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Order-Dependent Timing of Unimodal and Multimodal Stimulation Affects Prenatal Auditory Learning in Bobwhite Quail Embryos

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ABSTRACT: *This study examined the relationship between unimodal and multimodal sensory stimulation and their effects on prenatal auditory learning in bobwhite quail embryos. Embryos exposed to a maternal call in the 24 hr prior to hatching (unimodal condition) significantly preferred this familiar call over an unfamiliar call in postnatal testing, but failed to demonstrate this preference when the maternal call was presented concurrently with non-synchronized patterned light (multimodal condition). To further explore this interference effect, we provided one group of embryos concurrent exposure to a maternal call and patterned light for 12 hr followed by 12 hr exposure to the call alone (multimodal→unimodal call). This group failed to prefer the familiar call during postnatal testing. In contrast, reversing the order of presentation during prenatal exposure (unimodal call→multimodal) led a second group of subjects to significantly prefer the familiar call, suggesting that the order-dependent timing of sensory stimulation can significantly impact prenatal auditory learning. Experiment 3 examined the influence of modality versus timing of sensory stimulation on prenatal auditory learning by providing three groups of embryos with exposure to a maternal call during the 12 hr prior to hatching and by varying the duration of visual stimulation. Results indicate that 12 hr unimodal exposure to patterned light does not support prenatal auditory learning when it is followed by 12 hr exposure to multimodal stimulation (light→multimodal), but can facilitate prenatal auditory learning when it is followed by unimodal exposure to the call alone (light→call). Results are discussed in terms of intersensory relationships during perinatal development.* © *2001 John Wiley & Sons, Inc.* Dev Psychobiol 38: 1–10, 2001

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Sensory stimulation encountered by young organisms can influence the development of perceptual and behavioral responsiveness. Recent investigations have uncovered several aspects of sensory stimulation that appear to significantly affect emerging perceptual capabilities. For example, early perceptual development can be influenced by the *type* of stimulation provided to the young organism (McBride & Lickliter, 1994; Radell & Gottlieb, 1992; Sleigh, Columbus, & Lickliter, 1996) as well as the *timing* of this stimulation relative to the experiential history of the organism (Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992; Sleigh & Lickliter, 1998; Turkewitz & Devenny, 1995).

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Although there are several ways in which the type of sensory stimulation can be classified, a fundamental distinction is whether it is provided to a single sensory modality (unimodal) or concurrently across two or more sensory modalities (multimodal). Recent research at both the neural and behavioral levels points to a functional distinction between unimodal and multimodal stimulation in early perceptual organization in both avian and mammalian infants (Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992; Sleigh, Colombus, & Lickliter, 1998; Stein & Meredith, 1993; Stein, Meredith, & Wallace, 1994; Wallace & Stein, 1997). These studies indicate a complex relationship between the effects of unimodal and multimodal sensory stimulation during development, which is currently not well understood. For example, the significance of unimodal versus multimodal sensory stimulation appears to differ as a function of the organism's stage of development.

As a case in point, precocial avian embryos are able to demonstrate species-typical perceptual responsiveness under conditions of unimodal sensory stimulation, but fail to demonstrate normal patterns of responsiveness under multimodal conditions (Gottlieb et al., 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). In contrast, following hatching avian chicks demonstrate species-typical perceptual responsiveness under multimodal conditions, but can show developmental delays following unimodal exposure to sensory stimulation (Colombus, Sleigh, Lickliter & Lewkowicz, 1998; Sleigh et al., 1998). Thus, it seems that although prenatal multimodal stimulation can interfere with normal patterns of perceptual and behavioral responsiveness, postnatal multimodal stimulation appears necessary for the species-typical development of these patterns.

