Following-Response Initiation in Ducklings: Age and Sensory Stimulation

Abstract. *On the basis of visual stimulation alone, younger ducklings are much less apt than older ducklings to follow a moving model. When the model emits both visual and auditory stimulation, the following-response of the ducklings is greatly enhanced at all ages.*

When ground-nesting ducklings are exposed to a vocalizing, moving model during a relatively restricted period after hatching and their subsequent responsiveness is tested by exposing them to the auditory and visual aspects of the model *independently,* some of the ducklings respond more strongly to the auditory aspect and others respond more strongly to the visual aspect (*1*). Depending on the conditions under which the bird is reared, these relatively balanced (polymorphic) behavioral tendencies are found to be related or unrelated to the developmental age of the duckling at the time of its initial exposure to the vocalizing model (*2*). Specifically, when a hatchling is reared in social isolation under conditions which preclude visual and locomotor experience, its competence or preference for visual imprinting (as determined by testing) becomes more highly developed when its initial exposure to the vocal model occurs during the second half or later portion of the critical period, while its competence or preference for auditory imprinting (as determined by testing) is related to initial exposure to the vocal model during the early portion of the critical period. Thus, under these conditions, the sensory aspects of imprinting are serially related to developmental age (young = auditory, older = visual). When ducklings are reared communally under conditions that do not preclude visual and locomotor experience, visual and auditory imprinting occur with equal likelihood and are unrelated to age at initial exposure.

In the present study two corollaries of the results reported for ducklings reared under conditions of reduced visual and locomotor opportunity are examined. These corollaries involve predicting the ducklings' behavior upon their *initial* exposure to a silent or vocal model. First, in such ducklings the likelihood or strength of following a moving model on the basis of only visual stimulation should heighten with increasing age, becoming maximal during the later portion of the critical period. This prediction tests the notion that the visual competence of these ducklings increases with age (*2*). Second, in line with the suggestion that sound plays an attentional or activating role in visual imprinting (*1, 2*), augmenting the visual stimulative characteristics of the model by having it emit auditory stimulation should exert an enhancing effect on the following-response of the ducklings at all ages. These corollaries were tested by determining the effect of the presence and absence of auditory stimulation on the initiation of the following-response of Peking ducklings (*Anas platyrhynchos*) exposed to a moving model at different developmental ages and at different ages after hatching.

The 170 duck eggs were subjected to a refrigeration procedure before they were incubated. This procedure allowed the ducklings' developmental age (in days and hours from onset of incubation) to be calculated with reasonable accuracy (*3*). Once the eggs had hatched, the ducklings were placed in individual closed boxes in a brooder. During one of three developmental age ranges, when their age after hatching was from 8 to 50 hours, the ducklings were individually exposed for 20 minutes to a moving, multicolored model (a male Mallard decoy) as the model traversed a 14-foot circular course in 58 seconds, including two 4-second pauses (*4*). (The experiment was repeated with the same pattern of results when the speed of the model was reduced to 166 seconds for the course, including six 4-second pauses, except that the best dividing line for visual responsiveness proved to be 13 hours rather than 17 hours after hatching.) Eighty birds were exposed to the model as it moved silently, and 90 birds were exposed to the model as it moved and emitted the exodus call of the Wood duck (*Aix sponsa*) (*5*). The following-response of the birds was measured by the same criteria employed in previous studies (*2*). The results of the present study can be depicted in terms of the *incidence* as well as the *strength* of following. On the basis of previous findings (*1, 2*) it was possible in terms of developmental age to predict the specific point (27½ days from the onset of incubation) at which Peking ducklings should begin to become more responsive to a silent moving object. No specific point could be predicted with confidence for the posthatch age baseline.

Table 1. Average strength of following (as measured by time in seconds) addressed to silent and vocal model. According to the Mann-Whitney test, the older birds followed the silent model more strongly than the younger birds according to both age baselines ($p < .02$). There was a profound increase in strength of following the vocal model (compared to the silent one) in both the younger and older birds: developmental age 27 days, 0 to 11 hours ($p = .002$), 27 days, 12 to 23 hours ($p = .00003$), and 28 days, 0 to 11 hours ($p = .01$); posthatch age 8 to 17 hours ($p = .001$) and 18 to 50 hours ($p = .001$).

