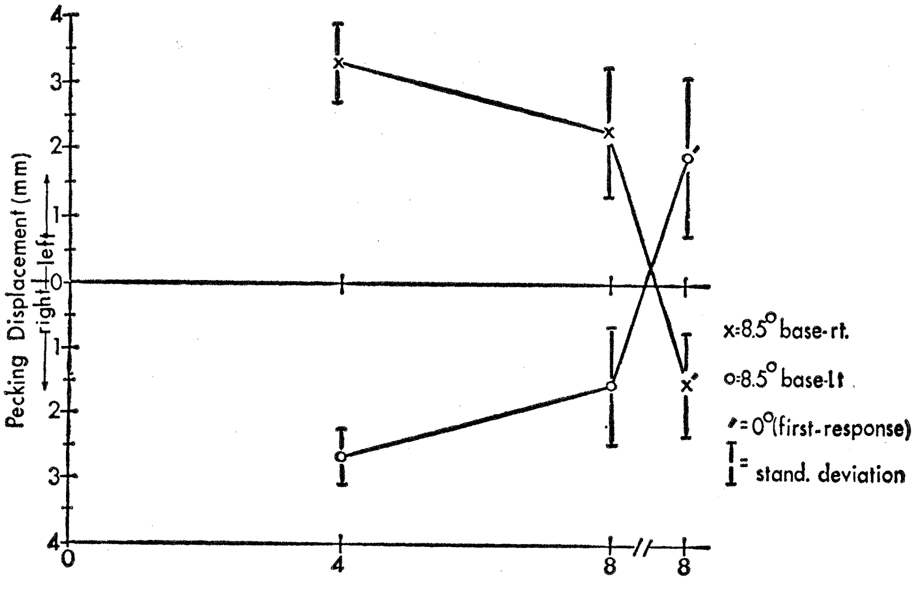

Fig. 2. Mean lateral displacement errors for two prism types during an 8-day exposure and mean initial lateral displacement errors for first responses elicited after substitution of 0° displacement plates for each prism type.

lateral deviations. The main effect of repeated trials, which was the day-4 to day-8 improvement effect, was significant at $P < .0005$ [the analysis of variance F ratio for 1 and 9 degrees of freedom (df) $= 80.89$]. The effects of base orientation and the interaction between base orientation and repeated trials were not significantly different, although, of course, the direction of the errors was opposite for base-right and base-left subjects.

A total of 14 chicks responded at day 8 when first wearing control hoods containing 0° clear plates (the 11 chicks mentioned above, plus three which failed to respond at day 4 and hence could not be included in the earlier analysis). No subject returned to 0 mm average pecking displacement. All but two of the 14 responded in the direction opposite to their initial displacement (negative aftereffect). The average negative aftereffect was 1.285 mm in the optically predicted directions. These results are significant at $P < .005$ [$t = 3.38$, 13 df (one-tailed test)] when compared to the hypothetical no effect predicted by Hess (*2*).

The existence of the negative aftereffect is in direct opposition to the concept that visual direction relationships in domestic fowl cannot be modified through experience. It would appear that it is the significant negative aftereffect rather than adaptation which is the more important finding. The pecking response of the chick requires that he make a directional choice at a distance with little or no opportunity for in-flight correction of aim. The test of negative aftereffect used in this experiment closely approximates the blind pointing or reaching without visual feedback measures of human (*8*) and higher primate (*9*) adaptation to lateral optical displacement, and thus these results can be used as a second and perhaps more useful index of comparative adaptation capacity.

PATRICK J. ROSSI
Department of Psychology,
Arizona State University, Tempe

References and Notes

1. H. Pfister, thesis, University of Innsbruck (1955).
2. E. Hess, *Sci. Amer.* **195**, 71 (1956).
3. R. Gregory, *Eye and Brain: The Psychology of Seeing* (World Univ. Library, New York, 1966), p. 209.
4. The cat, a mammal, can adapt to monocular up-down reversal of its visual field. These results are found in H. Bishop, thesis, University of Chicago (1959).
5. The presence of the sand results in increased scratching behavior which may contribute to the overall adaptation.
6. P. Rossi, thesis, University of California, Riverside (1967).
7. B. Winer, *Statistical Principles in Experimental Design.* (McGraw-Hill, New York, 1962).
8. R. Held and S. Freedman, *Science* **142**, 455 (1963).
9. J. Bossom, *Psychon. Sci.* **1**, 377 (1964); J. Bossom and C. Hamilton, *J. Comp. Physiol. Psychol.* **56**, 769 (1963).
10. Supported by PHS grant NB-04717. This work was done at the University of California, Riverside. I thank Drs. Austin H. Riesen, Arlo K. Myers, and Paul D. Wilson for assistance.

