to the fact that the stationary models simply failed to attract attention during the training period.

The data from the control group confirm our earlier finding: in the absence of an exposure to a moving model during the training period, few responses and no significant preferences are recorded.

These results can be reasonably interpreted in one of two ways. Perhaps there are several characteristic features by means of which imprinted objects are identified by chicks, with different cues being seized upon under different conditions. In the case of moving models, it might be that the stimuli associated with movement become of primary importance, while actual color or pattern becomes the dominating cue when the models are at rest. The studies of James (5) on visual flicker as a releaser of the following-response provide some basis for a belief that the painted model gives a more effective impression of movement (due to an increase in retinal flicker) than does the plain model. Alternatively, the imprinting experience itself may have a very much more limited effect than is commonly believed, with the preferences resulting from imprinting being limited to specific situations. Lorenz (6), in fact, suggests something akin to this when he speaks of his jackdaws as having been imprinted on separate Kumpans for sexual and social functions. Our suggestion implies a yet more drastic separation of functions.

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References and Notes

1. P. H. Gray, *J. Gen. Psychol.* **68**, 333 (1963).
2. E. H. Hess, *Science* **130**, 3368, 133 (1959); P. H. Klopfer, *Am. Naturalist* **98**, 173 (1964); E. Q. Salzen, in *Evolutionary Aspects of Animal Communication. Proceedings of a symposium held by the Society and Association for the Study of Animal Behavior, London 8–9 Nov. 1961* (Zoological Society of London, 1962), symposium No. 8, pp. 199–217.
3. P. H. Klopfer and J. P. Hailman, *Science* **145**, 1333 (1964); *Z. Tierpsychol.* **21**, 755 (1964).
4. W. Schein, *ibid.* **20**, 462 (1963).
5. H. James, *Canad. J. Psychol.* **13**, 59 (1959).
6. K. Lorenz, *J. Ornithol.* **83**, 137, 289 (1935).
7. I am, as usual, indebted to J. P. Hailman, in collaboration with whom this line of inquiry was originally begun. W. Schleidt and J. Hatch have kindly read and criticized the manuscript. This paper is dedicated to Professor Otto Koehler on the occasion of his 76th birthday.

30 September 1964

Single-Unit Activity in the Cat's Visual Cortex: Modification After an Intense Light Flash

Abstract. *In response to a brief, intense light flash at the retina, the cells of the visual cortex in the* cerveau isolé *preparation of the cat show prolonged excitation of a type not normally produced by physiological stimulation.*

In the human being, intense brief visual stimuli provoke a characteristic persistence of sensation, commonly referred to as an after-image (*1*). After-images fade and reappear with a periodicity dependent upon such factors as brightness and color. The fading effects are known to be in part retinal (*2*) and are probably in part centrally determined (*3*). The images may persist for 30 minutes; it has been suggested that their time course is dependent on the regeneration of visual pigment (*4*).

Visual stimuli, both brief and prolonged, have been shown to induce transient modifications in the level of firing of single units recorded in the animal cortex (*5*), but there is no evidence of the effect on single-unit activity of a brief stimulus of an intensity which would be expected to produce a prolonged after-image in the animal. We have performed such an experiment in the cat, using the *cerveau isolé* preparation (6), the results of which show that modification of single-unit activity persists for as long as 30 minutes after the primary stimulus. This modification consists of a marked increase not only in overall firing level but also, rather unexpectedly, in the frequency of firing within bursts (*7*).

Four animals were used in successive stages of the experiment, all preparations being identical. After mid-collicular section of the brainstem (*8*) the cat was allowed to recover from the anesthetic (ether), and extracellular recordings of unit activity in the visual cortex were made by means of glass microelectrodes. Recordings were stored on tape for later analysis.