Another factor that has been shown to influence perceptual development is the timing of the presentation of a given type of sensory stimulation in relation to the experiential history of the organism. Timing can also be defined according to several distinct classifications. For example, timing can refer to when in development a specific type of sensory stimulation is presented to an organism (age-dependent timing), or to the order in which different types of stimulation are presented (order-dependent timing). The unimodal/bimodal research outlined above represents age-dependent timing in that the effects of unimodal and multimodal stimulation were found to be contingent upon when (prenatally or postnatally) the stimulation was presented. Sleigh and Lickliter (1998) provide an example of order-dependent timing. They found that early perceptual functioning in bobwhite quail is sensitive to the order of presentation of stimulation. Specifically, embryos exposed to conspecific contentment calls followed by conspecific distress calls showed an accelerated pattern of postnatal visual responsiveness, whereas embryos exposed to the distress call followed by the contentment call showed deficits in postnatal visual responsiveness. In a similar vein, although it has previously been shown that bobwhite quail embryos are able to learn an individual maternal call in the period prior to hatching (Lickliter & Hellewell, 1992; Sleigh et al., 1996) demonstrated that altering the type of sensory stimulation that precedes the presentation of the maternal call can affect the capacity of embryos to learn the maternal call. Specifically, when the maternal call was preceded by contentment vocalizations embryos were able to learn the maternal call, whereas when the maternal call was preceded by distress vocalizations they failed to demonstrate a preference for the familiar maternal call.

In light of these findings, it appears that the type and timing of sensory stimulation can interact in shaping early perceptual responsiveness. However, little is known about how the order-dependent timing of unimodal and bimodal stimulation affects prenatal perceptual capacities. Although prior research has examined how unimodal and multimodal stimulation differ as a function of alterations in age-dependent timing (e.g., Gottlieb et al., 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992), no study to date has examined how these types of stimulation can affect the influence of the other during prenatal learning. It is conceivable that the reported interference effect of concurrent multimodal stimulation on prenatal perceptual learning may be influenced by antecedent or subsequent experience with unimodal or multimodal stimulation. The present study was an initial examination of the nature of these effects in the domain of prenatal auditory learning. In particular, we asked whether concurrent multimodal stimulation (Gottlieb et al., 1989; Radell & Gottlieb, 1992; Lickliter & Hellewell, 1992) is sufficient in and of itself to interfere with prenatal learning, or whether the interference is contingent upon antecedent or subsequent sensory experience. This was explored by altering the presentation order (i.e., order-dependent timing) of unimodal (auditory alone) and multimodal (concurrent auditory and visual) stimulation during late prenatal development and subsequently assessing chicks' preference for an individual maternal call presented in the period prior to hatching. In addition, we also varied the specific type of stimulation that comprised unimodal stimulation to assess whether the effects of visual stimulation differ from that of auditory stimulation during late prenatal development.

GENERAL METHOD

Certain features of the experimental design were common to all experiments, so these features are described before presenting the particular details of each individual experiment.

Subjects

Subjects were 160 maternally naïve, incubator-reared bobwhite quail (*Colinus virginianus*) chicks. Fertile, non-incubated eggs were received weekly from a commercial supplier and were set in a Petersime Model I incubator that maintained a temperature of 35°C and a humidity of 85%. After 20 days of the 23-day incubation period, the eggs were transferred to a hatching tray located in the bottom of the incubator. To control for possible effects of variations in developmental age, only those chicks that hatched on Day 23 were used in this study. The possible between-batch variation was controlled by selecting subjects for each experimental group from at least two different hatches (i.e., weeks) of eggs. Due to their incubator rearing, the only sounds available to the embryos were their own and their broodmates' embryonic and postnatal vocalizations along with the low-frequency background noise of the incubator's fan and motor. Following hatching, subjects were placed in large plastic tubs that were stationed in a sound-attenuated room illuminated by 100 W brooder lamps. These lamps were suspended above the plastic tubs and maintained an ambient air temperature of 30°C. Food and water were continuously available to the subjects throughout each experiment.

Procedure

To ensure that the embryos could see and hear prenatal visual and auditory stimulation, a portion of the upper shell and the inner shell membrane located above the air space of the egg was removed for each subject during the second half of the 21st day of incubation. It is at this time that the embryo's bill normally penetrates the air space on the large end of the egg, coinciding with the onset of respiration and vocalization (Freeman & Vince, 1974). This egg-opening procedure has been shown not to affect postural orientation, onset of hatching, survivability, or species-typical perceptual behavior (Banker & Lickliter, 1993; Lickliter, 1990). After the eggs were opened, they were placed in a portable Hovi-bator incubator that maintained a constant temperature and humidity as before. Following hatching the chicks were placed in the rearing tubs described above.

