

THE ROLE OF STIMULUS MATCHING IN THE DEVELOPMENT OF
INTERSENSORY PERCEPTION IN BOBWHITE QUAIL

by

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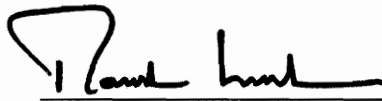
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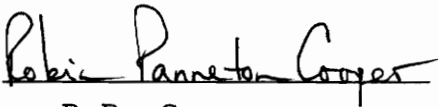
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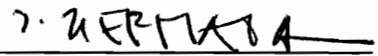
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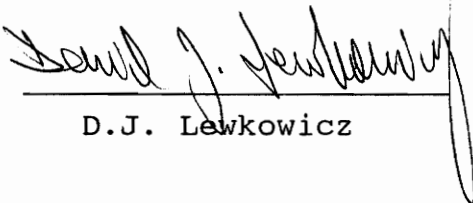
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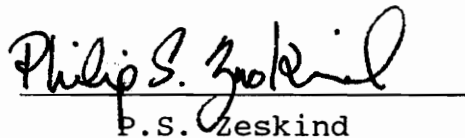
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(ABSTRACT)

The present study examined the role of the relationship between the type and amount of prenatal and postnatal stimulus cues in directing the perceptual preferences of bobwhite quail chicks. Results reveal that chicks prefer postnatal stimulus cues that matched the particular type of prenatal stimulation they received as embryos over stimulus cues that match the amount of prenatal stimulus cues they received. Specifically, when chicks were tested with novel stimuli, or when the preference for matching types of stimulus cues was controlled for, chicks exposed to prenatal auditory/visual cues showed a preference for combined auditory/visual cues over auditory cues presented alone. These findings suggest that exposure to enhanced prenatal auditory/visual stimulation can accelerate chicks perceptual responsiveness. However, this effect can be masked depending upon the relationship between the specific type of auditory stimulus cues used during prenatal exposure and subsequent postnatal testing. Further results indicate that preference for familiar type of stimuli can account for why

exposure to enhanced prenatal stimulation does not always appear to accelerate responsiveness to combined auditory/visual cues. Therefore, studies examining the effects of prenatal sensory manipulations on postnatal perceptual responsiveness must take into account the specific nature of the relationship between the type and amount of prenatal and postnatal stimulus cues employed in the experiment. In a more general sense, these results suggest that the study of early perceptual development requires the incorporation of complex, dynamic, and hierarchically based notions about the mechanisms associated with behavioral development.

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Introduction

Research concerning intersensory development has demonstrated that the manipulation of young animals' early sensory stimulation history can either accelerate or interfere with subsequent intersensory functioning (Foreman & Altaha, 1991; Gottlieb, Tomlinson & Radell, 1989; Kenny & Turkewitz, 1986; Lickliter, 1990a, 1990b; Lickliter & Stoumbos, 1991; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). These studies have used a variety of animal neonates, stimulus manipulations, and testing conditions to demonstrate the effects of enhanced early experience on subsequent perceptual functioning.

The purpose of the present study was to examine the effects of various prenatal sensory manipulations in order to identify the specific experiential conditions under which sensory stimulation serves to accelerate bobwhite quail chicks' postnatal responsiveness to combined auditory/visual maternal cues. It is important to note that acceleration of perceptual functioning is determined by comparison with unmanipulated control chicks. That is, acceleration refers to the result of an experimental manipulation in which subjects exhibit a preference for stimulus or stimuli at an earlier age than do unmanipulated control subjects. Subjects are said to exhibit a preference for a stimulus if they selectively approach that stimulus over another

stimulus during the course of a simultaneous choice test (see General Method section).

Empirical research which has demonstrated effects of enhanced or unusually early experiential factors on subsequent perceptual functioning will be reviewed in the next section. In particular the procedures and testing stimuli used in each study are described in some detail in order to identify possible factors that may account for apparent inconsistencies in the existing data. For example, factors such as the specific types of stimulation used, the amount of stimulation provided, and the relationship between the nature of prenatal stimuli and testing stimuli may be important variables in determining why some experimental manipulations accelerate auditory/visual responsiveness and others do not accelerate responsiveness under similar conditions. The present experiments are designed to examine the potential roles of these factors in determining which manipulations are likely to accelerate subsequent perceptual functioning.

Review of The Effects of Early Experience on Intersensory Functioning

Research on sensory system development has revealed that the onset of sensory function within the various modalities proceeds in an invariant sequence for both avian and mammalian species, including humans: tactile-vestibular-

chemical-auditory-visual (Alberts, 1984; Gottlieb, 1971a). Since sensory systems develop at different rates, there are limitations on the sensory function of maturing modalities at varying times during early development (Turkewitz & Kenny, 1982).

This sequential emergence of function in sensory systems has recently been shown to be an important factor in determining the nature of intersensory relationships in early development. Results of a number of recent studies utilizing precocial birds have shown that manipulating the experiential history of the sensory systems can result in significant changes in responsiveness to species-specific perceptual cues (see Lickliter, 1993 for a review).

Pattern of Perceptual Development in Unmanipulated Chicks

Before discussing the effects of experimental manipulations on perceptual responsiveness, however, it is necessary to discuss the typical pattern of responsiveness observed in unmanipulated subjects, since acceleration of perceptual responsiveness is determined relative to the pattern of responsiveness seen in control chicks. Lickliter and Virkar (1989) described the developmental trajectory of perceptual functioning for normally hatched (unmanipulated), group-reared bobwhite quail. Under normal conditions, bobwhite quail embryos are exposed to a prenatal stimulative environment which includes auditory self-stimulation in the form of embryonic vocalizations (Stoumbos and Lickliter,

1990), auditory stimulation from clutchmates (Vince, 1966, 1973), and little or no patterned visual stimulation inside the enclosed egg.

Normally hatched bobwhite chicks that have been reared in groups of siblings after hatching selectively approach bobwhite auditory cues (i.e., a bobwhite maternal call) over non-maternal auditory cues when tested at 24 hr and 48 hr of age. By 72 hr after hatching normally hatched (unmanipulated), group-reared bobwhite chicks do not respond to auditory cues presented alone, but rather exhibit a preference for a stuffed bobwhite hen paired with a recording of a bobwhite maternal call. In other words, normally hatched, group reared bobwhite chicks require only the bobwhite maternal call to direct their preferential responding during the first two days following hatching. However, by 72 hr following hatching combined auditory and visual maternal cues (i.e. the bobwhite maternal call paired with the bobwhite hen model) was found to be necessary to successfully direct bobwhite chicks' social preferences (Lickliter & Virkar, 1989).

In addition, hatchlings show a significant visual preference for a bobwhite hen model over a scaled quail hen model when both are emitting the same bobwhite maternal call by 72 hr following hatching (but not at earlier ages). Since both hens are emitting the same call, the auditory cues provided by the call do not provide a basis for

discrimination. Therefore, subjects have to utilize the available visual information provided by the hens to direct their preferential responsiveness (Lickliter & Virkar, 1989). It is important to note that the static visual cues provided by the hen models are not sufficient to elicit preferential responsiveness when presented alone. Rather, it was found that maternal visual cues must be presented with the maternal call to be effective at all ages tested (Figure 1).

Interestingly, McBride and Lickliter (1993) found that normally hatched bobwhite chicks reared in isolation, partial isolation, or with non-conspecific scaled quail chicks did not exhibit this pattern of preferential responsiveness to species-specific auditory/visual cues by 72 hr. In addition, Banker and Lickliter (1993) found that normally hatched bobwhite quail chicks whose eyes were occluded after hatching likewise did not respond to species-specific maternal auditory/visual cues at 72 hr after hatching, despite the fact that they were reared in groups with siblings. Finally, McBride and Lickliter (1994) found that normally hatched, group reared bobwhite chicks that were exposed to recordings of bobwhite distress vocalizations postnatally did not exhibit preferential responsiveness toward bobwhite maternal auditory/visual cues at 72 hr, a response reliably seen in controls. In contrast, hatchlings exposed to bobwhite contentment calls

or chicken distress calls did show a species-specific auditory/visual preference when tested at 72 hr of age.

