

Experiential Canalization of Behavioral Development: Results

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In exploring the possible experiential canalization of development, it was found that the mallard duck embryo's contact call plays a canalizing role in species-specific perceptual development. When mallard ducklings were prevented from hearing the contact call, they were susceptible to developing a preference for an extraspecific maternal call over the mallard maternal call. Exposure to the contact call prevented the ducklings from developing a preference for the extraspecific maternal call. Thus, normally occurring experience, in concert with genetic and other activities, can canalize behavioral development. Canalizing influences account for developmental stability, so that what we think of as normal or typical for a species repeats itself generation after generation. In order for evolution to occur, through genetic mutation or otherwise, the canalizing influences associated with normal development must be overcome. Canalization is thus a conservative feature of development that prevents evolution from occurring in a ready fashion.

My preceding article (Gottlieb, 1991a) established the theoretical framework for examining the possibility that normally occurring experience can canalize behavioral development. The present article presents empirical evidence for the experiential canalization of species-specific maternal attachment. The present hypothesis is that normally occurring experience helps to achieve species-specific development by making the developing organism unresponsive to extraspecific influences. For example, if the mallard duck (*Anas platyrhynchos*) embryo is devocalized, the usually highly selective response to the mallard maternal call is weakened: After hatching, the duckling is as responsive to a chicken (*Gallus gallus*) maternal call as to a mallard maternal call in a simultaneous-choice test (Gottlieb, 1978). Exposing otherwise devocalized embryos to a recording of mallard embryo contact vocalizations causes them to show the usual preference for the mallard call versus the chicken call in the postnatal test (Gottlieb, 1985). Exposure to other types of sibling vocalizations in embryo, or exposure to the contact call after hatching, is ineffective, so the kind of experience and the timing of the experience are highly specific.

If the experiential canalization hypothesis is correct, embryonic devocalization should make the mallard embryo and hatchling more susceptible to exposure to an extraspecific maternal call, assuming that the contact vocalization is acting as a canalizing or buffering experience. With the necessary control groups, five experimental conditions are necessary to test the canalization hypothesis, as indicated in Table 1.

In Table 1, X indicates the predicted preference and X---X indicates prediction of no preference. The two most critical

groups are 4 and 5. It is essential to demonstrate the induction of a preference for the chicken call in devocal-isolates and the buffering effect when vocal-isolates are exposed to the embryo contact call and the chicken call. The other groups are necessary control groups.

Method

Subjects

Peking ducklings are a domestic form of mallard duck. Despite their domestication, this breed has been shown to be similar to their wilder counterparts in the specificity of their auditory perception of maternal calls, as well as in various other forms of species-typical behavior (Gottlieb, 1971; Johnston & Gottlieb, 1981; Miller, 1977, 1980; Miller & Gottlieb, 1981). Unincubated eggs were received weekly from a large commercial supplier and incubated in the laboratory under conditions described in previous publications (Gottlieb, 1971, 1975).

Conditions

1. *Vocal-communal*. The vocal-communal mallards were incubated together and brooded together in groups of 15 to 25 in individual opaque boxes after hatching. Thus, they could hear themselves and each other both before and after hatching but could not see each other after hatching.

2. *Vocal-isolated (VI)*. At the beginning of Day 24 of incubation, 2 to 3 days before hatching, when the embryo is first able to vocalize, the VI mallards were put in individual soundproof incubators where they were able to hear their own vocalizations but not those of siblings. These birds served as controls for the devocal conditions below.

3. *Devocal-isolated (DI)*. As indicated in Figure 1, 2 to 3 days before hatching, during the first 8 hours of Day 24 of incubation, these embryos were muted and placed in individual soundproof incubators. They were muted in a brief operation in which their syringeal ("voice box") membranes were coated with a nontoxic surgical glue (collodion). Collodion forms a rigid sheath over the membranes, and when they are thus rigidified, the embryo (and later the hatchling) cannot vocalize (Gottlieb & Vandenberg, 1968). Our "hit" rate on devocalization is around 90%; if an embryo or hatchling can utter even the scratchiest vocalization it was eliminated from the experiment. There

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Table 1
Conditions Favoring Canalization or Malleability of Species-Specific Perceptual Preference

Condition	Predicted preference	
	Mallard	Chicken
1. Vocal communal	X	
2. Vocal-isolated	X	
3. Devocal-isolated	X	-----X
4. Devocal-isolated, exposed to chicken call		X
5. Vocal-isolated, exposed to chicken call and mallard duck embryo contact vocalization	X	

Note. X = preference; X ----- X = no preference.

is a small toll associated with the operation: About 10% fewer birds hatch than from unopened eggs.