Testing

Testing occurred at 24 hr ($\pm$1 hr) after hatching. The testing procedure took place in a circular arena, 160 cm in diameter, surrounded by a wall 24 cm in height. The walls of the apparatus were lined with foam to attenuate echoes and covered by an opaque black curtain to shield the observer from the subject's view. The floor of the arena was painted flat black. Two rectangular approach areas (32×15 cm) on opposite sides of the arena were demarcated by green stripes painted on the floor. These approach areas represent 5% of the total area of the arena. Mid-range dome-radiator speakers were hidden behind the curtain in each of the two approach areas. Each speaker received input from a Tascam Model 122-B cassette tape recorder located on a control table. The experimenter sat at this table and observed the subject's activities by means of a large mirror positioned above the testing arena. A system of stopwatches was used to record the latency and duration of response, as described below.

Testing involved placing each subject in the arena equidistant from the two approach areas. All birds were given an individual 5-minute simultaneous choice test between two variants of the bobwhite maternal assembly call (hereafter referred to as Call A and Call B). Each call emanated from one of the speakers located in the two approach areas. These two maternal calls were recorded in the field and have been shown to be generally similar in phrasing, call duration, repetition rate, dominant frequency, and frequency modulation (Heaton, Miller, & Goodwin, 1978). The sound intensity of each call was adjusted to peak at 65 dB (A scale, fast response), measured at the point where the chicks were introduced in the arena. The locations of the maternal calls (Call A and Call B) presented during testing were counterbalanced across individual trials to prevent possible side-bias.

Each subject was tested only once. Subjects were scored on both the latency of approach and the duration spent in each of the two approach areas. Latency was defined as the amount of time (in seconds) that elapsed from the onset of the trial until the subject entered an approach area. Duration was defined as the cumulative amount of time (in seconds) the subject remained in an approach area during the 5-minute test. A chick that did not enter either approach area received a score of 300 s for latency (i.e., the length of the trial) and 0 s for duration, and was considered a non-responder. A "preference" for a given stimulus was scored if a chick that stayed in an approach area for twice the time spent in the opposing approach area. "No preference" for a stimulus was scored if a chick approached both areas during a trial without showing a preference for either.

Data Analyses. The data of interest in each experiment were differences in (1) the latency of approach, (2) the duration of time spent in each approach area, and (3) the number of subjects showing an individual preference which was assigned to any subject that stayed in an approach area for more than twice as long as the other. The differences in latency and duration of approach were evaluated using the Wilcoxin matched-pairs signed-rank test. Differences in the number of individual preferences were evaluated by the χ^2-test. Significance levels of $p < .05$ (two-tailed) were used in all analyses.

EXPERIMENT 1: EFFECTS OF CONCURRENT MULTIMODAL STIMULATION ON PRENATAL AUDITORY LEARNING

As a first step in investigating sensory stimulation effects on prenatal auditory learning, this experiment was designed to replicate previous findings (Lickliter & Hellewell, 1992). Specifically, we first sought to determine whether bobwhite quail chicks display a naïve attraction to either variant (Call A and Call B) of the bobwhite maternal assembly call. Second, we asked whether chicks exposed prenatally to a particular variant of the maternal call would prefer this call over an unfamiliar maternal call. Finally, we re-examined the finding that delivering a maternal call in the presence of patterned light serves to interfere with embryos' prenatal capacity to learn that maternal call.