Taken together, these findings indicate that normally hatched bobwhite chicks reared in groups with siblings and allowed the opportunity for visual experience with these siblings during rearing display species-typical visual responsiveness by 72 hr after hatching (Banker & Lickliter, 1993; Lickliter & Virkar, 1989; McBride & Lickliter, 1993; McBride & Lickliter, 1994). However, birds receiving modified postnatal experience often do not display a typical pattern of early visual responsiveness.

Acceleration of Responsiveness to Auditory/Visual Cues

The developmental trajectory described by Lickliter and Virkar (1989) has been prenatally manipulated in subsequent studies to produce different developmental outcomes. Specifically, the method of "experiential enhancement" has been employed to alter the embryos' prenatal sensory experience. Experiential enhancement involves providing stimulation above and beyond what is normally present in the typical rearing environment. That is, the organism is exposed to more stimulation than it would normally encounter (Gottlieb, 1977).

For example, Lickliter (1990a, 1990b) found that unusually early (prenatal) visual stimulation during the last several days prior to hatching accelerates species-typical postnatal visual functioning in group-reared

bobwhite quail. That is, chicks exposed to patterned light as embryos responded to combined species-specific maternal auditory/visual cues at an earlier age than unmanipulated control chicks. Thus, subjects' responsiveness to combined auditory/visual cues appeared to be accelerated relative to controls. In addition, group-reared chicks that received prenatal visual experience demonstrated an altered pattern of early sensory dominance, shifting from auditory to visual dominance earlier in development than control chicks (Lickliter, in press).

It is interesting to note that postnatal visual experience is necessary for maintenance of the effects of prenatal visual experience. Banker and Lickliter (1993) reported that bobwhite chicks exposed to premature visual stimulation as embryos and subsequently denied visual exposure to conspecifics in group rearing did not exhibit accelerated responsiveness to species-specific auditory/visual cues.

In addition, enhanced prenatal auditory experience has also been found to accelerate species-specific visual responsiveness in bobwhite chicks (Lickliter & Stoumbos, 1991). Normally hatched, group reared bobwhite chicks that received augmented amounts of exposure to their own embryonic vocalizations prior to hatching responded to combined species-specific maternal auditory and visual cues at an earlier postnatal age than did unmanipulated control

chicks. It is important to note that exposure to enhanced auditory stimulation did not alter chicks' responsiveness to maternal auditory cues (Lickliter & Stoumbos, 1991). This may be due to the fact that the auditory system is already well developed by the last few days of incubation and may therefore be less malleable or sensitive to altered stimulation regimes (Gottlieb, 1971; Lickliter & Virkar, 1989; Lickliter, in press).

Taken together, the results from Lickliter (1990a, 1990b) and Lickliter and Stoumbos (1991) indicate that experiential enhancement of either auditory or visual stimulation can accelerate chicks' use of visual information (when presented with auditory cues) to guide preferential responding to maternal cues.

Interference With Responsiveness to Auditory and Visual Cues

While unusually early visual experience and augmented prenatal auditory experience has been found to accelerate the normal pattern of visual responsiveness in bobwhite quail chicks, related research has reported that unusually early visual experience can also interfere with species-typical auditory responsiveness (Lickliter, 1990a, 1990b). The term "interference" is used here to refer to the result of an experimental manipulation in which subjects do not exhibit preferential responsiveness to a stimulus or stimuli at an age at which subjects that have not received that manipulation reliably exhibit preferential responsiveness to

those stimuli. For example, whereas normally reared chicks show a significant preference for the bobwhite maternal call at both 24 hr and 48 hr following hatching (Lickliter & Virkar, 1989), chicks exposed to patterned light as embryos do not exhibit a preference for the bobwhite maternal call presented without visual cues at either 24 hr or 48 hr following hatching (Lickliter, 1990b).

Furthermore, premature visual stimulation presented concurrently with prenatal auditory exposure to an individual maternal call has been found to interfere with prenatal auditory learning in both bobwhite quail embryos (Lickliter & Hellewell, 1992) and duck embryos (Gottlieb, Tomlinson & Radell, 1989). Whereas both bobwhite quail embryos and duck embryos reared normally can learn the individual features of a maternal call prior to hatching, quail and duck embryos exposed to visual stimulation concurrently with prenatal exposure to an individual maternal call failed to prefer that familiar call in postnatal choice tests. In contrast, embryos exposed to non-concurrent auditory and visual stimulation did learn the individual maternal call. (Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992).

Augmented amounts of prenatal vestibular stimulation has likewise been found to interfere with auditory learning in duck embryos (Radell & Gottlieb, 1992). Radell and Gottlieb (1992) found that duckling embryos exposed to concurrent

tactile-vestibular and auditory stimulation fail to learn an individual mallard duck maternal call. Ducklings not exposed to concurrent stimulation were capable of learning the distinctive features of an individual maternal call as embryos (Gottlieb, 1988). Conversely, vestibular stimulation did not interfere with auditory learning when it was either nonconcurrent with auditory stimulation or when the concurrent vestibular stimulation was reduced to a level which did not greatly exceed the typical amount of vestibular stimulation normally encountered by the embryos during the late embryonic period (Radell & Gottlieb, 1992). These results parallel those of Gottlieb, Tomlinson, & Radell (1989) and Lickliter & Hellewell (1992), in that intersensory interference (i.e., lack of early auditory learning) occurred only when two or more sensory systems were concurrently stimulated prenatally.

Taken together, findings reviewed to this point demonstrate that altering sensory experience in one modality can affect the functioning of other sensory modalities by either interfering with or accelerating subsequent responsiveness. However, the specific mechanisms underlying this dynamic nature of prenatal sensory/perceptual organization have not been systematically studied. The next section reviews literature dealing with possible mechanisms by which experiential history could affect intersensory functioning.

Possible Underlying Mechanisms of Early Perceptual Organization

Turkewitz and Kenny (1982) proposed that premature stimulation to a later developing system (i.e., visual) can interfere with an earlier developing system by taking over neurons and/or synaptic connections that would normally be allocated to the earlier developing system. That is, premature visual stimulation could result in a take over of cerebral neural space normally allocated to auditory functioning. This scenario suggests that any early deficit in perceptual functioning would be a long-lasting one.

In contrast to this view, Gottlieb, Tomlinson and Radell (1989) argued that the mechanism for intersensory interference is not competition for neuronal space. Gottlieb et al. (1989) found that embryos exposed prenatally to early visual stimulation were still able to learn a specific maternal call postnatally. Similarly, Radell and Gottlieb (1992) found that while augmented tactile/vestibular stimulation interfered with prenatal auditory learning when the stimuli were presented concurrently, the subjects were able to learn the call when re-exposed to it following hatching. Gottlieb et al. (1989) concluded from these findings that intersensory interference is transitory in its effect and occurs only when two competing stimuli are presented concurrently. Gottlieb et al. (1989) suggest that concurrent stimulation potentially increases experiential

competition between the modalities when both are still undergoing maturation. They propose that the embryo is not capable of adequately attending to concurrent sensory stimulation, in that the intensity of concurrent stimulation effectively overwhelms the young organism's attentional capabilities. Based on their findings from enhanced vestibular stimulation in duck embryos, Radell and Gottlieb (1992) proposed that the amount of sensory experience normally encountered by a developing organism can be seen as optimal for its species-typical perceptual development. Radell and Gottlieb (1992) argue that any substantial and enduring deviation from the normal amount of sensory experience typically encountered by the developing individual should lead to functional deficits in perceptual capacity. In contrast, exposure to species-typical or only slightly augmented levels of sensory experience should result in typical or even facilitated intersensory development, which may help explain the accelerated pattern of visual responsiveness seen in bobwhite quail chicks exposed to enhanced prenatal auditory experience (Lickliter & Stoumbos, 1991).