4. *Devocal-isolated, exposed to chicken call.* The DIs exposed to the chicken call received that exposure in their soundproof incubator compartments, where a speaker repetitively broadcast a single burst of a chicken maternal call for 30 min per hour from Day 24 until 48 hr after hatching, at which time the birds were tested. (The call was actually on for 22.5 min of the 30-min period.) The call peaked at 65 dB (Scale B, fast) in the incubator and in the test (described below).

5a. *Vocal-isolated, exposed to chicken call.* These birds were treated the same as above with the exception that they could hear themselves vocalize, as well as being exposed to the 30-min chicken call each hour. (In Groups 5a and 5b, the embryos' heads were extricated from the shell in the same manner as for Group 3 and 4 birds, but they were not devocalized.) The prediction here, as indicated in Table 1, was the failure of the exposure to the chicken call to induce a preference for it because the birds had been permitted to hear their own contact call.

Although I did not monitor the vocalizations of these particular birds, I knew from unpublished observations that isolated birds produce the contact call numerous times both before and after hatching.

5b. *Vocal-isolated, exposed to chicken and embryo contact calls.* These VIs were treated the same as Group 5a, except that they were exposed to 10 min of the variable-rate embryonic contact call (Gottlieb, 1985) after 30 min of exposure to the chicken call each hour. Because I did not monitor the self-produced vocalizations of the birds in Group 5a, this group provided a more precise fix on a known amount of exposure to the contact call that is required for the buffering effect. The choice of the amount of exposure to the contact call was originally arbitrary. In the 10-min period, the call was actually on for 4.6 min, which we now know from monitoring studies is at the bottom of the range produced by individual birds in isolation (4.8–6.2 min per hour, from unpublished observations). This amount of "sib stimulation" is well below the amount that would be received under natural incubation and brooding conditions, in which the birds would be exposed to as many as 8 to 13 conspecific siblings. Thirty min per hour of exposure (actually 22.5 min) to the extraspecific chicken call was shown to be effective in a previous study of malleability in devocalized ducklings (Gottlieb, 1987a), but those ducklings were tested with the chicken call versus the wood duck maternal call, not versus the mallard maternal call. The presence of the mallard call in the simultaneous auditory choice test with the chicken call provided a much sterner test of malleability than using two extra-specific maternal calls.

Test. Each bird was tested individually at 48 hr (± 4 hr) after hatching, as illustrated in Figure 2.

A speaker was mounted behind each of the two elliptical areas, each broadcasting the chicken or mallard calls over the 5-min test period. As the bird entered the elliptical area in the vicinity of a speaker, the duration of its stay (in seconds) was measured. The duration scores for each call were analyzed by the Wilcoxon test to get a preference for each group (condition) in the experiment. A further measure of preference for each bird was derived as follows: If a bird stayed in one approach area more than twice the time it spent in the opposing area, a preference was registered. This measure of preference gives a useful