19 March 1968

Androgen Control of Territorial Marking in the Mongolian Gerbil

Abstract. *Gerbils mark objects with the secretion of a midventral sebaceous gland. Both the behavior and the gland integrity are under androgen control, as indicated by castration and replacement with testosterone propionate. The integrity of the gland seems less important for marking than an influence on the central nervous system, although the gland can be used as an external measure of androgen levels. It is possible that the secretion acts as a pheromone to signal territorial possession.*

The Mongolian gerbil (*Meriones unguiculatus*) is rapidly becoming a significant target for biological research (*1*). Members of this species (order Rodentia; family Cricetidae) weigh about 70 to 90 g as adults, are highly exploratory and tractable, and require no water other than that derived as a metabolic by-product. Recently, we have described for the gerbil an abdominal skimming response that we interpret as territorial marking (*2*). In brief, both males and females rub a ventral sebaceous gland over low-lying objects, leaving a sebum that is oily to the touch and musky in smell. The response is highly discrete, involving rapid approach to an object, sniffing of the object, mounting it and then pressing the ventral sebaceous gland against its surface, and finally a forward dismount. Males mark objects about twice as frequently as females, corresponding in a rough way to the sex difference in the size of the sebaceous gland. When a male enters a territory already masked by the sebum from another animal its marking frequency is reduced (*2*). In a well-developed male the gland is a midventral, orange, fusiform pad approximately 3 cm long, 0.7 cm wide, and 0.2 cm thick. Its histology has been described and, in the male, its integrity is dependent on the gonads (*3*). Generally the gland is enfolded by ventral body hairs but can be detected by the orange stain from the sebum or exposed by clipping or shaving the surrounding hair (*4*). This report on the male emphasizes the effects of castration and testosterone therapy on the marking behavior and the morphology of the ventral sebaceous gland.

Marking behavior and activity were assessed in an area (1 m^2) on a wooden floor marked off into 16 squares of equal size. A roughened Plexiglas peg, 2.6 cm long, 1.2 cm wide, and 0.7 cm high, was permanently positioned at each of the nine lined intersections. The field was surrounded by gray wooden walls 47 cm high, each of which held one 15-watt light bulb shielded at the top and focused into the interior of the field.

Sixty male Mongolian gerbils, obtained from Tumblebrook Farms in New York and approximately 80 days old, began the experiment. Each animal was given one 5-minute trial in the field every 3rd day until six trials were complete. A trial consisted of placing the gerbil in the middle of the field and recording the number of peg marks and

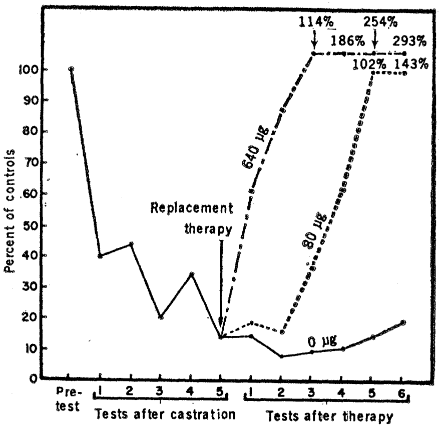

Fig. 1. Effects of castration and testosterone propionate therapy on territorial marking.

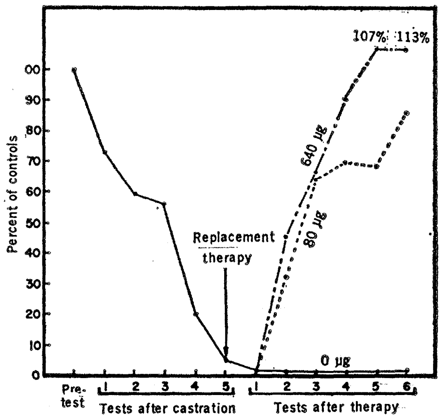

Fig. 2. Effects of castration and testosterone propionate therapy on size of the ventral gland.