Imprinting: A Reassessment

Abstract. *Chicks exposed to a moving model during their critical period for imprinting will subsequently demonstrate a preference for that model if it is stationary. In preference tests with moving models, other preferences appear to over-ride the effects of the imprinting experience.*

The young of many precocial species can be induced to follow moving objects that possess a variety of shapes and colors. This behavior is elicited only during a particular interval shortly after hatching, the so-called "critical period." Presumably as a consequence of following during the critical period there develops a more or less long-lasting preference for the object originally followed. It is as if the image of an object can be imprinted upon a *tabula rasa* only during a relatively brief labile period. Once imprinted, the *tabula* retains the image. Such, briefly, is the classical view of the phenomenon of imprinting. For a history of this concept, see (*1*); for a discussion of its experimental parameters, see (*2*).

We have recently published results of experiments that, to our surprise, confounded this view (*3*). Initially, we merely demonstrated that the exposure to a moving model during the critical period was indeed necessary if our subjects (domestic vantress-cross chicks and domestic peking ducklings) were to show the following-response outside of the critical period. We then divided our experimental animals into two groups; individuals of each group were exposed to one or the other of two models during the critical period. One of these models was a white papier-mâché mallard decoy (plain model); the other was an identical decoy that was painted a variety of bright colors. Twenty-four hours after the original exposure the animals were allowed a simultaneous choice between the two models. They chose to follow the brightly colored model regardless of which of the two they had originally been exposed to (Table 1). It must emphasized that during the initial exposure, both models, the plain and the colored, had elicited the same following from the same number of chicks or ducklings.

We interpreted the foregoing to mean that the imprinting experience—that is, the exposure to a model during the critical period—served merely to activate the following-response. The preferred characteristics of the object being followed were apparently fixed in some other way, presumably independently of the visual experience of the subjects (all subjects were reared and kept in the dark except during the 20-minute training and testing sessions). It is possible that the preferred shape or some other feature of the object followed is influenced by experiences during the critical period. This we cannot judge, since color (or brightness) and pattern were our only variables. Nonetheless, the results of these experiments were sufficiently startling that it became necessary to ask a number of new questions. Most important of these was the question of whether the preferred following-surrogate, in this case, the painted model, was also preferred in other contexts. For instance, even though the imprinting experience might not determine the characteristics of the preferred following-surrogate, it might be important for determining the characteristics of the preferred objects of sexual attentions (for example, *4*).

Our procedure was identical to that described previously (*3*) (see Table 2). In brief, each chick was exposed to one of the training conditions for 20 minutes while between the ages of 21 days and 15 hours to 22 days and 5 hours, as measured from the onset of incubation. Twenty-four hours after this initial exposure, all animals were tested by being exposed simultaneously to their original training model and the other model, both models being stationary. Following was scored (in seconds) whenever the animal was moving with the model and within a certain distance of its tail or side; an "approach", in the case of the stationary models, was recorded whenever the subjects were within 30 cm of either model. The models themselves were suspended at opposite ends of a table, 1.5 m in diameter. The models emitted a recorded "come, come, come" sound, both during the training and testing sessions, our preliminary trials having demonstrated that stationary, silent models evoke very few responses. It should be noted that our subjects were not in any way constrained to make a choice: the size of the testing apparatus was sufficiently large so that they could wander about in a random fashion without a choice ever having to be recorded. Thus, our criteria for a preference were rather rigorous (compare *1*).

Table 1. Preference tests with moving models (in each group, $N = 42$).

Groups	Mean score during test (seconds)		Probability of chance difference*
	Painted model	Plain model	
1. Trained to moving, plain model	137.0	98.0	< .01
2. Trained to moving, painted model	156.5	72.2	< .01
3. Untrained controls†	32.2	29.2	> .2
4. Untrained controls‡	36.4	33.5	> .2

* Wilcoxen signed rank, matched pairs, two-tailed test. † Tested at usual training age. ‡ Tested at usual testing age.

Table 2. Preference tests with stationary model (in each group, $N = 45$).