While attentional limitations are a possible explanation for why concurrent stimulation serves to interfere with early auditory learning, it does not explain why enhanced prenatal stimulation can also accelerate the use of visual cues. Research reviewed by Turkewitz (in press) examining the

effects of early stimulation in one modality on functioning in other modalities provides some possible insights into this issue.

Homing behavior in newborn kittens is initially under olfactory and thermal control (Freeman & Rosenblatt, 1978), with a gradual transition to joint visual and olfactory control, and is finally primarily under visual control (Rosenblatt, Turkewitz & Schneirla, 1969). That is, kittens initially rely upon thermal and olfactory cues in order to successfully find their home corner. They gradually come to rely upon visual information to find home in the weeks following birth. Eye opening in kittens is a gradual process. There is therefore a gradual increase in visual input which does not disrupt or interfere with olfactory based homing behavior.

The visual system in kittens is functional well before the age of eye opening (Hubel and Weisel, 1963). However, when patterned visual information first becomes available, the kitten may not utilize visual cues in directing its behavior and may continue to behave in accordance with the pattern it had developed in the absence of vision. Similarly, bobwhite quail have visual information available to them after hatching, but they continue to use auditory cues during the first several days after hatching to direct their social behavior and do not typically utilize visual

information until some 72 hr after hatching (Lickliter & Virkar, 1989).

How then can experiential enhancement (increasing the amount of prenatal or postnatal stimulation) lead to the facilitation of visual responsiveness? There is evidence that early eye opening in rats is associated with a tendency to rely on information from visual stimuli more so than if their eyes had opened normally. When tested under circumstances in which tactile and visual cues are in conflict (as in a visual cliff task), rat pups ignore visual differences on the two sides of the cliff and respond instead to their tactile similarity (Kenny, 1984). In other words, rats use tactile information shortly after normal eye opening, but later in development rat pups respond to the visual rather than the tactile aspects of the cliff by preferentially descending on the shallow side of the cliff (Kenny, 1984).

According to Turkewitz (in press) these findings suggest that vision is salient for the rat at this time and this visual salience is responsible for the disruption of homing behavior. That is, when rat pups' eyes were opened approximately one week prior to the typical age of eye opening they did not exhibit the characteristic disruption of homing behavior; rather, these pups improved their homing behavior at an age when their littermate controls showed a decline in homing behavior (Kenny & Turkewitz, 1986). This

could be because the pups are relying on the use of visual cues for homing as a result of the early eye opening and therefore do not have to make the transition from olfactory guided behavior to visually guided behavior, which is associated with disruption of homing behavior.

Subsequent research supports the notion that the early eye opened rat pups were relying on visual information for homing behavior. When visual differences between cage regions was reduced, experimental animals behaved like controls and exhibited the same decline in homing behavior toward the second week of life (Kenny & Turkewitz, 1986). This evidence suggests that the observed difference between early eye opened pups and controls is based on a difference in their use of available visual information.

Furthermore, Calenza et al. (1984) reported that rat pups whose eyes were opened earlier than normal failed to discriminate between shavings from their home cage and shavings with other odors at an age when their littermate controls were able to do so. These findings suggest that these pups were not making use of available olfactory cues and were, as the findings of Kenny and Turkewitz (1986) indicate, using available visual cues instead.

In a similar vein, Tees, Buhrmann, and Hanley (1990) reported that light reared rats benefited more than dark reared rats on a water maze task from viewing the room/pool from a platform in the correct location. Furthermore,

visually experienced rats remembered the location of the platform more than dark reared rats when retested one month later. Apparently, rats who had prior visual experience were more likely to make use of visual information on the water maze task. Similarly, Tees and Symons (1987) reported that dark reared rats were less successful than light reared rats in acquiring an initial discrimination involving visual events.

Gottlieb, Tomlinson, and Radell (1989) found that ducklings that were given premature exposure to visual experience by having their heads extended from the egg (which enabled them to see other ducklings) failed to learn the characteristics of a mallard maternal call. Dark reared ducklings preferred the call to a novel one. Perhaps as a result of the early visual exposure, the ducklings were making increased use of visual information rather than relying solely upon auditory information. Similarly, Lickliter and Hellewell (1992) found that bobwhite quail exposed to unusually early visual stimulation by having their heads exposed as embryos failed to show a preference for familiar species-specific maternal auditory cues, whereas control chicks who were not exposed to early visual stimulation did prefer the familiar auditory cues.

Taken together the results from these various studies suggest that early visual experience may lead to more reliance on visual information to guide behavior. This

insight may help explain the findings of Lickliter (1990a, 1990b), in which early visual experience accelerated visually guided functioning in bobwhite quail. It is still not clear, however why enhanced auditory stimulation also accelerates visual functioning (Lickliter & Stoumbos, 1991). The next section reviews research concerning intensity based responsiveness in young organisms which may explicate the mechanisms for such cross modal effects of early sensory stimulation.

The Intensity Hypothesis of Early Perceptual Functioning

According to Schneirla (1959, 1965) young organisms respond to the net intensity of a stimulus rather than to its modality of presentation. Furthermore, the effects of stimulation in one modality can be added to one another or substituted for one another. Turkewitz, Lewkowicz & Gardner (1983) reviewed evidence that infants are responsive to quantitative aspects of stimulation and that the source of the stimulus input is relatively unimportant. According to Turkewitz et al. (1983), young infants respond to overall amount of stimulation rather than to the manner in which the amount is achieved. Additions and substitutions could occur within and across modalities. That is, stimulation from different modalities is additive, the effects of stimulation in different modalities would combine, with responses and preferences determined by the overall amount of stimulation.

For example, adding a sound to a light would produce a response equivalent to that given to a more intense light.

It may be possible that the overall amount or intensity of stimulation the organism is exposed to prenatally, regardless of modality of presentation, can influence subsequent responsiveness. This may help explain why the addition or enhancement of both auditory and visual stimulation prenatally resulted in the acceleration of bobwhite chicks' responsiveness to combined auditory and visual stimuli postnatally (Lickliter, 1990a, 1990b; Lickliter & Stoumbos, 1991). Perhaps enhanced stimulation of any type (auditory or visual) can effectively accelerate responsiveness. This explanation implies that the amount of stimulation to which the organism is exposed is the critical factor in affecting early perceptual responsiveness.

Indeed, Gardner, Lewkowicz, Rose and Karmel (1986) found that regardless of modality (auditory or visual) visual preferences varied systematically with changes in prior stimulation, such that there was an inverse relationship between amount of pre-stimulation and preferred temporal frequency. Gardner et al. (1986) found that human infants looked less as temporal frequency increased and looked more as temporal frequency decreased as a function of increasing amounts of pre-stimulation. Prior exposure to a faster frequency shifted visual preferences toward slower temporal frequencies in a manner similar to that which occurs when the

arousal level of the infant is increased. These results suggest that, in neonates, the effects of prior stimulation on subsequent visual preferences may be more related to the operation of a non-specific response mechanism dealing with amount or intensity of stimulation rather than to any specific properties of the stimuli. Gardner et al. (1986) concluded that additional stimulation (internal or external in origin) influences neonates' visual attention through general rather than stimulus-specific effects on arousal. Therefore, effects of prior stimulation can be cross-modal.

