On the Epigenetic Evolution of Species-Specific Perception:

The Developmental Manifold Concept

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Abstract

As evolution proceeds, natural selection operates to preserve adaptive phenotypes. The adaptive phenotypes are produced during the course of individual development. Thus, natural selection favors animals that have had a particular developmental history, including, but not restricted to, their genes. This point is demonstrated by the importance of normally occurring embryonic sensory stimulation in the development of instinctive perception in two species of ducklings.
That natural selection plays a role in evolution is indubitable. However, the exact nature of that role is often misunderstood. For example, evolutionary psychologists think that natural selection causes adaptations: "natural selection is the only known causal process capable of producing complex functional organic…adaptations" (Buss et al., 1998, p. 533). On the contrary, natural selection operates on already-developed adaptive phenotypes--it does not cause these phenotypes. The role of natural selection is to preserve adaptive phenotypes once they have surfaced as an outcome of development.

As so insightfully stated by the biologist J.A. Endler (1986, p. 51), "natural selection cannot explain the origin of new variants and adaptations, only their spread."

Thus, natural selection works on phenotypes that have had a particular developmental history. Although natural selection doesn't care about the details of that developmental history, it is in effect selecting for that developmental history in order for the adaptive phenotype to be produced reliably generation after generation. Because the development of all phenotypes involves genes, genes will always be a part of that developmental history. But learning (or more broadly speaking, a developing animal's experience with its past stimulative environment) can also be a part of that history. Natural selection favors animals that have benefited from their past experience, whether that experience occurred embryologically in the prenatal period or after birth or hatching in the postnatal period. In effect, natural selection favors animals that have experienced certain prior interactions at the genetic, cellular, organic, or at the whole organism-environment level of analysis. Ever since the advent of experimental embryology in the late 1800s, it has been appreciated--at least in some quarters--that development involves interactions. We are now safe in generalizing that conclusion to all levels of analysis:
An organism's genetic activity, anatomy, physiology, behavior, and psychological makeup are always a consequence of such interactions. In order to capture the flavor of the manifoldness of these interactions, I coined the term *developmental manifold* in 1971. Thus, the DM includes both nature (biology) and nurture (experience broadly defined to include the spontaneous or evoked activity of neurons, hormonal influences and the like, as well as organism-environment coactions).\(^1\) My own research on instinctive behavior--species-specific perceptual development, in this case--forced the developmental manifold view on me, in contrast to the then-prevalent idea that the developmental history of instinct should be conceptualized as genetic activity $\rightarrow$ nervous system $\rightarrow$ instinctive behavior in a strictly feed-forward manner. Rather, in the spirit of the theme of this special issue, the organism coactionally constructs itself anew in each generation in relation to its internal and external environment. (See the various reviews converging on this point in Oyama, Griffith, & Gray, 2001.) This is an active, bidirectional process that involves coactions both within and between all levels of analysis from the genes to the external social and physical environments. But I am getting ahead of my story.

During the course of conducting my dissertation involving a laboratory study of imprinting in ducklings (Gottlieb, 1961), it became obvious that, even at the height of the sensitive period, not all of the ducklings followed the imprinting object (something that would not be likely to be happening in nature). Consequently, my wife Nora and I began to observe imprinting in several species of ducks in nature to see what was going on in the "real world" of ducklings. In both hole-nesting wood ducks (*Aix sponsa*) and ground-nesting mallard ducks (*Anas platyrhynchos*), we observed that the hen uttered a species-
specific maternal call to entice her young from the nest. Imprinting as studied in the laboratory was thought to be largely a visual phenomenon: young birds had been shown to learn the visual characteristics of a large array of artificial objects. When the species-specific maternal call was added to standard visual objects in the laboratory experiments, I found that now 100% of the birds would follow, as was apparent in nature. Not only that, but it became apparent that the different species had a foreknowledge of the maternal call of their species: ducklings and chicks hatched in incubators would selectively approach and follow the maternal call of their species without having been previously exposed to it! Thus, species identification was instinctive as far as the auditory modality was concerned. In examining the relative importance of the visual and auditory aspects of the hen, wood ducklings and mallard ducklings hatched in the laboratory preferred the disembodied maternal call of their species to a moving but silent stuffed hen of their species (Gottlieb, 1968).