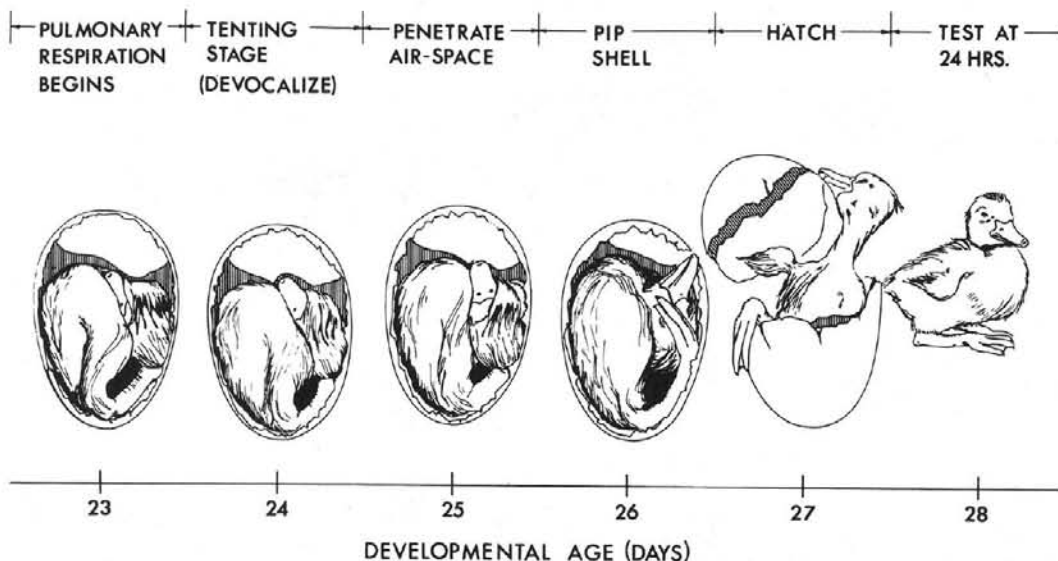


Figure 1. Pulmonary respiration begins on Day 23 of incubation in the domestic mallard duck embryo and is well established by Day 24. When respiration is established, the embryo survives the devocalization operation, which requires extricating its head from the eggshell and painting its syringeal membranes with surgical glue.

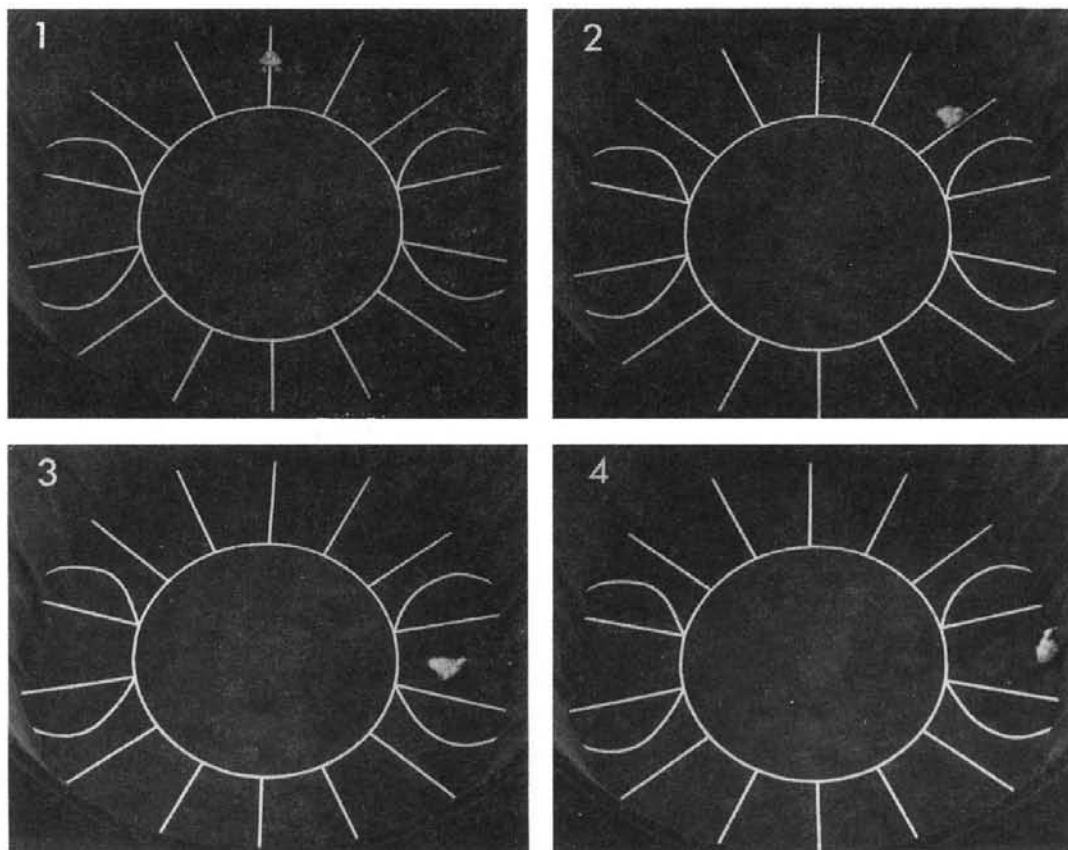


Figure 2. Overview of simultaneous auditory-choice test. (1) Duckling placed equidistant between two speakers (not visible), in front of which are painted elliptical approach areas. (2) Duckling on its way toward approach area on its left. (3) Duckling in approach area. (4) Duckling snuggling to curtain and orienting to nonvisible speaker broadcasting a maternal call of its own (or another) species.