For example, Lewkowicz and Turkewitz (1981) found that infants tested on a visual preference test following auditory pre-stimulation preferred to look at low intensity stimuli, whereas controls preferred intermediate stimuli. Lawson and Turkewitz (1980) found similar results using a number of cubes as the visual stimuli. Lewkowicz and Turkewitz (1980) also tested the hypothesis that the modality of stimulus input is largely irrelevant since the principle determinant of responsiveness is the amount of stimulation. Infants were first habituated with a white light of a constant intensity presented for 1 sec every 20 sec for 20 trials. The infants were then given a cross-modal generalization test in which they were presented with white noise stimuli that ranged in intensity from 70 to 80 dB (74dB was the intensity that was found to be subjectively equivalent to the light). The dependent measure was change in heart rate in response to the

presentation of the various stimuli. Results were consistent with the prediction that the responses to the auditory stimuli should describe a U-shaped function, in that the auditory stimulus that was the least discrepant in intensity in relation to the light elicited a response of relatively small magnitude (because they were already habituated to that intensity), whereas auditory stimuli that were perceived as more discrepant should elicit a response of greater magnitude (as if it was a novel intensity).

Perhaps the strongest support for an "intensity" hypothesis is the work of Spear and his colleagues. If responding is based upon intensity rather than modality, intersensory effects of conditioning should be similar to intrasensory effects in that both could be related to amount of stimulation presented. In conditioning studies with rats, Kucharski and Spear (1985) found evidence that pups treat two simultaneously occurring stimuli as a single stimulus composed of the net intensity of each individual stimulus. If a compound CS stimulus is comprised of stimulus A and stimulus B, the consequences of this interaction are tested by comparison to conditioning of stimulus A alone. Kucharski and Spear (1985) report that adult rats were more likely to exhibit overshadowing (stimulus A is learned less effectively in the presence of stimulus B than when presented alone), whereas preweanling rats were more likely to exhibit potentiation (i.e. stimulus A is learned more effectively in

the presence stimulus B than when presented alone). When the stimuli were presented sequentially, both preweanlings and adults tended toward overshadowing. In preweanlings this facilitation of conditioning is exhibited with both intermodal and intramodal stimuli. These findings suggest that inter- and intrasensory effects are not readily distinguishable in the rat pup. Preweanlings' responding was instead based upon the overall intensity of the stimulus. That is, pups responded to the combined A/B stimuli as a single stimulus with the net intensity of both A and B and conditioned more strongly to this more intense stimulus. In contrast, adults treated the compound CS as two separate stimuli. As a result, the presence of stimulus B interfered with the learning of Stimulus A.

The intensity hypothesis described above provides some possible clues as to the cross modal effects by which experiential enhancement can accelerate visually guided functioning in bobwhite quail. It appears that embryos exposed to enhanced stimulation, regardless of modality (i.e., auditory or visual), respond to combined auditory/visual cues at an earlier age than unmanipulated chicks (Lickliter & Stoumbos, 1991; Lickliter, 1990a, 1990b). This result implies that amount of stimulation is an important factor in accelerating auditory/visual responsiveness. That is, exposure to amounts of stimulation greater than that which is typically present prenatally

serves to accelerate postnatal responsiveness to combined auditory and visual stimuli, regardless of the specific modality stimulated. The term "amount of stimuli" refers to the amount of sensory stimuli presented relative to control conditions. For example, subjects receiving enhanced auditory stimuli are receiving extra auditory stimuli above that which is present in unmanipulated control conditions. Also, visual stimuli paired with auditory stimuli is a greater amount of stimuli than auditory presented alone.

Previously mentioned research by Lickliter (1990a, 1990b) and Lickliter and Stoumbos (1991) is consistent with this hypothesis, since in all cases experiential enhancement of either auditory or visual stimulation accelerated responsiveness to combined auditory and visual stimuli. Furthermore, when embryos were exposed to enhanced stimulation they did not demonstrate preferences for auditory stimuli alone (Lickliter, 1990a, 1990b). Thus, prenatal exposure to enhanced stimulation resulted in a preference to respond to more stimulus cues (i.e. auditory combined with visual) than is typically observed at that age. If it were the case that exposure to greater than normal amounts of stimulation accelerates functioning, then enhanced stimulation of any kind should accelerate responsiveness to combined auditory/visual stimuli.

This "amount" hypothesis is supported by recent work on the effects of attenuation of prenatal sensory stimulation

from siblings. Lickliter and Lewkowicz (under review) found that bobwhite chicks that were incubated in physical isolation, and therefore received attenuated vestibular, tactile, and proprioceptive stimulation from siblings, did not respond to combined bobwhite auditory and visual cues at 72 hr of age, as observed in communally incubated chicks. Rather, the isolate-incubated subjects continued to respond to auditory cues presented alone at 72 hr of age. In other words, subjects that received attenuated amounts of prenatal stimulation responded to less stimulation postnatally than communally incubated embryos.

Taken together the research reviewed above indicate that the amount of prenatal stimulation is an important factor in determining the amount of stimulation subjects respond to when tested postnatally. That is, subjects exposed to attenuated prenatal stimulation respond to auditory cues alone whereas enhanced prenatal stimulation accelerates responsiveness to combined auditory and visual stimuli rather than auditory cues alone. Although the research reviewed above suggests that enhanced prenatal stimulation of any kind accelerates responsiveness, the specific modality of stimulus presentation may be an important factor. It is possible that enhanced auditory and visual stimulation accelerates responsiveness to combined auditory/visual stimuli. If this is the case, this possibility may help further explain the findings of Gottlieb et al.(1989), and Lickliter and

Hellewell (1992). In these experiments, subjects were stimulated prenatally with concurrent auditory and visual stimuli (i.e. bobwhite maternal call and patterned light). Subjects were then tested postnatally for their preference between two auditory stimuli presented alone (i.e., familiar and unfamiliar maternal calls both presented without concurrent visual stimulation). In each study hatchlings did not display a preference for the familiar maternal call. In contrast, control birds that were exposed to the call only and tested with the call only displayed a preference for the familiar call presented alone. In other words, the lack of early auditory learning only occurred in hatchlings that were exposed prenatally to two or more concurrently presented stimuli (auditory and visual) and were subsequently tested with only auditory stimulation.

Thus, there was a mismatch between the nature of the stimulation provided during prenatal exposure and testing, which may have affected the subjects' performance in the testing trial. It is possible that the concurrent presentation of visual stimulation did not, in and of itself, interfere with the learning of the call. Rather, chicks' lack of responsiveness to the familiar call may have been due to the fact that embryos exposed to early visual stimulation do not respond to auditory cues presented alone, but require combined auditory and visual cues (Lickliter, 1990a, 1990b). Had the chicks been tested with combined auditory/visual

cues, they may have shown a preference for the familiar maternal call. This finding would be consistent with a model which predicts that prenatal exposure to enhanced auditory/visual stimulation accelerates postnatal responsiveness to combined auditory/visual stimulation.

The data reviewed above suggest a pattern in which prenatal exposure to enhanced stimulation in the form of auditory and visual experience accelerates postnatal responsiveness to combined auditory/visual cues. This may be only partially true, however, since all of the available data are still not accounted for. For example, there is evidence that not all types of enhanced auditory stimulation accelerates responsiveness. The term "type of stimulus" refers to the specific kind of stimulus used, such as a specific variant of a bobwhite call.

For example, enhanced auditory experience does not accelerate perceptual functioning under all conditions. Lickliter and Stoumbos (1991) exposed bobwhite quail embryos to increased amounts of their own normally occurring embryonic vocalizations during the days immediately prior to hatching. When tested postnatally, these birds showed an accelerated pattern of responsiveness to species-specific maternal visual cues. In contrast, bobwhite quail embryos exposed to bobwhite embryonic vocalizations with a faster repetition rate than normal (4.5 notes per sec rather than the normal rate of 3.2 notes per sec) did not show an

accelerated pattern of postnatal visual responsiveness (Lickliter & Stoumbos, 1991). This finding suggests that the type of stimulation provided must also be taken into account in constructing how sensory experience affects subsequent perceptual abilities.