Developmental Manifold and Probabilistic Epigenesis

Having been influenced by the epigenetic thinking about instinctive behavior put forward by Kuo (1976), Schneirla (1960), and Lehrman (1970), I embarked on a long series of experiments to determine whether normally-occurring embryonic auditory experience had anything to do with the selective response to the maternal call of the species after hatching. Embryos begin to vocalize several days before hatching and even
though these vocalizations do not sound like the maternal call, I wondered whether they might be involved in establishing the selective response. After eighteen months of exploration, with the assistance of John Vandenbergh, I devised a technique to devocalize embryos (Gottlieb & Vandenbergh, 1968) in a way that otherwise did not harm them. That technique allowed the experimental study of the instinctive selectivity for the maternal call of the species in the absence of prior normally-occurring vocal-auditory experience. As shown in Table 1, the selectivity of the devocalized mallard duckling was negatively affected by not experiencing their embryonic vocalizations: devocalized mallards were as apt to prefer a chicken maternal call as the mallard maternal call. The control group of devocalized birds that were allowed to hear their own embryonic vocalizations for 18-21 hours before they were devocalized (Delayed group) preferred the mallard maternal call over the chicken maternal call. Thus, I was able to conclude:

The present results indicate that the epigenesis of species-specific auditory perception is a probabilistic phenomenon, the threshold, timing, and ultimate perfection of such perception being regulated jointly by organismic and sensory stimulative factors. In the normal course of development, the manifest changes and improvements in species-specific perception do not represent merely the unfolding of a fixed or predetermined organic substrate independent of normally occurring sensory stimulation. With respect to the evolution of species-specific perception, natural selection would seem to have involved a selection for the entire developmental manifold, including both the organic and normally occurring stimulative features of ontogeny. (Gottlieb, 1971, pp. 156-157)

In order to avoid having these results and conclusions cast as a victory for nurture in the ongoing nature-nurture debate, I (1971, p. 157) went on to say,
One of the main questions in the ontogeny of behavior concerns the contribution of genetic (molecular) and other biochemical factors. While there is agreement that such factors provide an indispensable impetus to neural maturation, the exact nature or mechanics of the molecular and biochemical control of early neural maturation is not yet known.

Building on the writings of my aforementioned predecessors, I had first put forward the concept of probabilistic epigenesis in 1970, in a review of conceptions of behavioral embryology. In reviewing the literature, I found two dominant conceptions of behavioral embryology, one of which I labeled predetermined epigenesis and the other, probabilistic epigenesis. Initially, I thought the main dividing point of the two conceptions was their view of the structure-function (S-F) relationship. In the predetermined view, the S-F relationship was unidirectional (S→F), whereas in the probabilistic view it was bidirectional (S↔F). Phrased in this way, these conceptions became empirically testable (i.e., does function influence the maturation of structure?). In 1976, I extended these notions to the genetic level, and elaborated on this topic in reviews published in 1983 and 1991a as follows:

**Predetermined Epigenesis**

**Unidirectional Structure-Function Development**

Genetic activity (DNA → RNA → Protein) →

structural maturation → function, activity, or experience

**Probabilistic Epigenesis**

**Bidirectional Structure-Function Development**

Genetic activity (DNA ↔ RNA ↔ Protein↔)

structural maturation ↔ function, activity, or experience
As it applies to the nervous system, structural maturation refers to neurophysiological and neuroanatomical development, principally the structure and function of nerve cells and their synaptic interconnections. The unidirectional S-F view assumes that genetic activity gives rise to structural maturation that then leads to function in a nonreciprocal fashion, whereas the bidirectional view holds that there are reciprocal influences among genetic activity, structural maturation, and function. In the unidirectional view, the activity of genes and the maturation process are pictured as relatively encapsulated or insulated, so that they are uninfluenced by feedback from the maturation process or function, whereas the bidirectional view assumes that genetic activity and maturation are affected by function, activity, or experience. The bidirectional or probabilistic view applied to the usual unidirectional formula calls for arrows going back to genetic activity to indicate feedback serving as signals for the turning on and off of genetic activity. The usual view, as in the central dogma of molecular biology, calls for genetic activity to be regulated by the genetic system itself in a strictly feed-forward manner. The central dogma of molecular biology has been a highly influential and outstanding example of predetermined epigenesis. It was not until 1998 that I was finally able to publish a comprehensive empirical review of bidirectionality from behavior and the external environment to the genetic level, in the context of a critique of the central dogma.