summary tabulation of the behavior of each bird in the experiment and allowed further statistical treatment of preference in terms of the chi-square test (between conditions) and the binomial test (within conditions). The latter almost always agreed with the duration measure described earlier and thus lent strength to the results, whether for a preference or the absence of a preference in the choice test. A preference was indicated by a two-tailed p value of .05 or less. P 's greater than .05 were indicative of no preference. In all cases but one, the results of the binomial test and the Wilcoxon test were in agreement as to the presence or absence of a preference, so to conserve space and avoid repetition, only the former are reported in detail. The single exception concerned Group 5b's performance at 48 hr, for which the binomial was nonsignificant and the Wilcoxon indicated a mallard preference.

To assess the "durability" of the 48-hr test results, each bird in Groups 4, 5a, and 5b was retested at 65 hr. Because exposure to the chicken call (and contact call) was terminated at 48 hr, the 65-hr test results give some indication of the enduring effect of the earlier experience.

Results

As can be seen in Table 2, the vocal-communal and VI birds showed, as expected, a unanimous preference for the mallard call over the chicken call, whereas the unstimulated DIs did not

show a preference. Furthermore, as predicted, the DI birds exposed to the chicken call showed a preference for the chicken call over the mallard call at 48 hr and continued to show that preference at 65 hr. Also as predicted, the VI birds exposed to the chicken call (Group 5a) did not develop a preference for it, as evidenced by their behavior in the 48- and 65-hr tests. The buffering effect of the contact call was even more clearly in evidence in Group 5b, in which the birds received explicit exposure to the contact call, as well as the chicken call: These birds preferred the mallard over the chicken call in both tests. The results from Group 5a indicate a blockage of the chicken preference by self-stimulation, but, to maintain the species-typical preference for the mallard call in the face of exposure to the chicken call, exposure to contact calls produced by siblings is required (Group 5b). Group 5b heard the broadcast of only one sibling's calls, which would be considerably less than would occur under normal incubation and brooding conditions in nature.

According to the chi-square test, when the preferences of the groups are compared across conditions, the unstimulated vocal-intact (Group 2) birds showed a greater preference for the mallard call than did the unstimulated DI (Group 3) birds. As predicted, the DI birds that were exposed to the chicken call

Table 2
*Preferences of Mallard Ducklings in Simultaneous
 Auditory-Choice Test*

Condition	N	N responded	Preference		
			Mallard call	Chicken call	Both
1. Vocal-communal	30	24	24***	0	0
2. Vocal-isolated	20	14	14***	0	0
3. Devocal-isolated	83	43	26	15	2
4. Devocal-isolated, exposed to chicken call	26	21	3	17**	1
Retest	23	17	2	15**	0
5a. Vocal-isolated, exposed to chicken call	36	26	11	15	0
Retest	36	30	16	12	2
5b. Vocal-isolated, exposed to chicken and contact calls	41	31	19	12	0
Retest	38	28	20*	6	2

Note. Results of Conditions 1 and 3 are from Table 2 in "Development of Species Identification in Ducklings: IV. Change in Species-Specific Perception Caused by Auditory Deprivation" by G. Gottlieb, 1978, *Journal of Comparative and Physiological Psychology*, 92, p. 380. Copyright 1978 by the American Psychological Association. In the first test of Group 5b, the binomial test is nonsignificant, whereas the Wilcoxon analysis of differences in approach duration scores favoring mallard is significant ($p < .02$). Otherwise, all Wilcoxon outcomes agree with the presence or absence of preference according to the binomial test.

* $p < .01$. ** $p \leq .004$. *** $p < .00006$.

(Group 4) showed a greater preference for it than did the unstimulated DI (Group 3) birds. As predicted, the stimulated DI (Group 4) birds also showed a greater preference for the chicken call than did the stimulated VI (Group 5b) birds, which showed a greater relative preference for the mallard call. For all of the above differences, $p < .00006$.