Method

Sixty bobwhite quail embryos, divided into three experimental groups, served as subjects. All embryos in each group underwent the egg-opening procedure. One group of embryos was reared without exposure to either variant (Call A and Call B) of the maternal call. A second group of embryos was exposed to an individual maternal call (Call B) in groups of 12–14 for 10 min each hour for the 24-hour period prior to hatching. Auditory stimulation began on the second half of the 21st day of incubation and continued through the second half of the 22nd day of incubation. The recording of the individual maternal call was broadcast through a speaker connected to an amplifier that received input from a Sony portable compact disc player. The sound intensity inside the incubator was adjusted to a peak intensity of 65 dB as measured by a Bruel & Kjaer Model 2232 sound level meter. All the normally occurring acoustic components of the maternal call were present and unaltered. A third group underwent the same experimental procedures of Group 2, with the exception that embryos were exposed to temporally patterned light that was concurrently provided with the delivery of the maternal call. These subjects were exposed to both a maternal call (Call B) and patterned (i.e., flashing) light for 10 min/hr for the 24 hr prior to hatching. The temporally patterned light (maximum flash energy = 4-W/s) flashed at a rate of 1 cycle/s and was not precisely synchronized with the maternal call. Special care was taken to insure that the presence of light did not alter the ambient air temperature or humidity within the incubator. Each group was tested at 24 hr after hatching in a simultaneous choice test between the two individual maternal calls (see General Methods for details).

Results and Discussion

Results of testing are depicted in Tables 1 and 2. Acoustically unmanipulated chicks who underwent the egg-opening procedure (Group 1) failed to show a significant preference for either maternal call. That is, the two variants of the bobwhite maternal calls were equally attractive to naïve chicks in the period following hatching. Analysis of latency and duration supported this finding, in that there were no significant differences in latency or duration of approach to either of the two maternal calls. In contrast, quail embryos exposed to a variant of the bobwhite maternal call (Group 2) demonstrated a significant preference ($p = .002$) for that familiar maternal call (Call B) over an unfamiliar maternal call (Call A) at 24 hr following hatching. Although there was no significant difference in the latency of approach, there was a significant difference in the duration ($p = .025$) of response to the familiar call (Table 2). Embryos exposed to patterned light concurrently with exposure to the maternal call (Group 3) failed to prefer the familiar maternal call following hatching. Chicks showed no preference for either maternal call during testing and there were no significant differences in latency or duration scores for either maternal call during test trials.

These results replicate previous findings from bobwhite chicks (Lickliter & Hellewell, 1992) and are consistent with parallel results from mallard ducklings (Gottlieb et al., 1989; Radell & Gottlieb, 1992), lending further support to a functional distinction between prenatal unimodal and multimodal stimulation. The results of the present experiment are consistent with the distinction that the type of sensory

Table 1. Preference of Chicks in Simultaneous Auditory Choice Tests at 24 hr Following Hatching

			Preference		
Experiment	*n*	*n* responding	Maternal Call A (unfamiliar)	Maternal Call B (familiar)	No Preference
Experiment 1					
Group 1 (No exposure)	20	20	9	9	2
Group 2 (Call alone)	20	20	4	14*	2
Group 3 (Call & Light)	20	17	7	8	2
Experiment 2					
Group 1 (Call & Light→Call)	20	19	3	6	10
Group 2 (Call→Call & Light)	20	19	1	15*	3
Experiment 3					
Group 1 (No Exposure→Call)	20	20	5	7	6
Group 2 (Light→Call & Light)	20	18	8	8	4
Group 3 (Light→Call)	20	19	4	14*	1

*$p < .002$ (χ^2 test).

stimulation (unimodal/multimodal) encountered prenatally can influence early perceptual learning. Specifically, quail embryos are able to learn a particular variant of the bobwhite maternal call when the call is presented alone (unimodal condition, Group 2), but appear unable to learn the individual call when delivered in the presence of concurrent visual stimulation (multimodal condition, Group 3).

EXPERIMENT 2: ORDER-DEPENDENT EFFECTS OF MULTIMODAL STIMULATION ON PRENATAL AUDITORY LEARNING

This experiment was designed to explore possible relational effects that unimodal and multimodal sensory stimulation may have on interference with auditory learning in the late prenatal period. Specifically, we examined whether the order of presentation of unimodal and multimodal stimulation would affect embryos' ability to learn an individual maternal call.