Teasing Apart the Developmental Manifold

The fact that devocalized ducklings lacked the auditory perceptual specificity of their vocal counterparts did not in itself provide sufficient evidence that the
developmental manifold plays a constructive role in the ontogeny of instinctive behavior. In the same year (1971) that my monograph was published, Roger Sperry (1971, p. 32) was writing, "In general outline at least, one could now see how it could be entirely possible for behavioral nerve circuits of extreme intricacy and precision to be inherited and organized prefunctionally solely by the mechanisms of embryonic growth and differentiation." This was an extension of what Sperry had written earlier (1951, p. 271), "Development in many instances . . . is remarkably independent of function, even in . . . [the] sense [of] . . . function as a general condition necessary to healthy growth." In order to document the constructive role of embryonic auditory experience in the development of auditory perceptual specificity it was necessary (1) to document the specific perceptual deficit in the devocalized duckling and (2) show which aspect of the embryonic vocalization the embryo needed to be exposed to in order for that deficit to be rectified in the hatchling. (At that time, ethologists did not believe that the development of instinctive behavior required specific, as opposed to rather general, experiential inputs.) The accomplishment of aims (1) and (2) took fourteen years of experimentation (summarized in Gottlieb, 1997).

Insert Table 2 about here

It turned out that, of the two main perceptual deficits, high-frequency insensitivity and repetition-rate generality, the former belatedly but only temporarily rectified itself (possibly through the contribution of spontaneous neural discharges in the auditory system--Gottlieb, 1997, pp. 53-57), whereas the latter could be rectified only by the
embryo hearing its contact call in all the variations of repetition rate that would normally
be produced by the embryo itself. The embryo's contact call changes in the hatchling,
such that it no longer has the appropriate frequencies or ranges of repetition rates to "fix"
the embryonic deficit. Also, the embryo must experience the embryonic contact call in
the embryonic state; exposing devocalized hatchlings to the embryonic contact call does
not rectify the repetition-rate deficiency. These were striking findings in the sense of
demonstrating the remarkable specificity of the developmental manifold, in terms of
timing and stimulus parameters, as well as calling our attention to the often non-obvious
role of normally occurring experience. As shown in Table 2, the embryo had to
experience embryonic vocalizations in their typically produced repetition-rate range from
2-6 notes/second in order to come to prefer the mallard maternal call at its species-typical
rate of 4 notes/second. In the absence of hearing the full range, the devocalized hatchling
did not prefer the species-typical 4 notes/second maternal call at the usual time (24 hr.)
after hatching but continued to be equally responsive to the mallard maternal call at both
4 notes/second and 2 notes/second (the latter artificial alteration being the repetition rate
of the chicken maternal call). Although the requisite embryonic auditory experience
could be considered perceptual learning of sorts, it certainly was not as straightforward as
imprinting. In fact, as shown in Table 2, devocalized embryos exposed to the embryonic
call at 4 notes/second did not prefer the 4 notes/second maternal call at 24 hrs. after
hatching, as would have been predicted by a straightforward learning hypothesis.

---------------------------------------------
Insert Table 3 about here
---------------------------------------------
The importance of hearing species-specific embryonic vocalizations was also shown to be the case for wood ducklings, in which frequency modulation rather than repetition rate is the critical acoustic feature of the wood duck maternal call. While mallard ducklings can remain on their species-specific perceptual trajectory by hearing either embryonic calls produced by themselves or siblings, wood ducklings must hear the calls of siblings, auditory self-stimulation being ineffective in that species (Gottlieb, 1984). The requisite specificity of normally occurring experience is as striking in the wood ducklings as it is in the mallards. A descending frequency modulation (FM) around 1300 Hz is the critical acoustic feature of the wood duck maternal call. As shown in Table 3, communally reared wood ducklings prefer a synthetic wood duck maternal call with a descending FM over an ascending FM. Aurally isolated wood ducklings do not show a preference. The wood duckling's calls contain an exaggerated descending FM between 5,000-3,000 Hz. When the duckling's call is played backwards it has an ascending FM and does not work to rectify the perceptual deficit in aurally isolated wood ducklings; the duckling's call must be played in the forward direction (descending FM) to rectify the deficit (Table 3).