Age	Time (sec)	
	Silent	Vocal
< 27½ days (developmental)	41.8	252.8
> 27½ days (developmental)	67.2	300.4
8–17 hours (posthatch)	6.0	102.4
18–50 hours (posthatch)	84.9	346.4

Figure 1 shows that the likelihood of a duckling's following the silent model significantly increased with developmental age, with proportionately more ducklings following after 27½ days of development ($\chi^2 = 7.26, p = .007$). The same picture holds for posthatch age (Fig. 2), with propor-

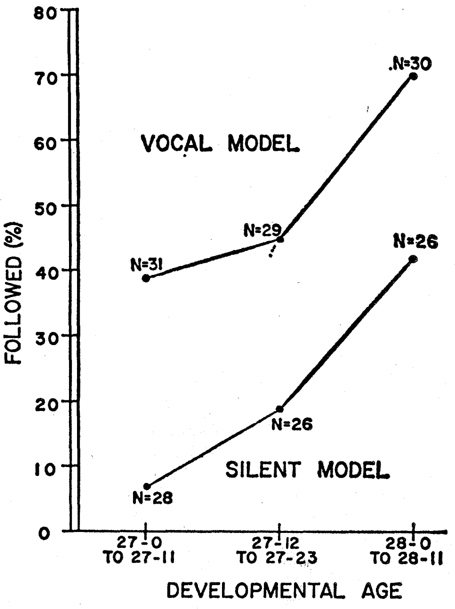

Fig. 1. Proportion of ducklings which followed silent and vocal model at each developmental age (in days and hours from onset of incubation).

tionately more ducklings following when their posthatch age was more than 17 hours ($\chi^2 = 6.71$, $p < .01$). Analyses of the strength of following in the young and older ducklings (Table 1) indicate that the older birds also followed the silent model more *strongly* than the younger ones (Mann-Whitney Tests, $p < .02$ in both age base lines).

As can be seen further in Fig. 1, Fig. 2, and Table 1, vocal stimulation exerted a very potent effect on the instigation and the strength of following at all ages in both baselines. The statistical information concerning the increase in incidence of following addressed to the vocal model over the silent one follows: posthatch age 8 to 17 hours ($\chi^2 = 10.9$, $p < .001$) and 18 to 50 hours ($\chi^2 = 7.67$, $p = .005$); developmental age 27 days, 0 to 11 hours ($\chi^2 = 9.9$, $p = .002$), 27 days, 12 to 23 hours ($\chi^2 = 5.33$, $p = .02$), and 28 days, 0 to 11 hours ($\chi^2 = 5.57$, $p = .02$). The statistical analyses concerning the increase in strength of following the vocal model over the silent one are consistent with the above results and are presented in Table 1.

The present evidence indicates that the duckling's ability to follow a model sheerly on the basis of visual stimulation increases with age and that auditory stimulation plays an important activating or attention-directing function at all ages. These findings are consonant with the implications of the previous work outlined in the introduction of this report. In addition, the present laboratory demonstration of the enhancing effect of auditory stimulation coordinates well with the naturalistic observation (*6*) that auditory stimulation is a prominent component of "imprinting" as it occurs in the wild (*7*). At present there is no evidence to suggest that tactile, thermal, or olfactory stimulation play a significant role in instigating the following-response (*8*).

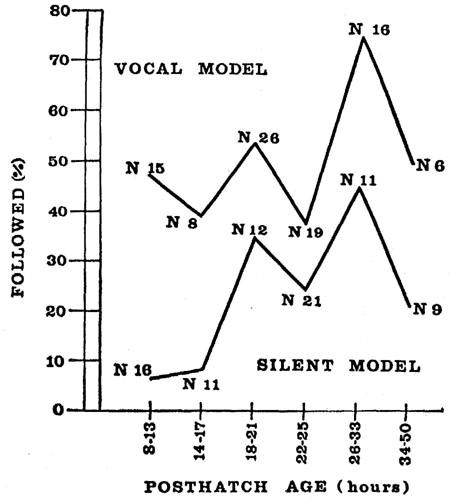

Fig. 2. Proportion of ducklings which followed silent and vocal model at each posthatch age range.