Method

Subjects were 40 bobwhite quail embryos, divided into two experimental groups. All subjects underwent the same experimental procedures described in Experiment 1, receiving exposure to an individual maternal call (Call B) for 10 min/hr during the 24 hr prior to hatching. However, one group of chicks (Group 1) received concurrent visual stimulation across the *first* 12 hr of the 24 hr period prior to hatching (Call B & Light→Call B). The second group (Group 2) was exposed to the concurrent visual stimulation for the *final* 12 hr of the 24 hr period prior to hatching (Call B→Call B & Light). Thus, both groups received equivalent amounts of unimodal auditory and multimodal sensory stimulation, but the order of presentation was reversed between the two experimental groups. All chicks were tested 24 hr after hatching as described in the General Methods.

Results and Discussion

Results are shown in Tables 1 and 2. Embryos receiving exposure to the maternal call (Call B) concurrently with light for 10 min/hr across the first set of 12 hr followed by the maternal call alone for the final 12 hr prior to hatching (Group 1) failed to show a significant preference for the familiar maternal call. No significant differences in latency and duration

Table 2. Latency and Duration Scores of Chicks in Simultaneous Auditory Choice Tests

Condition	n	Latency: Call A (unfamiliar)	Latency: Call B (familiar)	Duration: Call A (unfamiliar)	Duration: Call B (familiar)
Experiment 1					
Group 1 (No exposure)	20	73	82	27.5	56.5
Group 2 (Call alone)	20	128.5	54.5	12.5	77*
Group 3 (Call & Light)	17	126	69	39	46
Experiment 2					
Group 1 (Call & Light→Call)	19	57	61	58	69
Group 2 (Call→Call & Light)	19	104	40*	5	179*
Experiment 3					
Group 1 (Light→Call & Light)	20	59.5	30.5	46	63
Group 2 (No Exposure→Call)	18	55	56.5	53.5	56
Group 3 (Light→Call)	19	300	41*	0	98*

*$p < .03$ (Wilcoxon test).

scores were found. In contrast, embryos who first experienced unimodal exposure to the call and were then exposed to concurrent patterned light in the final 12 hr of the 24 hr period prior to hatching did exhibit a significant preference ($p < .001$) for the familiar maternal call (Call B) over the unfamiliar maternal call (Call A). Analyses of latency and duration scores further supported this finding in that these chicks showed shorter latencies ($p = .02$) and longer duration ($p = .001$) of response to the familiar call.

These results are consistent with previous findings from studies of bobwhite quail (Sleigh & Lickliter, 1998) and suggest that differences in the timing of sensory stimulation can yield differential effects on early perceptual learning. Given that each group received equal amounts of exposure to a maternal call (10 min/hr for 24 hr) and equal amounts of visual stimulation (10 min/hr for 12 hr), the crucial factor for fostering prenatal auditory learning appeared to be that unimodal auditory exposure preceded concurrent auditory and visual exposure.

It is important to note, however, that these findings could be due to differences in age-related rather than order-dependent timing effects. That is, given the nature of the experimental design, age was confounded with order. Specifically, in addition to differences in the order of stimulus presentation, the groups differed according to what age they receive unimodal and multimodal exposure to sensory stimulation. In this case, Group 1 received unimodal exposure to the maternal call at a younger age than did Group 2. Given the relatively rapid rate of development that occurs in the days prior to hatching, it is plausible that these age-related differences may also have had an impact on the results obtained.

In any case, the results of the present experiment indicate that the previously reported interference effect associated with concurrent prenatal multimodal stimulation (Gottlieb et al., 1989; Lickliter & Hellewell, 1992) appears to be contingent upon the relative timing of unimodal and multimodal exposure. In particular, it seems that antecedent unimodal auditory experience can offset the interference associated with subsequent multimodal (auditory and visual) experience. However, whether this order-dependent timing is also mediated by the source of stimulation (auditory vs. visual) remains unresolved. The next experiment was designed to explore this issue.