Experiential Canalization of Behavioral Development

In 1991, much to my surprise, I found that, in the absence of hearing their own or sib vocalizations, devocalized mallard embryos remained malleable, in the sense that
exposing them to a recording of a chicken maternal call resulted in their development of a preference for the chicken call over the mallard call. As shown in Table 4, vocal-isolated embryos were buffered against developing a preference for the chicken call and merely exposing them to recorded embryonic vocalizations (10 minutes/hour) allowed them to retain their preference for the mallard despite being exposed to the chicken call (30 minutes/hour for 96 hours). This study lent further support to the developmental manifold concept, showing that

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, …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. (Gottlieb, 1991b, p. 35)

As the present experiments make clear, developmental canalization does not emanate merely or solely from the genetic level, as advocated by Waddington (1957, p. 36, Figure 5), but it also involves normally occurring experiences as well--ones that influence neural and behavioral development and can serve as signals for gene activation (Gottlieb 1998).

Malleability

A feature of probabilistic epigenesis and developmental theory more generally speaking is the embryological concept of equifinality, meaning that the same developmental outcome can be reached by different routes (or from different starting
points).\textsuperscript{2} Miller (1997) has made an explicit study of multiple pathways to the same developmental outcome in the instinctive alarm-call responsivity of devocalized ducklings. In a companion study to the one mentioned above, in which devocalized embryos could become imprinted to a chicken call, I (1991c) demonstrated equifinality by showing that rearing vocal ducklings communally in social groups resulted in their becoming imprinted to a chicken call over the mallard call (Table 5). Since vocal individuals reared in isolation do not become imprinted to the chicken call (Table 5), my research assistants and I monitored the activities of the isolate- and group-reared birds. We found that the isolates slept less and were highly aroused before, during, and after the playbacks of the chicken call, whereas the grouped birds slept more and were much less aroused than the isolates (Gottlieb, 1993). Because the imprinting to the chicken call was effective only in the vocal ducklings reared communally, I called this the "social induction of malleability." It turned out (Gottlieb, 1993) that the malleability (and correlated reduced arousal) was a consequence of tactile contact afforded by the social rearing. When the otherwise socially reared birds were not permitted tactile contact, their arousal level mirrored that of isolates and their malleability was absent. It gives one pause to realize that generations of imprinting studies were carried out with birds reared in isolation, the most widely used method of rearing animals for laboratory research on imprinting since the 1950s. A young bird's imprintability is dependent on its learning ability. The normal learning ability of the ducklings is present only when they are reared normally (in a social group as would be the case in nature) and impaired when they are reared atypically (social isolation).
Developmental Intersensory Interference

The developmental manifold concept holds that interferences or changes in the sensory aspect of species-typical developmental conditions will alter usual developmental outcomes. With an eye on the crib of the prematurely born human infant, two graduate students and I removed the shell over the airspace in late duck embryos and prematurely exposed them to a low level of patterned visual stimulation while exposing them to a recording of a particular mallard hen's call (Gottlieb, Tomlinson, & Radell, 1989). Under similar conditions, but without the premature visual stimulation, the embryos learned the particular characteristics of the maternal call to which they were exposed (Table 6, darkened incubator condition). The embryos that were prematurely exposed to visual stimulation did not learn the call to which they were exposed (Table 6, lighted incubator condition). Turkewitz and Kenny (1982, 1985) had theorized that the sequential development of sensory function (tactile, vestibular, chemical, auditory, visual) prevented competition between the systems and they provided some empirical evidence that prematurely exposing young animals to stimulation in a later developing modality had negative consequences for the functioning of the early system with which it competed. Our study supported that hypothesis, but went on to show that the negative effect of premature visual stimulation on the embryo's auditory learning ability was transient, not permanent as Turkewitz and Kenny had theorized. After hatching, the prematurely visually stimulated embryos' auditory learning ability was intact (Table 6, postnatal
exposure to maternal call groups). Nonetheless, these results and others like them from laboratories around the world (reviewed in Lickliter, 2000) have had an impact on changing the sensory environment of prematurely born infants in neonatal intensive care units (NICUs). In hospitals in the USA, thirty states now employ methods to reduce overall light and sound levels in NICUs to more closely approximate the typical level of sensory stimulation that the prematurely born fetus would encounter in the uterine environment.