Group	Mean score during test (seconds)		Probability of chance difference*
	Training model	Other model	
1. Trained to moving, plain model	353.1	87.6	< .01
2. Trained to moving, painted model	273.2	97.4	0.02–0.03
3. Trained to stationary, plain model	81.8	22.8	0.1–0.15
4. Trained to stationary, painted model	71.2	27.6	> .2
5. Control (empty apparatus during training)	69.6	42.3	> .2

* Wilcoxen signed rank, matched pairs, two-tailed test.

The data indicate that in the case of chicks originally exposed to a moving model, a preference for the training model is evident when the tests are conducted with stationary models. This is in accord with the traditional view of imprinting. It is quite a different result from that described earlier where moving models were used during the test, and a preference for the painted model was shown by all experimental subjects.

Of the 90 birds exposed to a moving model, only 33 actually followed their model for 60 seconds or more during the training period. These 33 birds showed a much greater preference for their training model (by a factor of more than two) than did the other 57 birds. Thus, the unselected data given in the table actually underestimate the strength of the preference for the training model, due to the presence of a substantial proportion of totally unresponsive or "sleepy" birds.

The birds that were exposed to a stationary model showed no significant preference for the training model. However, it is of interest that of the eight birds that approached the model during training, six showed a strong preference for their training model during the test. Most of the others were unresponsive. Thus, the lack of any significant preference in the group of stationary-trained birds as a whole is probably due 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

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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.

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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

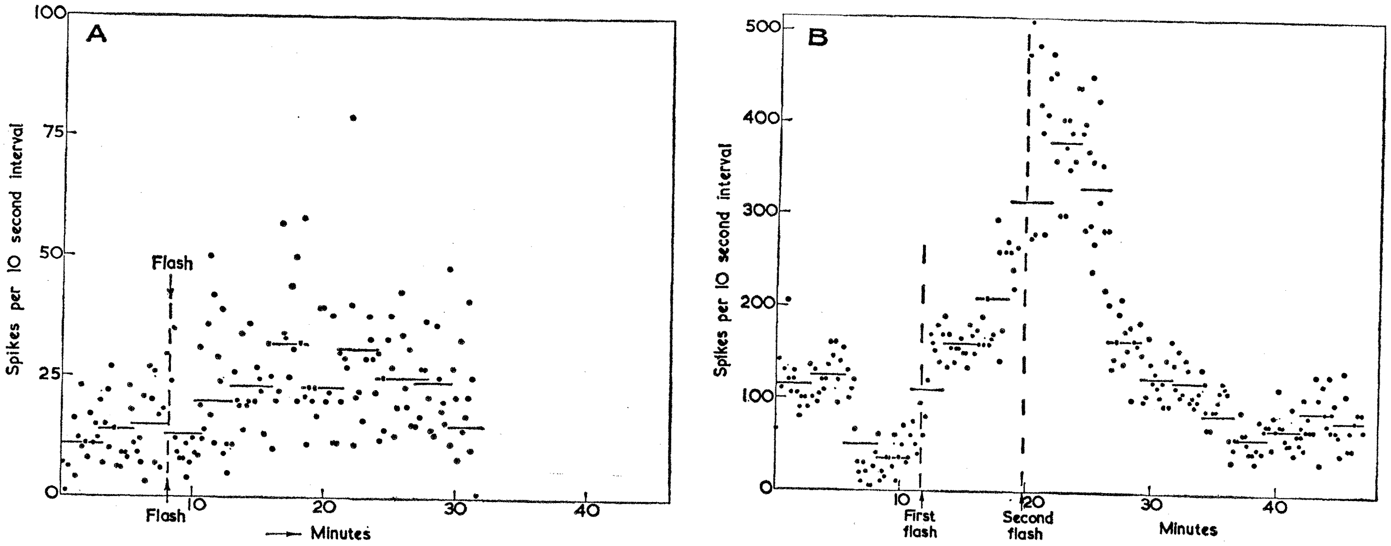

Fig. 1. Changes in the rate of firing following one (*A*) or two (*B*) intense flashes of light to the retina. Horizontal bars represent mean values of spikes per 10-second interval over 2.5-minute periods.