EXPERIMENT 3: EFFECTS OF VISUAL STIMULATION PRECEDING MULTIMODAL STIMULATION ON PRENATAL AUDITORY LEARNING

In this experiment we examined the effects of initial exposure to visual stimulation prior to concurrent auditory and/or visual stimulation on subsequent prenatal auditory learning. In particular, we were interested in whether the inability of embryos in Group 3 of Experiment 1 (Call & Light) and those in Group 1 of Experiment 2 (Call & Light→Call) to learn an individual maternal call could be attributed to either (a) the order-dependent timing of the light and maternal call (i.e., unimodal/multimodal effect) or (b) to interference associated with the age-dependent timing of visual experience. That is, it could be that initial early exposure to light disrupts ongoing and/or subsequent prenatal auditory learning regardless of whether it is presented with or without concurrent auditory stimulation.

To address this issue, three groups of quail embryos were exposed to an individual maternal call across the final 12 hr prior to hatching (rather than the entire 24 hr prior to hatching as in the former experiments). Groups differed according to the duration of time embryos were exposed to patterned light. One group was provided only the maternal call without any unusual visual stimulation (No Stimulation→Maternal Call). A second group received unimodal exposure to light across the first 12 hrs followed by multimodal exposure to the call and light across the final 12 hrs prior to hatching (Light→Call & Light). A third group received initial unimodal exposure to light prior to unimodal exposure to a maternal call (Light→Call). If initial exposure to light always interferes with prenatal learning (an age-dependent timing effect), the responsiveness of Groups 2 and 3 to the familiar maternal call should be equivalent (Group 2 = Group 3). Alternatively, if the influence of visual experience on prenatal auditory learning is dependent upon subsequent unimodal or multimodal stimulation (order-dependent timing effect) then differences in responsiveness should emerge between Groups 2 and 3 (Group 2 $\neq$ Group 3).

Methods

Sixty bobwhite quail, divided equally into three groups ($n = 20$), served as subjects. One group (Group 1) was exposed to a maternal call (Call B) for 10 min/hr across the final 12 hr prior to hatching (No Stimulation→Call B). A second group (Group 2) received patterned light for 10 min/hr for the entire 24 hr prior to hatching. However, an individual maternal call (Call B) was also concurrently presented during the final 12 hr (Light→Call B & Light). A third group (Group 3) was presented with patterned light alone for 10 min/hr across the first set of 12 hr followed by 10 min/hr of a maternal call (Call B) across the final set of 12 hr prior to hatching (Light→Call B). Each group was tested 24 hr after hatching in a simultaneous auditory test as described in the General Method.

Results and Discussion

As shown in Tables 1 and 2, quail embryos exposed to a maternal call (Call B) during the final 12 hr prior to hatching (Group 1) failed to show a significant preference for that familiar maternal call over an unfamiliar maternal call (Call A) after hatching. Analyses of latency and duration scores further support this finding, with no significant differences in either measure of response. Likewise, embryos initially receiving unimodal patterned light for 10 min/hr across the first 12 hr followed by the concurrent delivery of the same patterned light and a maternal call for 12 hr (Group 2) also showed no preference for either maternal call during testing. Again, latency and duration scores supported this finding, with no significant differences in scores for either the familiar or unfamiliar call. In contrast, embryos exposed to patterned light alone across the first 12 hr followed by maternal call alone across the final 12 hr prior to hatching did demonstrate a significant preference ($p = .001$) for the familiar maternal call (Call B). This finding was further supported by shorter latency ($p < .01$) and longer duration ($p < .01$) scores in subjects' response to the familiar maternal call.

As outlined above, the primary motivation for conducting this experiment was to determine whether the inability of embryos to learn the maternal call in conditions where visual stimulation was presented initially (Group 3/Experiment 1 and Group 1/Experiment 2) could be attributed to (a) initial exposure to light (age-dependent timing) or (b) to the order-dependent relationship between auditory and visual stimulation within the unimodal/multimodal framework. Although Group 2 of the present experiment (Light→Call & Light) displayed no preference for the familiar maternal call, Group 3 (Light→Call) did demonstrate a significant preference for the familiar call. This finding suggests that initial exposure to light (age-dependent timing) is not the crucial factor affecting the interference effect of visual stimulation on prenatal auditory learning. Prenatal visual experience does not always interfere with prenatal auditory learning. On the contrary, it appears that visual experience can facilitate prenatal auditory learning under unimodal conditions.