Discussion

To my knowledge, this is the first explicit demonstration of the canalizing influence of normally occurring sensory experience. Exposure of mallard ducklings to their variable-rate contact call not only fosters species-specific perceptual development (i.e., ensuring selective responsiveness to the maternal call of the species), it also buffers the duckling from becoming responsive to social signals from other species. In the absence of exposure to the contact call, the duckling is capable of becoming attached to the maternal call of another species even in the presence of its own species call (in simultaneous auditory-choice tests). My previous demonstration of malleability in devocalized mallard ducklings (Gottlieb, 1987a) involved the induction of a preference for either a chicken maternal call or a wood duck (*Aix sponsa*) maternal call; the birds were tested with the chicken versus wood duck calls, not the mallard maternal call. To be quite frank, I did not believe that it was possible to demonstrate malleability in the presence of the species-

specific maternal call. It was only when I began to think of the possible canalizing effect of experience that it became apparent that devocalization might permit such a degree of malleability that exposure to an extraspecific maternal call would override the "innate" attractiveness of the species maternal call. Clearer thinking about what genes do and do not do in individual development gave rise to the idea that canalization must take place not only at the genetic level but at all levels of the developing system (Gottlieb, 1991a, Figure 1), including the developing organism's usually occurring experiences. The fact that canalizing influences are potentially present at all levels of the developing system has not been widely appreciated. Because the developmental ramifications of canalization were described fully in the foregoing article (Gottlieb, 1991a), I limit the present discussion to the evolutionary implications of canalization.

Canalization and Evolution

Canalizing influences account for developmental stability, so that what we think of as normal or typical for a species repeats itself generation after generation. For evolution to occur, through genetic mutation or otherwise, the canalizing influences associated with normal development must be overcome. Canalization is thus a conservative feature of individual development that prevents evolution from occurring in a ready fashion.

Elsewhere (Gottlieb, 1987b), I took Kuo's (1976) idea of behavioral neophenotypes and applied it to the problem of evolution. In essence, the creation of a new behavioral phenotype (behavioral neophenogenesis) requires a change in normal or usual rearing circumstances that ordinarily function to canalize development along species-typical lines. An altered behavioral phenotype causes the affected individuals to change their way of life, exploiting new habitats, diets, and so on, which will eventually lead to morphological change and perhaps eventually to genetic change (through long-continued selective breeding among the descendants of the affected individuals). Behavioral change is widely considered to be the first step in the pathway to evolutionary change (Bonner, 1983; Hardy, 1965; Lamarck, 1809/1984; Larson, Prager, & Wilson, 1984; Leonovicová & Novák, 1987; Piaget, 1978; Reid, 1985; Sewertzoff, 1929; Wyles, Kunkel, & Wilson, 1983), and behavioral change is most readily accomplished by overcoming or changing the experiential canalizing influences that are present in the usual course of individual development. Behavioral neophenogenesis allows evolution to proceed at a much more rapid rate than is the case when a species must await a severe environmental change or catastrophe such as oceans drying up or months of darkness to prune individuals that are capable of adapting to the change from those that are not. Such extreme environmental changes are rare and widely spaced in time compared with the frequency and tempo of evolution that could be instigated by behavioral neophenotypes.

Thus, an understanding of the experiential canalization of behavioral development has potentially significant implications for our understanding of evolution (and especially the resistance to evolution). The present proposal is unconventional in relation to the neo-Darwinian concept of evolution in that it postulates an extragenetic "behavioral mutation" rather

than a genetic mutation as the instigator of evolutionary change. Along these lines, it has been demonstrated that certain extragenetic behavioral and morphological changes are "heritable" in the sense that they recur in subsequent generations (Clark & Galef, 1988; Denenberg & Rosenberg, 1967; Ho, 1984; Skolnick, Ackerman, Hofer, & Weiner, 1980).

It is important to realize that although experimentally produced genetic mutations and selective breeding have produced many new varieties or subspecies, such mutations have never produced a new species, even when the experimental program extended over 30 years and involved tens of thousands of generations (e.g., Goldschmidt, 1933). Ever since the time of W. Bateson (1894), a minority of biologists have despaired of a new species evolving from a new variety that has been produced by genetic mutation and selective breeding. Thus, while I do not want to present the behavioral mutation idea as a mutually exclusive alternative to genetic mutation, I do think that it is worthwhile to consider the experiential dissolution of canalization and the behavioral route to evolutionary change as a potentially valid pathway. The behavioral–developmental pathway to evolutionary change is described in detail in Gottlieb (1991b).

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