The procedure was as follows. A spontaneously active single unit in the primary visual area, firing according to the usual criteria of constant amplitude and wave form, was located. After a

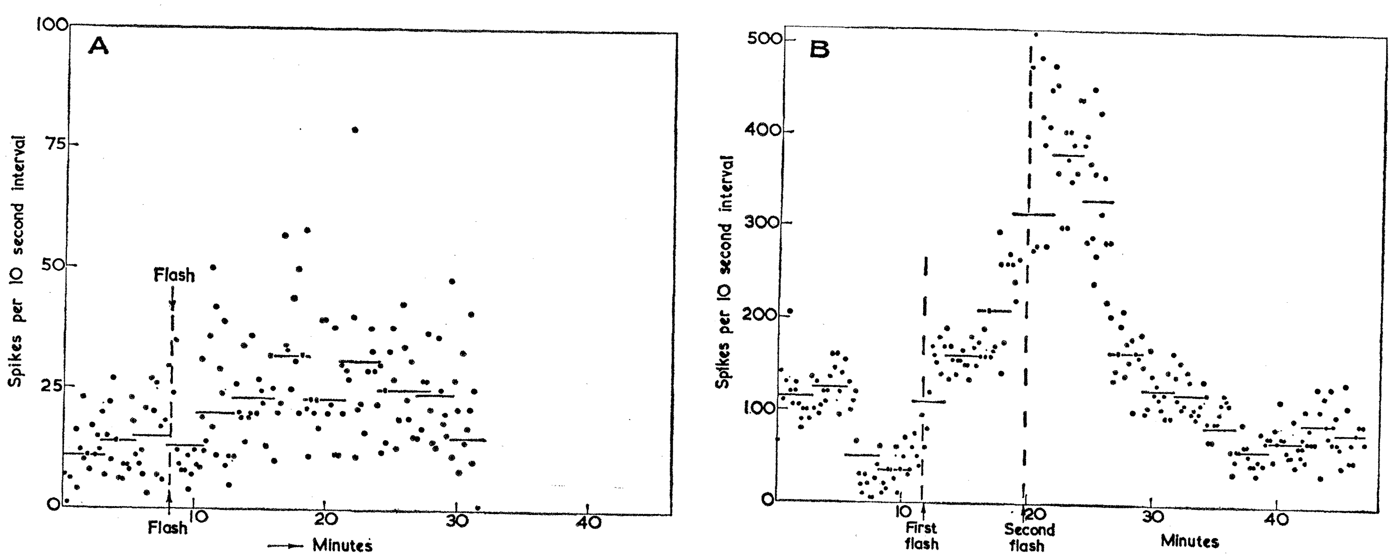

Fig. 1. Changes in the rate of firing following one (*A*) or two (*B*) intense flashes of light to the retina. Horizontal bars represent mean values of spikes per 10-second interval over 2.5-minute periods.

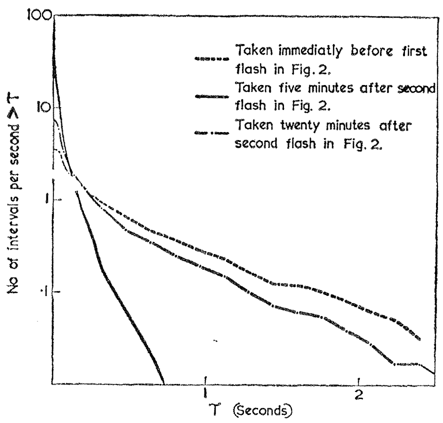

Fig. 2. Three-minute interval histograms taken immediately before first flash in Fig. 1*B*, 5 minutes after second flash in Fig. 1*B*, and 20 minutes after second flash in Fig. 1*B*, respectively.

control period of 30 minutes of firing, an intense flash was given to the contralateral retina; this emanated from a 1000-joule flash-bulb located 15 cm from the cat's eye, the pupil of which had been dilated with atropine. Room illumination was kept low and constant throughout the experiment.

Figure 1*A* indicates the change in rate of firing following the flash. The firing rate increased gradually to a relatively high peak after 10 minutes; next followed a slow decline until the original control level was roughly matched after 30 minutes. Figure 1*B* shows data for a second unit; two flashes were given 5 minutes apart, and the figure shows an apparent summation effect. Once again, after approximately 30 minutes, firing fell to the mean pre-flash level. The interval histograms in Fig. 2 indicate that not only did the overall firing rate increase, but that the firing rate within bursts also increased.