Summary and Conclusions

When one reads the older literature on the evolution and development of species-specific or instinctive behavior, it’s common to read that such behavior is an outcome of heredity. That is, natural selection favored animals whose genes dictated adaptive behavior:

Genetic Activity → Species-Specific Behavioral Development

As it became clearer that the genes must be specifying the neural development underlying the behavior rather than the behavior as such, the progression was envisaged as:

Genetic Activity → Neural Maturation → Species-Specific Development
Then in the 1950s with the discovery that normally occurring sensory experience was necessary to at least maintain already developed nerve cells and neural connections (synapses), the picture became:

Genetic Activity → Neural Maturation → Experience → Species-Specific Development

The present results suggest an even greater importance of normally occurring sensory experience, not merely a maintenance role but an essential constructive function of such experience:

Genetic Activity ↔ Neural Maturation ↔ Experience ↔ Species-Specific Development

In this latter view, the nervous system does not develop fully or normally without the benefit of normally occurring experience. Thus, experience in this case plays a constructive role in the development of the nervous system and species-specific behavior. This is a significant departure from the notion that normally occurring experience only comes into play once the nervous system has been fully constructed by the activity of the genes. In the present view, the normal activity of the genes themselves is dependent upon signals arising from the internal and external environment during the course of normal development (evidence presented in Gottlieb, 1998).

Along with the elaboration of the developmental manifold idea by West and King (1987) and by Lickliter and Ness (1990), it is encouraging that, recently, several publications in developmental and evolutionary biology have appeared that are consonant with, and significantly extend, the developmental manifold notion. These articles
represent a move away from the nondevelopmental genocentric tradition of biology
expressed so succinctly in the following quotation:

Traditionally, evolutionary biologists have viewed mutations within individual genes as
the major source of phenotypic variation leading to adaptation through natural selection,
and ultimately generating diversity among species. (Ochman & Moran, 2001, p. 1096)

The developmental manifold holds that natural selection operates on outcomes of
development that include genes but that development is not controlled or determined by
genes in the sense of genes providing a blueprint or program for development. Evelyn
Fox Keller (2000), in her book, The Century of the Gene, has shown not only the
conceptual but the empirical inadequacy of genetic blueprints or genetic programs for
development. She advocates replacing the genetic program idea with a developmental
program. Jason Scott Robert (2001) has taken Keller's notion to a further degree of
refinement in his critical analysis of the role of the ubiquitous homeobox genes in
development and evolution, in this case moving from a genocentric view of development
and evolution to a developmental systems view of gene action and evolution. Among
other things, the developmental systems view holds that selection acts directly on
phenotypes not genotypes. This idea itself is not new and can be traced back to Mivart
(1871), who pointed out that adaptations arise before they are selected for, i.e., they are
the product of development. What Mivart could not have known in advance of
experimental studies of embryology and developmental genetics was the absolute
importance of developmental (epigenetic) conditions in recreating the changed phenotype
generation after generation. This idea has been significantly elaborated by Newman and
Müller (2000), and by Weiss and Fullerton (2000), who point out that, during the course
of evolution, the genes associated with a given morphological outcome (phenotype) may
change while the evolved outcome is kept stable by *epigenetic* mechanisms, a conclusion consonant with the developmental manifold idea but one that certainly goes beyond it in addressing the genetic component. Not to claim too much, this particular view (developmental systems thinking), as pointed out by Robert, Hall, and Olson (2001), has not yet permeated the thinking of evolutionary developmental biologists. Nonetheless, it is gratifying to see that the epigenetic evolutionary implications of research on instinctive behavioral development is consonant with some of the recent thinking about morphological evolution. Certainly, a change is in the wind in the way development is now being invoked in relation to evolution in the biological literature (*cf.* True & Haag, 2001). It is all the more encouraging to see epigenetic mechanisms being emphasized with respect to human evolutionary psychology (Caporael, in press), which has traditionally had a genocentric focus beginning with its roots in sociobiology.
References


Footnote to Title Page

I apologize in advance for the self-centered exposition in this essay. It took a rather long time to understand and to experimentally tease apart the developmental manifold. It was not--and still is not--a "hot" topic, so that explains the relative paucity of citations to the empirical work of others.