It is important to note that embryos exposed to embryonic vocalizations with faster than normal repetition rates exhibited a preference for a bobwhite maternal call with a faster repetition rate over a bobwhite maternal call with a normal repetition rate (Lickliter and Stoumbos, 1992). Perhaps bobwhite chicks that were exposed to faster than normal embryonic vocalizations as embryos would display an accelerated visual preference if they were tested in a choice test in which each hen was paired with the fast version of the bobwhite maternal call. That is, if the testing stimuli are closely matched to the early exposure stimuli, subjects may show an accelerated auditory/visual preference. There is reason to expect this result since bobwhite chicks prefer repetition rates (Lickliter & Stoumbos, 1992) as well as maternal calls (Lickliter & Hellewell, 1992) in postnatal tests that closely match those to which they had been exposed prenatally.

Early visual experience also does not interfere with auditory responsiveness under all conditions. For example, Lickliter (1990a, 1990b) found that bobwhite embryos exposed to prenatal visual stimulation do not respond to auditory

cues presented alone at 24 and 48 hr after hatching. In contrast, Lickliter and Hellewell (1992) found that embryos exposed to prenatal visual stimulation and enhanced auditory stimulation (non-concurrently) did respond to auditory cues presented alone. One possible explanation for these apparently contradictory findings may involve the relationship between the nature of the stimulation used during prenatal exposure and the stimuli used during testing. Specifically, in the Lickliter and Hellewell (1992) study the prenatal auditory stimulus was identical to the testing stimuli for which the subjects exhibited a preference. In other words there was a match between the type of prenatal stimuli and the testing stimuli. The Lickliter (1990a, 1990b) studies did not employ such a match.

Hypothesis and Predictions

After reviewing previous research it appears that there are several factors that may play important roles in determining the effect an experiential manipulation has on subsequent perceptual responsiveness. These factors include 1) the amount of stimulation (in terms of experiential enhancement or experiential attenuation) present relative to control conditions, 2) the type of stimulation (i.e. auditory or visual) provided, and 3) the match between the nature of the prenatal exposure stimuli and the postnatal testing stimuli employed (in terms of amount or type of stimulation).

The present study was designed to examine the roles and relative importance of each of these factors. The present study was also designed to determine whether these factors could account for the fact that some experiential manipulations accelerate auditory/visual responsiveness while others do not.

As a first step in examining the relative importance of type and amount of stimulation Experiment 1 presented chicks with a direct choice between a match for type versus a match for amount of stimulus cues. Specifically, Experiment 1 examined whether chicks exposed to enhanced prenatal stimulation would prefer a match between the amount of stimulation (i.e. exhibit a preference for novel auditory and visual cues combined) or the type of stimulation (i.e. exhibit a preference for matching auditory cues presented alone. If subjects' responsiveness is guided primarily by a match between the amount of prenatal and postnatal stimulation, then subjects should show a preference for the combined auditory/visual cues. If, on the other hand, responsiveness is guided by a match between the type of prenatal and postnatal stimulation, then subjects should exhibit a preference for the familiar auditory cues.

Experiment 2 further investigated the role of type matching. Specifically, Experiment 2 examined whether the match between the type of prenatal exposure stimuli and testing stimuli could explain why Lickliter and Stoumbos

(1991) found that different types of prenatal auditory stimulation did not all accelerate auditory/visual responsiveness. If chicks require a match between prenatal and postnatal auditory stimuli to guide their responsiveness, then subjects exposed to enhanced prenatal stimulation should not exhibit accelerated auditory/visual responsiveness when the testing stimuli do not match the prenatal stimuli. They should, however, exhibit accelerated auditory/visual responsiveness if the testing stimuli matches the prenatal stimulation.

Previous research suggests that enhanced prenatal stimulation can accelerate responsiveness to combined auditory and visual cues (Lickliter, 1990a, 1990b; Lickliter and Stoumbos, 1991). Experiment 3 examined the possibility that this effect can be masked by the use of familiar testing stimuli. That is, chicks may exhibit a preference for familiar auditory stimuli presented alone during testing despite having experienced enhanced prenatal stimulation. If this type matching is controlled for, embryos exposed to auditory and visual stimulation should require combined auditory and visual cues in order to direct their filial preferences after hatching and should not respond to auditory cues presented alone.

Experiment 4 examined whether such a preference for a match between amount of stimuli could account for the findings of Lickliter and Hellewell (1992), in which subjects

exposed to concurrent auditory and visual stimulation prenatally did not exhibit a preference for familiar auditory cues presented alone during postnatal testing. If subjects in the Lickliter and Hellewell (1992) study did not exhibit a preference for the familiar call due to an impoverished testing situation, then chicks exposed to the same prenatal auditory and visual cues should show a preference for the familiar call if it is paired with species-specific visual cues during testing.

General Methods

Subjects

Maternally naive, incubator-reared bobwhite quail chicks (Colinus virginianus) served as subjects. Fertile, unincubated eggs were received weekly from a commercial supplier and set in a Petersime Model I incubator, maintained at 37.5 °C and 80-83% humidity. After 20 days of incubation the eggs were transferred to a hatching tray located in the bottom of the incubator. Only those birds that hatched between the second half of day 22 and the first half of Day 23 of incubation were used as subjects (by convention, Day 23 of incubation begins at 23 day, 0 hr and ends at 23 day, 23 hr). This constraint was employed to control for possible effects of variation in developmental age. The possible influence of between-hatch variation in behavior was controlled by drawing subjects for each experiment from at least three different batches of eggs.

After hatching, chicks were placed in large plastic tubs (45 x 25 x 15 cm) which contained 10-12 same-aged chicks. This group size was chosen to mimic naturally occurring brood conditions (Stoddard, 1931; Stokes, 1967). The room in which the hatchlings were kept was illuminated by a 100-W brooder lamp suspended above the plastic tubs, which maintains an ambient air temperature of approximately 30 °C. Food and water was continuously available throughout the course of the experiments.

Egg Opening Procedure

During the second half of the 21st day of incubation (21 day, 1200-1600 hr), the shell and inner-shell membrane over the air space of the egg of each subject was removed and the embryo's head was gently pulled out of the shell. The embryo's bill usually penetrates the air space early on Day 21, and it is at this time that the embryo begins to respire and vocalize (Vince, 1973). As a result, exposing the embryo's head at this time (the body remains confined within the shell) does not interfere with incubation nor does it adversely affect survivability (Heaton & Galleher, 1981). This procedure produces no bleeding and requires about 1 minute per egg. Following removal of part of the shell, opened eggs were placed in a Hovi-bator portable incubator for the last 36 hr of incubation. This incubator is outfitted with a Plexiglass top, allowing both observation and stimulation of the embryos within. Temperature and humidity was maintained as during incubation, and as a result, experimental embryos and control embryos did not differ in their developmental age at hatch.

Apparatus

The testing apparatus was located in a sound-attenuated room and consisted of a large circular arena, 160 cm in diameter, surrounded by a black curtain that shields the observer from the subject's view. The walls of the apparatus

are lined with foam to attenuate echoes and the floor is painted flat black. Two rectangular approach areas (32 x 15 cm) are delineated on opposite sides of the arena by green lines painted on the floor. A mid-range dome radiator speaker is positioned behind the curtain in each of these approach areas, equidistant from the point at which each subject was placed in the apparatus. These speakers allow the presentation of maternal auditory cues during the test trial. Each speaker is connected to a Tascam model 122-B cassette tape recorder located at a control table. The observer was seated at this table and observed each subject's activity through a large mirror positioned above the arena. A system of hand-operated stop-watches was used to score the latency and duration of response, as described below. The testing room was maintained at approximately 25 °C throughout the study.