The influence of visual stimulation appears to be contingent, however, upon the unimodal and/or multimodal relationships within which it is embedded. For instance, multimodal exposure involving visual stimulation tends to interfere with prenatal auditory learning, except under conditions where there has been previous exposure to unimodal auditory stimulation. On the other hand, antecedent unimodal visual experience does not offset the interfering effects of subsequent multimodal exposure, suggesting specific types of unimodal stimulation differentially moderate the influence of subsequent multimodal stimulation. However, there are conditions under which unimodal visual and unimodal auditory stimulation can generate similar effects. For example, a maternal call can be learned during the final 12 hrs prior to hatching when its delivery is preceded by 12 hrs exposure to either unimodal auditory (Group 2/Experiment 1) or unimodal visual stimulation (Group 3 / this experiment). Thus, it does not appear to be visual stimulation per se that interferes with prenatal auditory learning, but rather the specific influence (i.e., interfering, facilitative, or no effect) of unusually early visual stimulation seems to depend upon the (1) the initial mode(s) of presentation (auditory and/or visual), (2) the subsequent type(s) of stimulation (auditory and/or visual), and (3) the amount of exposure to auditory and visual stimulation.

GENERAL DISCUSSION

The differential effects of unimodal and multimodal stimulation on early perceptual and behavioral responsiveness have received increasing attention within developmental science in recent years (Bahrick & Lickliter, 2000; Gottlieb et al., 1989; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992; Richards, 2000; Stein & Meredith, 1993). Whereas prior investigations have typically explored effects on perception in terms of the unique stimulus features of unimodal and multimodal stimulation, the current study is among the first to examine the relational effects of these types of sensory stimulation. In so doing, this study unites several recent insights concerning the influence of the type and timing of sensory stimulation during the prenatal period. In particular, the results of this study show that the relational influences of unimodal and multimodal stimulation on prenatal auditory learning are determined in part by the specific types of stimuli initially presented, the order of presentation of unimodal and multimodal stimulation, and the overall amount of auditory experience with the target stimuli provided to the young organism. Our results suggest that previously reported interference effects associated with prenatal multimodal stimulation can be offset by antecedent unimodal auditory stimulation, indicating that the influence of unusually early visual stimulation on prenatal auditory learning depends upon the timing, types, and amounts of unimodal and/or multimodal stimulation within which it is embedded.

Additionally, this study provides an example of how stimulation received in one sensory modality can bring about functional changes in a different sensory modality (Experiment 3). Embryos were unable to learn a maternal call with only 12 hr of unimodal auditory exposure, but did learn the call if this unimodal auditory exposure was preceeded by unimodal visual experience. Several investigators have argued that structured limitations arising from the sequential emergence of sensory functioning (see Gottlieb, 1971 for review of sensory emergence) during prenatal development can serve as an organizational foundation for early perceptual development (Gottlieb et al., 1989; Lickliter, 1993; Spear, 1984; Turkewitz & Kenny, 1982, 1985). From this view, premature experience in a later developing modality (e.g., visual) may disrupt or impede development in an earlier developing modality (e.g., auditory) and is thought to be mediated by competition between the sensory modalities for limited attentional resources necessary for normal development and differentiation. In this study, we demonstrated that rather than disrupting early perceptual development, unusually early visual stimulation can facilitate emerging auditory abilities under some conditions. Specifically, we showed that although bobwhite quail embryos could not learn a maternal call presented for 10 min/hr across 12 hr (Group 1/Experiment 3), they could when the delivery of the call was preceded by unimodal visual stimulation (Group 3/Experiment 3). These findings suggest that under unimodal conditions, unusually early stimulation in a later-developing modality can facilitate (rather than compete with) the functioning of an earlier developing modality. However, the mechanism(s) through which this facilitation is achieved remain to be discovered.