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Footnote One

I use the term coaction instead of interaction because, in recent times, the latter has assumed subtle statistical connotations in association with the widespread use of the ANOVA and its derivatives that are not in keeping with the everyday meaning of interaction. Coaction builds on Dewey and Bentley's (1949) notion of transaction, which itself was introduced to go beyond the more narrow physico-chemical understanding of interaction in their time. Coaction refers to potentially bidirectional influences within and among the four major levels of analysis: genetic activity, neural activity, behavior, and the cultural, physical, and social aspects of the external environment. Causality is a relational term in this usage (Gottlieb, 1991a).
Footnote Two

At first blush it would seem that equifinality contradicts the developmental manifold idea, but it must be remembered that developmental outcomes are achieved by multiple influences operating at various levels, not just one factor at one level. For example, neurons are spontaneously active in the absence of exteroceptive stimulation, so, in the case of devocalized mallard ducklings, their auditory high-frequency sensitivity eventually develops (but is not maintained) in the absence of exposure to the embryonic contact call (Gottlieb, 1997, pp. 53-57). So, there is a maturational lag and the ability deteriorates in the absence of exteroceptive stimulation. Normal repetition-rate specificity does not develop in the absence of normal auditory stimulation (Gottlieb, 1978). The exploration of equifinality would seem especially fruitful for human cognitive development and may be the typically unacknowledged premise especially in intervention studies. As a striking example in the animal literature, the nonspatial memory of mice with gene knockouts can be "rescued" by rearing them in an enriched environment (Rampon et al., 2000). The enriched rearing environment most likely turns on genes (through intermediary mechanisms) that would otherwise be silent. Compensatory possibilities are hidden under normal or species-typical developmental conditions. The nature and effectiveness of potential compensating influences can only be identified when the developmental system is deprived of some normally occurring ingredient. The possibility of compensation is an important qualification of the developmental manifold concept but it is entirely in keeping with recent epigenetic formulations of morphological evolution discussed in the final section of this article.
Table 1
Preferences of Vocal and Devocalized Mallard Ducklings in Auditory Choice Tests

<table>
<thead>
<tr>
<th>Auditory Experience</th>
<th>Preference</th>
<th>Normal mallard call (4 notes/sec)</th>
<th>Normal chicken call (2 notes/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vocal-communal</td>
<td>24*</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Devocal-isolated</td>
<td>26</td>
<td></td>
<td>15</td>
</tr>
<tr>
<td>Delayed devocal-isolated</td>
<td>17*</td>
<td></td>
<td>1</td>
</tr>
</tbody>
</table>

* $p < .0001$, binomial test. (From Gottlieb, 1997.)
Table 2
Preferences of Vocal and Devocalized Mallard Ducklings in Auditory Choice Test with Mallard Maternal Call at Normal and Slowed (Chicken) Repetition Rates at 24 hr. after Hatching (5 min/hr Embryonic Exposure to Embryonic Contact Calls for 24 hr.)

<table>
<thead>
<tr>
<th>Auditory Experience</th>
<th>Preference</th>
<th>Normal mallard call (4 notes/sec)</th>
<th>Slowed mallard call (2 notes/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vocal-communal</td>
<td></td>
<td>26**</td>
<td>3</td>
</tr>
<tr>
<td>Devocal-isolated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No exposure to calls</td>
<td></td>
<td>26</td>
<td>14</td>
</tr>
<tr>
<td>Embryonic exposure to 4 notes/sec contact call</td>
<td></td>
<td>27</td>
<td>20</td>
</tr>
<tr>
<td>Embryonic exposure to 2, 4, &amp; 6 notes/sec contact calls</td>
<td></td>
<td>21*</td>
<td>8</td>
</tr>
</tbody>
</table>