Testing

One simultaneous choice test, 5 min in length, was given to each subject at either 48 hr or 72 hr (+/- 3hr) following hatching. The birds were tested for their preference between various auditory and/or visual stimuli presented on either side of the arena. Presentation of the stimuli was counterbalanced across subjects to prevent a possible side bias from affecting the results. In the test trials, each quail hatchling was placed singly in the test apparatus, equidistant from the two approach areas. The latency and

duration of a subject's response to the audio-visual stimuli was scored as follows: As the bird entered each approach area, its choice, the latency (amount of time elapsed in seconds from the onset of the trial), and duration (the cumulative amount of time in seconds the bird remained in the approach area) of response was recorded. When over the course of the 5-minute test, a chick stayed in one approach area for more than twice the time it spent in the opposing area, a preference was registered. Occasionally a bird entered both approach areas during a test without showing a preference for either one. This behavior was scored as "no preference" in the tables showing the test results. If a subject did not enter either approach area, it was considered a "non-responder" and received a score of 300 seconds for latency (the length of the trial) and 0 seconds for duration for both audio-visual stimuli. This usually occurred because the subject either "froze" (that is crouched and remained motionless throughout the trial) or because the subject ran around the testing arena for the duration of the trial without stopping in either approach area. This method of data collection allowed information regarding whether the subjects exhibited a preference for one stimulus, approached both stimuli without showing a preference for either one, or did not respond to either stimulus during a test trial.

Data Analysis

Before performing any statistical analyses, duration

scores of less than 10 seconds was replaced with a score of zero, to avoid scoring accidental responses as subjects move about the area. The corresponding latency score was replaced with a score of 300 sec (the length of the testing trial). The primary data of interest in this study were measures of preference for the auditory and visual stimuli presented during the trials. Three such measures of preference were analyzed: (a) differences in the latency of approach to each stimulus and (b) the differences in the duration of time spent in proximity to each stimulus by a subject in a group were evaluated by a paired t-test performed on the mean latency and duration scores of each stimulus, and (c) an individual preference, assigned to any subject that stayed in proximity to one stimulus for more than twice as long as the other (duration), was evaluated by the chi-square test. These data were used to determine whether or not subjects exhibited preferential responsiveness, and significance levels of $p < .05$ were used to evaluate results.

Since the purpose of this study was to determine what stimulative conditions accelerate perceptual responsiveness, comparisons between experimental and control group data were made in order to determine whether subjects' responsiveness was accelerated. Specifically if experimental subjects exhibited a preference at an earlier age than controls, it was concluded that those subjects exhibited accelerated responsiveness.

Experiment 1: The Effects of Enhanced Prenatal Auditory and Visual Stimulation on Responsiveness to Auditory Versus Combined Auditory/Visual Cues

The review of research on early perceptual development in the introduction suggests that the amount and the type of stimulation to which an embryo is exposed can affect its perceptual preferences for different types and amounts of stimuli presented postnatally (Lickliter, 1990a,b; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, under review). It seems likely that these two factors (type and amount of stimulation) both operate to determine the outcome of a particular manipulation. Therefore it is important to examine the respective roles of each in order to see how they could account for the outcomes of the experiential manipulations revealed in earlier studies. As a first step in assessing the roles of both type and amount of stimulation, this experiment compared subjects' preferential responding to a match between the amount of stimulation present during prenatal exposure during postnatal testing versus chicks' preference for a match between the specific type of stimulation subjects were exposed to prenatally and during testing.

In previous research Lickliter and Hellewell (1992) found that bobwhite embryos exposed to both an individual maternal call and to prenatal visual stimulation presented

non-concurrently exhibited a significant preference for that maternal call over an unfamiliar maternal call at 24 hr after hatching. In other words, embryos exposed to both auditory and visual stimulation prenatally responded to auditory cues presented alone at 24 hr after hatching. This finding apparently conflicts with previous findings by Lickliter (1990a, 1990b), which showed that bobwhite embryos exposed to prenatal visual stimulation required combined auditory/visual cues to direct their preferential responding and did not respond to auditory cues presented alone at 24 hr after hatching.

These apparently contradictory findings may be due to the relationship between the type of auditory stimuli used during exposure and during testing in each study. For example, in the Lickliter and Hellewell (1992) study embryos were exposed prenatally to visual stimuli (patterned light) and a bobwhite maternal (call B). Subjects were subsequently tested in a choice test between that same call (call B) and another bobwhite maternal call (call A). Thus the prenatal auditory stimulus was identical to the auditory stimulus used in testing. Under these conditions, the presence of visual stimuli did not interfere with the learning of the familiar call.

On the other hand, in the Lickliter (1990a, 1990b) studies subjects were not presented with matching auditory stimuli during exposure and testing. Instead, subjects were

exposed to prenatal visual stimulation in addition to their own embryonic vocalizations and were then tested for their preference for a bobwhite maternal call. These subjects did not exhibit a preference for the bobwhite maternal call at 24 hr or 48 hr after hatching.

A possible explanation for these contradictory findings may simply be that subjects responded to the familiar stimuli. That is, subjects in the Lickliter and Hellewell (1992) study may have responded to the auditory cues presented alone, despite prenatal visual exposure, because they were identical to the prenatal auditory stimulus to which the subjects have previously been exposed. It is important to note that subjects in that study were not tested with combined auditory/visual cues in the subsequent choice test.

Thus, two factors, the amount of stimulation (in terms of experiential enhancement) and the match between the type of prenatal and testing stimulation may play important role in determining subjects' perceptual responsiveness. This experiment attempted to address the relative importance of these two factors. Specifically, subjects exposed prenatally to non-concurrent visual (patterned light) and auditory (bobwhite call B) stimulation were tested for their preference between the familiar bobwhite call (call B) presented alone versus an unfamiliar variant of the bobwhite call (call A) combined with species-specific visual cues to

determine whether subjects prefer a match between amount or type of stimulation. That is, chicks exposed to auditory and visual stimulation as embryos were required to demonstrate their preference for either a) combined auditory and visual cues postnatally or, b) a match between the specific type of auditory stimuli encountered prenatally (i.e. the individual maternal call). If subjects prefer the match between the specific type of stimulation, then subjects should respond to the familiar auditory cues. If subjects prefer a match between the amount of stimulus cues, then subjects should respond to the combined auditory/visual cues, despite the fact that the testing stimuli are unfamiliar to the subjects.

Method

Sixty-three bobwhite quail, drawn from at least three separate hatches served as subjects. The experimental subjects (n=24) underwent the egg-opening procedure during the second half of day 21 and received 10 min/hr of exposure to a variant of the bobwhite maternal call (call B) during the 24 hr period prior to hatching. Subjects were also exposed to a 15-W light pulsed at three cycles per second (maximum flash energy = 4-W/s) for another 10 min/hr during the 24 hr period. In other words, embryos received non-concurrent auditory and visual stimulation. The call was played on a Marantz model PMD 221 portable cassette recorder and was presented at a uniform peak intensity of 65 db as

measured by a Bruel & Kjaer model 2232 sound level meter. The temporally patterned light was located immediately above (4 cm) the plexiglass top of the portable incubator. Particular care was taken to insure that the presence of the light did not alter the ambient air temperature or relative humidity within the incubator.

Since acceleration of responsiveness is determined relative to control conditions, unmanipulated chicks were tested at 24hr and 72hr after hatching to provide comparison data by which to assess the perceptual responsiveness pattern of manipulated chicks. That is, unmanipulated chicks typically exhibit responsiveness to auditory cues at 24hr of age and respond to combined auditory and visual cues by 72hr after hatching. Therefore, if experimental chicks exhibit a preference for combined auditory and visual cues at 24hr after hatching, then their responsiveness is accelerated relative to controls. Control subjects (n=40) did not undergo the egg-opening procedure and did not receive enhanced prenatal stimulation. Previous research has demonstrated that the egg opening procedure alone does not, in and of itself, affect hatchlings' postnatal perceptual responsiveness (Lickliter, 1990a; Lickliter, in press). Following hatching, chicks were placed in groups containing 10-12 same-age chicks and individually tested at 24 hr or 72 hr of age in a simultaneous choice test between the familiar bobwhite call (Call B) presented alone versus an unfamiliar

variant of the maternal call (Call A) paired with a stuffed bobwhite hen replica. Choice and latency to approach were scored as described in the General Method section.