One possibility is that unimodal sensory stimulation fosters the organization or enhances the performance of the embryo's emerging attentional capacities. A general attention mechanism of this sort may mediate intersensory influences in early development, in that stimulation to one modality can serve to support emerging attentional mechanisms, thereby allowing for the subsequent improved processing of sensory information from different modalities. This proposed general attention mechanism is assumed to emerge and differentiate from the ongoing sensory and motor activities of the developing organism, and is closely tied to the organism's level of arousal. In this scenario, unimodal visual stimulation could facilitate auditory learning by increasing arousal levels in such a way as to boost subsequent attentional processing of the maternal call.

Applying this attention model to the relational effects of unimodal and multimodal stimulation reported in this study, the stimuli initially encountered by the quail embryo may serve to bias attention to those stimulus properties in subsequent stimulation. For instance, prior exposure to unimodal stimulation may bias the embryo's attention to modality-specific features of the familiar stimulation, even under subsequent multimodal conditions (Group 2/Experiment 2; Group 2/Experiment 3). If this account holds, then it is likely that chicks in Group 2/Experiment 3 (Light→Call & Light), despite failing to learn the maternal call, may have instead learned the modality-specific features of the unimodal visual stimulation. In a similar vein, when the embryo encounters initial multimodal stimulation, its attention may be biased toward certain amodal features of multimodal stimulation (e.g., rate or synchrony) rather than the modality-specific features of the individual maternal call, thus accounting for the inability to discriminate features of the individual maternal call during ongoing multimodal or subsequent unimodal exposure to the call (Group 3/Experiment 1; Group2/Experiment 2). Bahrick and Lickliter (2000) have recently reported a similar effect for human infants. In this study, 5-month-olds could discriminate a complex rhythm when presented redundantly across auditory and visual modalities, but were unable to discriminate rhythm when it was presented unimodally. However, less is known about how selective attention is deployed and how it affects perceptual functioning during the perinatal period.

The findings from the current study coincide with the notion that unimodal input tends to promote prenatal perceptual functioning, regardless of the specific sensory modality which receives this stimulation, whereas multimodal stimulation tends to interfere with prenatal perceptual functioning (Lickliter & Banker, 1994). However, the present study also demonstrates that the presentation order of unimodal and multimodal stimulation (order-dependent timing) can moderate the interference associated with multimodal stimulation. Further research is required to further delineate and describe this moderating effect.

It is interesting to note that the prenatal environment is structurally organized in such a way as to effectively attenuate the presence of multimodal stimulation relative to unimodal stimulation. Given the relatively buffered nature of the prenatal environment and the sequential onset of sensory functioning, it is likely that the developing embryo is primarily exposed to unimodal stimulation and has relatively fewer opportunities to experience multimodal stimulation (prior to the onset of visual experience). Becoming familiar with various sources of unimodal stimulation may initially provide a foundation for the subsequent processing of unfamiliar unimodal and multimodal sources of stimulation. Following the reasoning of Turkewitz and Kenny's (1982, 1985) intersensory interference hypothesis, these structural and functional constraints are not limitations to be overcome, but rather provide an organizational framework that serves to promote normal patterns of early perceptual and behavioral responsiveness. Whereas Turkewitz and Kenny's (1982, 1985) model focuses on the constraints provided by the sequential onset of the sensory system function during the prenatal period, the present results extend their model by emphasizing that the relationship between the order-dependent timing of unimodal and multimodal stimulation (without reference to the different degrees of modality maturity) can also provide considerable constraints that may influence early perceptual development. In particular, the results from the current study and from previous reports (Lickliter & Lewkowicz, 1995; Radell & Gottlieb, 1992) indicate that the interference associated with prenatal multimodal stimulation is likely influenced by the type and timing of stimulation within which it is embedded *and* the overall amount of stimulation to which the organism is exposed.

In the general sense, the results of the present study emphasize the idea that stimulus characteristics such as type of stimulation, timing of stimulation, amount of stimulation, and the organism's developmental history interact in shaping early perceptual and behavioral responsiveness (see Lickliter & Bahrick, 2000 for further discussion). As a result of this dynamic relationship, developmental causation should not be viewed as residing in either the organism or the environment alone, but rather in the structured interactions between the developing organism and its changing environment.

NOTES

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