*p = .02, ** p < .00006, binomial test. (From Gottlieb, 1997.)
Table 3
Wood Ducklings' Preferences in Auditory Choice Tests with Descending FM versus Ascending FM Synthetic Wood Duck Maternal Calls at 24 hr. after Hatching

<table>
<thead>
<tr>
<th>Auditory Experience</th>
<th>Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Descending</td>
</tr>
<tr>
<td>Vocal-communal</td>
<td>13*</td>
</tr>
<tr>
<td>Vocal-isolated</td>
<td>16</td>
</tr>
<tr>
<td>Vocal-isolated exposed to alarm-distress call</td>
<td>17*</td>
</tr>
<tr>
<td>(descending FM)</td>
<td></td>
</tr>
<tr>
<td>Vocal-isolated exposed to alarm-distress call</td>
<td>13</td>
</tr>
<tr>
<td>(ascending FM)</td>
<td></td>
</tr>
</tbody>
</table>

* $p < .05$, binomial test. (From Gottlieb, 1997.)
Table 4
Preference of Mallard Ducklings in Experiential Canalization Experiment

<table>
<thead>
<tr>
<th>Auditory Experience</th>
<th>Preference</th>
<th>Mallard Call</th>
<th>Chicken Call</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Vocal-communal</td>
<td></td>
<td>24***</td>
<td>0</td>
</tr>
<tr>
<td>2. Vocal-isolated</td>
<td></td>
<td>14***</td>
<td>0</td>
</tr>
<tr>
<td>3. Devocal-isolated</td>
<td></td>
<td>26</td>
<td>15</td>
</tr>
<tr>
<td>4. Devocal-isolated with chicken call</td>
<td></td>
<td>3</td>
<td>17**</td>
</tr>
<tr>
<td>Retest</td>
<td></td>
<td>2</td>
<td>15**</td>
</tr>
<tr>
<td>5. Vocal-isolated with chicken call</td>
<td></td>
<td>11</td>
<td>15</td>
</tr>
<tr>
<td>Retest</td>
<td></td>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>6. Vocal-isolated with chicken and</td>
<td></td>
<td>19</td>
<td>12</td>
</tr>
<tr>
<td>embryonic calls</td>
<td></td>
<td>20*</td>
<td>6</td>
</tr>
</tbody>
</table>
Ducklings were exposed to chicken call for 30 min/hr from two days before hatching till two days after hatching. They were first tested at 48 hr after hatching and then retested at 65 hr. Group 6 was exposed to chicken call for 30 min/hr and embryonic calls for 10 min/hr on same schedule as above.

* p < .01, ** p < .004, *** p < .00006, binomial test. (From Gottlieb, 1997.)
Table 5
Malleability of Socially-Reared and Socially-Isolated Vocal Ducklings

<table>
<thead>
<tr>
<th>Rearing Condition and Auditory Experience</th>
<th>Test and Retest (hr.)</th>
<th>Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mallard Call</td>
</tr>
<tr>
<td>Socially isolated exposed to chicken call</td>
<td>48</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>16</td>
</tr>
<tr>
<td>Socially reared exposed to chicken call</td>
<td>48</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>1</td>
</tr>
</tbody>
</table>

Exposure period same as in note to Table 4.
* \( p < .003 \), ** \( p < .00006 \), binomial test. (Data from Gottlieb, 1997.)
Table 6
Preferences of Mallard Ducklings in Auditory Choice Tests with Familiar and Novel Mallard Maternal Calls as a Function of Prenatal or Postnatal Exposure to Maternal Call and Prematurity of Patterned Visual Experience

<table>
<thead>
<tr>
<th>Experience</th>
<th>Preference</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Familiar Call</td>
<td>Novel Call</td>
</tr>
<tr>
<td>Prenatal exposure to maternal call</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Darkened incubator</td>
<td>19**</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Lighted incubator</td>
<td>18</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Postnatal exposure to maternal call</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Darkened incubator</td>
<td>36*</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Lighted incubator</td>
<td>18**</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

* $p = .0005$, ** $p = .00006$, binomial test. (Adapted from Gottlieb et al., 1989.)