Results and Discussion

The results of testing are shown in Tables 1 and 2. Experimental chicks tested at 24 hr after hatching showed a significant preference for the familiar bobwhite maternal call (Call B) presented alone over the unfamiliar bobwhite maternal call (Call A) paired with the stuffed bobwhite hen replica (Table 1, $p < .05$; $\chi^2 = 10.53$, $df=2$). Correspondingly, there were significantly longer durations ($t=2.77$, $df=40$ $p < .001$) and shorter latency scores ($t=2.03$, $df=41$, $p < .05$) in chicks' response to the familiar bobwhite maternal call (Table 2).

Results also showed that unmanipulated chicks tested at 24 hr after hatching did not display a preference for either the bobwhite maternal call "A" paired with a stuffed bobwhite hen or the bobwhite maternal call "B" presented alone (Table 1). Correspondingly, there were no significant differences in control subjects' latency or duration scores at 24 hr (Table 2). In contrast, control subjects tested at 72 hr after hatching displayed a significant preference for the bobwhite maternal call "A" paired with the stuffed bobwhite hen (Table 1, $p < .05$; $\chi^2 = 28.39$; $df=2$). Correspondingly, there were significantly longer durations ($t=7.51$, $df=16$

$p < .001$) and shorter latency scores ($t=6.90$, $df=17$ $p < .001$) in chicks response to the bobwhite call "A" paired with the bobwhite hen (Table 2). These results are consistent with previous findings that unmanipulated bobwhite chicks responsiveness is guided by auditory cues at 24 hr of age, and unmanipulated chicks do not utilize visual cues to guide their responsiveness until 72 hr after hatching (Lickliter & Virkar, 1989).

The results of this experiment indicate that experimental chicks preferred a match between the type of auditory stimulus presented prenatally and during testing over a match between the amount of stimulus cues presented prenatally and during testing. In other words, chicks showed a preference for a familiar auditory stimulus presented alone at 24 hr after hatching despite having been exposed to enhanced prenatal auditory and visual stimulation. In contrast, Lickliter (1990a,b) found that chicks exposed to prenatal visual stimulation required combined auditory/visual cues to direct their preferences and did not respond to auditory cues alone when tested with novel stimuli. In relation to the earlier findings of Lickliter and Hellewell (1992), it appears that the presence of a familiar auditory stimulus presented alone is sufficient to guide chicks' preferential responses despite exposure to early visual experience. Thus, it appears that type of stimulation presented prenatally and during testing is a more critical

variable than amount of stimulation. This notion is explored further in the next experiment.

Experiment 2: Effects of Auditory Matching on Auditory/Visual Responsiveness

The results of Experiment 2 indicate that subjects prefer a match between the type of stimulus presented prenatally and that presented postnatally. This preference for the familiar type of stimulation is apparently strong enough to overshadow the effects of prenatal visual experience. The match between type of stimuli therefore appears to be an important factor that must be accounted for when examining the effects of a manipulation of sensory experience on perceptual functioning. For example, such "stimulus matching" may have been a factor in the findings of Lickliter and Stoumbos (1991, 1992). Lickliter and Stoumbos (1991) exposed bobwhite quail embryos to increased amounts of their own normally occurring embryonic vocalizations during the days immediately prior to hatching. When tested postnatally, these birds showed an accelerated pattern of responsiveness to species-specific maternal visual cues. In contrast, bobwhite quail embryos exposed to bobwhite embryonic vocalizations with a faster repetition rate than normal did not show an accelerated pattern of postnatal visual responsiveness (Lickliter & Stoumbos, 1991), suggesting that different types of prenatal auditory

stimulation have different effects on postnatal perceptual responsiveness.

In a subsequent study Lickliter and Stoumbos (1992) reported that bobwhite embryos exposed to the same auditory stimulation (bobwhite embryonic vocalizations) at a faster repetition rate exhibited a preference for a bobwhite maternal call with a faster repetition rate over a bobwhite maternal call with a normal repetition rate. However, it is important to note that the embryos in that study were exposed prenatally to auditory stimulation with higher repetition rate but were tested with the bobwhite maternal call at normal repetition rate paired with species-specific visual cues. Therefore, there may have been a mismatch between the nature of the prenatal stimulation and the testing stimuli. It is possible that subjects would have exhibited accelerated auditory/visual responsiveness if the testing stimuli more closely matched the prenatal stimuli (in terms of repetition rate). If the match between the stimuli to which the embryo is exposed and the testing stimuli employed is important, then subjects should be able to respond to combined auditory/visual stimuli if the auditory stimulus used in testing matches the stimuli to which they were exposed prenatally, even if the auditory stimulation is "atypical" (not species-typical).

Therefore, in this experiment bobwhite embryos were exposed to modified bobwhite embryonic vocalizations with

faster than normal repetition rates as in the Lickliter and Stoumbos (1991) study and were then tested in a visual choice test with bobwhite maternal calls at faster repetition rates paired with a bobwhite hen or a scaled quail hen replica. Since bobwhite chicks exposed to fast embryonic vocalizations prefer a bobwhite maternal call with a matching (fast) repetition rate (Lickliter & Stoumbos, 1992), subjects were expected to exhibit accelerated auditory/visual responsiveness when tested with auditory stimuli that match the prenatal exposure stimuli in terms of repetition rate. In other words, chicks should prefer testing stimuli that more closely matched the prenatal auditory stimuli they experienced as embryos.

Method

Twenty-one bobwhite quail hatchlings, drawn from at least three separate hatches, served as subjects. Subjects underwent the egg opening procedure as described in the General method section. The embryos were then placed in a portable incubator and stimulated with recordings of bobwhite embryonic vocalizations with a faster repetition rate than normal. This was accomplished by halving the space between notes in a burst, resulting in a repetition rate of 4.5 notes per second rather than the typical repetition rate of 3.2 notes per second (see Figure 2). All other acoustical features of the embryonic vocalizations remained unaltered

and matched those of the normal (unmanipulated) stimulation tapes. Subjects received exposure to the recording for 10 min per hour during the last 24- to 36-hr period before hatching (mean exposure time = 260 min). The recording was looped to repeat continuously during the 10-min exposure period.

Following hatching all chicks were placed in rearing tubs with 10-12 same-aged chicks. Subjects were tested individually at 24 hr after hatching in a simultaneous choice test between a bobwhite maternal call with a faster repetition rate than normal (2.6 notes/sec, as opposed to the normal rate of 1.4 notes/sec, see Figure 2) paired with a stuffed bobwhite hen versus a fast bobwhite maternal call paired with a stuffed scaled quail hen. Since both hens were emitting the same call, auditory cues did not offer a basis for decision. Subjects were thus required to base their preference on the available visual cues provided by the hens. Choice and latency were scored as described in the General Method section.

Results and Discussion

The results of testing are shown in Tables 3 and 4. Experimental chicks tested at 24 hr after hatching exhibited a significant preference for the bobwhite hen paired with the fast bobwhite maternal call over the scaled hen paired with the fast bobwhite maternal call (Table 3, $p < .01$; $\chi^2 = 12.34$;

df=2). Correspondingly , there were significantly longer durations ($t=3.69$, $df=29$ $p < .001$) and shorter latency scores ($t=2.24$, $df=32$ $p < .05$) in chicks' response to the bobwhite hen paired with the fast bobwhite maternal call (Table 4).