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References and Notes

1. P. H. Klopfer and G. Gottlieb, *J. Comp. Physiol. Psychol.* **55**, 126 (1962).
2. G. Gottlieb and P. H. Klopfer, *ibid.*, p. 821.
3. G. Gottlieb, *Animal Behavior*, in press.
4. The apparatus has been described (*2*). From the standpoint of visual perception processes, it should be noted that the model appears at all points in the apparatus against a relatively homogeneous, "flat black" background from the ducklings' angle of regard. The apparatus also differs from that of other investigators in that it is not of the circular maze type—that is, in the present apparatus the model can be seen by the duckling at any point in the field should the duckling attend to the model.
5. Physical and other details of this call have been described by G. Gottlieb [*J. Comp. Physiol. Psychol.* **56**, 86 (1963)].
6. G. Gottlieb, *Science* **139**, 497 (1963).
7. Without benefit of detailed knowledge of the naturalistic situation, a number of researchers have implicitly or explicitly acknowledged the enhancing value of sound in instigating the following-response. The earliest reports were by: D. A. Spalding, *Macmillan's Magazine* **27**, 282 (1873); K. Lorenz, *J. Ornithol.* **80**, 50 (1935); E. Fabricius, *Proc. 10th Intern. Ornithol. Congr.* (1950), p. 3→ A. O. Ramsay, *Auk* **68**, 1 (1951).
8. Research supported by funds from the North Carolina Hospitals Board of Control and U.S. Public Health Service grant M-6039. The technical assistance of Carter Doran, Anne Smith, Frank Lane, and Linda Marsh Green is gratefully acknowledged.

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Biosynthesis of Streptococcal Cell Walls: A Rhamnose Polysaccharide

Abstract. *Protoplast membranes from* Streptococcus pyogenes *incorporated rhamnose into a preexisting polysaccharide when incubated with thymidine diphosphate rhamnose-*C^{14}. *This polysaccharide, when extracted from the membranes, did not give a precipitin reaction with group A antisera, but could be coprecipitated with added group A polysaccharide by acetone. It is presumed to be a precursor to group specific polysaccharide of the streptococcal cell wall.*

The group-specific antigen, or C-substance, of the cell walls of *Streptococcus pyogenes* is a polysaccharide. L-Rhamnose and *N*-acetyl-D-glucosamine have been identified as the only carbohydrate constituents of the C-polysaccharide (*1*) of the group A organism. A methylation study has shown that the glycosidic bonds between the rhamnose units involve carbon atoms 1 and 3. Side chains are attached at carbon atom 2 (*2*). Some of the *N*-acetylglucosamine is linked terminally and is responsible for the serologic response to antiserum to the group A streptococci (*2, 3*).

L-Rhamnose of the streptococcal cell walls is derived solely from D-glucose without scission or rearrangement of the glucose carbon skeleton (*4*). This conversion occurs through thymidine diphosphate sugar intermediates in other organisms (*5*). The same pathway occurs in group A streptococci.

We now describe an enzyme system in protoplast membranes of *S. pyogenes*, type 14, strain S_{23}, which transfers rhamnose from thymidine diphosphate L-rhamnose (TDP-Rh) to a rhamnose-containing polysaccharide present on the membranes. This particulate enzyme system is obtained from lysed protoplasts by the use of a purified lysin (*6*). That the enzyme preparation consists largely if not exclusively of protoplast membranes is deduced from the microscopic appearance, the absence of nucleic acids, the high lipid content, and the behavior with detergents. The TDP-Rh-C^{14} was prepared from glucose-C^{14}-1-phosphate (*5*) and contained 11 percent TDP-D-glucose-C^{14}, from which it could not be readily separated. In a typical experiment 40 to 50 percent of the radioactivity added as TDP-Rh-C^{14} was recovered in a polysaccharide extracted from the membranes after incubation (Table 1).

The product of the enzymic reaction

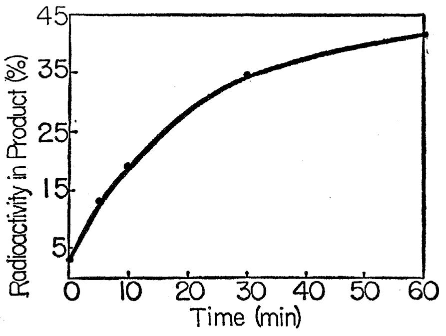

Fig. 1. Rate of incorporation of rhamnose-C^{14} from TDP-Rh-C^{14} into rhamnose polymer of protoplast membranes.