These responses showed an unusually long time course. The unit responses built up gradually, taking up to 10 minutes to reach their maximum; they then declined slowly to the control level for another 10 to 20 minutes. Relatively long effects of this sort have always been hard to produce and usually involved dramatic alterations of a cell's environment by, for example, topical application of strychnine or local polarization. Further, neither polarization nor stimulation with a regularly flashing light have been found to alter the slope of the short interval component of a histogram recorded from a visual cortical unit (*7*). In other words, the frequency of a unit's firing within bursts has hitherto seemed to be inflexible, even though the frequency and length of bursts have both increased. With an after-image which is known in the human to produce a persistent though varying and intermittent light sensation, changing information must pass up the optic tract for a considerable time. It seems likely that, if Burns's hypothesis of self re-exciting networks (*9*) is correct, an increased rate of firing within bursts reflects great increase in the amount of information circulating in networks of neurones within the visual cortex. [There is some evidence that a rise in intra-burst frequency represents increase in the number of impulses reaching a neurone from its neighbors (*10*).]

The question arises whether conclusions valid for the intact animal may be drawn from experiments on *cerveau isolé* preparations. Our preparations were responsive to visual stimuli and showed an electrocorticogram (ECG) with high frequency components. We believe that with healthy preparations the cortex is in an alert state and does not have slow, "spindly" wave forms in its ECG. The two most significant sensory pathways are still entirely intact, and several authors have commented on the efficacy of olfactory stimuli alone in producing arousal patterns in electroencephalograms recorded from *cerveau isolé* preparations (*11*).

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References and Note

→ W. Berry, *Amer. J. Pyschol.* **38**, 584 (1927).
2. K. J. W. Craik, *Nature* **145**, 512 (1940).
3. H. C. Bennett-Clark and C. R. Evans, *ibid.* **199**, 1215 (1963).
4. H. B. Barlow and J. A. Sparrock, *Science* **144**, 1309 (1964).
5. D. H. Hubel and T. N. Wiesel, *J. Physiol.* **160**, 106 (1962); B. D. Burns and G. K. Smith, *ibid.* **164**, 238 (1962).
6. F. Bremer, *Compt. Rend. Soc. Biol.* **118**, 1235 (1935).
7. G. K. Smith and D. R. Smith, *Nature* **202**, 253 (1964).
8. B. D. Burns and B. Grafstein, *J. Physiol.* **118**, 412 (1952).
9. B. D. Burns, *The Mammalian Cerebral Cortex* (Physiol. Soc. Monog. No. 5) (Williams and Wilkins, Baltimore, 1957).
10. A. D. J. Robertson, in preparation.
11. J. D. French, "The reticular formation," in *Handbook of Physiology* (Amer. Physiol. Soc.) (Williams and Wilkins, Baltimore, 1960), sect. 1, vol. 2.
12. Work carried out as part of the research program of the National Physical Laboratory; publication is by permission of the director.

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Choice Behavior in Rhesus Monkeys: Effect of Stimulation during the First Month of Life

Abstract. *Monkeys reared from birth away from other monkeys and handled by humans during the first month of life preferred humans to monkeys when tested at the age of 2 to 3 years. Animals having both early human handling and physical contact with other monkeys, or physical contact with other monkeys and no human handling, preferred monkeys. Subjects reared in complete isolation from humans and monkeys spent less time with either choice stimulus, but also preferred monkeys to humans.*

Persistent effects of early stimulation on later behavior have been demonstrated in many species. Studies of imprinting reveal effects of stimulation at "critical" periods in the life of the organism (*1*). Studies of primate behavior reveal persistent effects of early restriction on social, sexual, and maternal responses (*2–4*). This study concerns the effects of very early human handling on the preference of monkeys for humans or monkeys later in life.

We used six groups of rhesus monkeys that were reared in the laboratory. Some of these groups were reared in the laboratory nursery by the methods of Blomquist and Harlow (*5*). The important factor in nursery rearing for this study was the feeding of the monkeys by hand. The infant, cradled in the arms of the nursery worker (usually female), was fed from a baby's bottle. On the average, each infant was hand-fed once every 4 hours for 10 to 12 days after birth. When 11 to 25 days old the infant took its formula from a bottle on a wire rack where initially the infant was held in place by the nursery worker. When the infant could climb the rack, physical handling was minimal. Some animals were slow in developing ability to feed from the rack; to maintain their food intake, they received supplementary hand-feeding between days 12 and 20. Thus, for the first 10 days of life there was intimate physical contact between the infant monkey and the human, with progressively less physical contact thereafter, although close visual contact continued.

Animals in group 1 (handled, no peers) were nursery-reared from day 1 to approximately day 21. About day 22 they were placed in bare wire cages