These findings support the hypothesis that prenatal exposure to faster than normal bobwhite embryonic vocalizations can result in accelerated visual responsiveness under specific conditions. This result is consistent with the findings of Lickliter and Stoumbos (1991) in that prenatal exposure to bobwhite embryonic vocalizations was found to accelerate responsiveness to bobwhite maternal visual cues. This finding is also consistent with the findings of Lickliter and Stoumbos (1992) in that prenatal exposure to faster than normal bobwhite embryonic vocalizations results in a preference for a faster than normal bobwhite maternal call.

An important aspect of this experiment is the finding that different types of auditory stimulation can be shown to accelerate visual responsiveness if the appropriate testing stimuli are used. Again, the relationship between the type of stimuli used during prenatal exposure and during postnatal testing appears to be a critical factor. Previously it appeared that only a certain type of embryonic vocalizations had the effect of accelerating auditory/visual responsiveness (Lickliter & Stoumbos, 1992). It now seems that the "atypical" auditory stimulation used in the Lickliter and

Stoumbos study may have been sufficient to accelerate responsiveness, but the effects of acceleration were masked by the testing stimuli employed. It is therefore important to account for the relationship between exposure and testing stimuli when assessing the effects of a specific manipulation of sensory experience.

It is interesting to note that the stimuli used prenatally and postnatally do not have to be identical (as in Experiment 1) for type matching to affect subsequent responsiveness. In fact, although the repetition rates of the embryonic vocalizations and the maternal call used in testing in this experiment were both accelerated, they did not have identical repetition rates (Figure 2). Apparently some degree of similarity between stimuli is sufficient to guide chicks' preferential responding.

Experiment 3: Effects of Prenatal Auditory and Visual Stimulation on Responsiveness to Combined Auditory/Visual Cues

Taken together, Experiments 2 and 3 demonstrated that type matching can direct chicks' perceptual responsiveness under certain conditions. Having identified familiarity of type of auditory stimuli as an important factor, it is now possible to address the role of amount of stimulation while controlling for type matching. The following experiments were designed to determine if the relationship between amount

of stimulation during exposure and during testing could also account for patterns of responsiveness if type matching were controlled for. For example, it is possible that the prenatal auditory and visual stimulation presented in Experiment 1 potentially accelerated subjects' visual responsiveness, but the effect was masked in testing due to the presence of the matching auditory cues. To test for this possibility, this experiment examined whether exposure to enhanced auditory/visual stimulation accelerates responsiveness to combined auditory/visual cues when type matching is controlled. In other words, does exposure to more prenatal stimulation lead to a preference for more postnatal stimulation? If so, then embryos exposed to enhanced auditory and visual stimuli prenatally should require combined auditory/visual cues to successfully guide their postnatal filial preferences.

Embryos in this experiment were presented with non-concurrent auditory and visual stimulation and subsequently tested for their preference between the familiar auditory stimulus presented alone versus the familiar auditory stimulus presented with bobwhite hen visual cues. Since both auditory cues presented during testing were familiar, type matching was controlled for. Therefore, if subjects' responding is based solely upon familiarity of the auditory stimuli, then subjects should not exhibit a preference for either stimulus cue. On the other hand, if early visual

simulation does accelerate chicks' visual responsiveness (Lickliter, 1990a), then the subjects should require both auditory and visual cues to direct their preferential responding. That is, chicks that received early auditory and visual stimulation should exhibit a preference for the combined auditory and visual stimulus over the familiar auditory stimulus presented alone.

Method

Sixty bobwhite quail, drawn from at least three separate hatches served as subjects. The experimental embryos (n=20) underwent the egg-opening procedure during the second half of day 21 and received 10 min/hr of exposure to a variant of the bobwhite maternal call ("Call B") during the 24 hr period prior to hatching. Subjects were also be exposed to a 15-W light pulsed at three cycles per second (maximum flash energy = 4-W/s) during another 10 min/hr during the 24 hr prior to hatching. In other words, subjects received non-concurrent auditory and visual stimulation. The call was played on a Marantz model PMD 221 portable cassette recorder and was presented at a uniform peak intensity of 65 db as measured by a Bruel & Kjaer model 2232 sound level meter. The temporally patterned light was located immediately above (4 cm) the plexiglass top of the portable incubator. Particular care was taken to insure that the presence of the light did not

alter the ambient air temperature or relative humidity within the incubator.

Control subjects (n=40) did not receive enhanced prenatal stimulation. Following hatching, chicks were placed in social groups containing 10-12 same-age chicks and individually tested at 24 hr of age in a simultaneous choice test between the familiar bobwhite call (Call B) paired with a stuffed bobwhite hen replica versus the familiar variant of the maternal call (Call B) presented alone. Choice and latency were scored as described in the General Method section.

Results and Discussion

The results of testing are shown in Tables 5 and 6. Results show that chicks tested at 24 hr exhibited a significant preference for the bobwhite call paired with the bobwhite hen over the bobwhite call presented alone (Table 5, $p < .05$; $\chi^2 = 9.09$; $df=2$). Correspondingly, there were significantly longer durations ($t=2.53$, $df=37$ $p < .01$) and shorter latency scores ($t=2.81$, $df=36$ $p < .01$) in subjects' responses to the bobwhite call paired with the bobwhite hen over the bobwhite call presented alone (Table 6).

Results also showed that unmanipulated chicks tested at 24 hr after hatching did not display a significant preference for either the bobwhite maternal call paired with a stuffed bobwhite hen or the bobwhite maternal call presented alone

(Table 5). Correspondingly, there were no significant differences in control subjects' latency or duration scores (Table 6). In contrast, control chicks tested at 72 hr after hatching exhibited a significant preference for the bobwhite maternal call paired with the stuffed bobwhite hen (Table 5, $p < .05$; $\chi^2 = 20.02$; $df=2$). Correspondingly, subjects' had significantly longer duration scores ($t=4.56$, $df=9$ $p < .001$) and shorter latencies ($t=3.00$, $df=4$ $p < .001$) to approach the bobwhite maternal call paired with the stuffed bobwhite (Table 6).

These findings suggest that when familiarity factors are controlled for, enhanced prenatal auditory and visual stimulation accelerates responsiveness to combined auditory and visual cues. That is, whereas control chicks did not display such a preference until 72 hr of age, experimental subjects displayed a preference for combined auditory and visual cues at 24hr of age. Therefore, although the type of stimuli used appears to be the more powerful factor, subjects' responding is not based solely on the familiarity of type of stimulation presented. Rather, amount of stimuli also appears to be involved in guiding chicks' early perceptual responsiveness.

Experiment 4: Effects of Concurrent Auditory and Visual Stimulation on Responsiveness to Combined Auditory/Visual Cues

The results of Experiment 3 show that subjects exposed to prenatal auditory and visual stimulation exhibit a preference for familiar auditory cues paired with visual cues over familiar auditory cues presented alone. In other words, subjects exposed to prenatal auditory and visual stimulation as embryos did not respond to auditory cues presented alone, but rather prefer combined auditory and visual cues to direct their preferential responsiveness. This finding may explain why bobwhite embryos in a previous study exposed to the bobwhite maternal call and patterned light stimulation concurrently did not exhibit a preference for the familiar maternal call presented alone (Lickliter and Hellewell, 1992).

In this experiment, bobwhite embryos were exposed to patterned visual stimulation concurrently with a bobwhite maternal call as in the Lickliter and Hellewell (1992) study. Subjects were then tested for their preference for that familiar maternal call over an unfamiliar bobwhite maternal call. Unlike the Lickliter and Hellewell (1992) study, however, the maternal calls were presented with maternal visual cues present during testing (i.e. stuffed models of bobwhite hens). In other words, subjects received concurrent auditory/visual stimulation during prenatal exposure and also

during testing. Consequently, the amount of stimulation present postnatally more closely matched that of the prenatal stimulation period. In contrast to this experiment, subjects in the Lickliter and Hellewell (1992) study were tested with auditory cues presented alone. Consequently, there was a mismatch between the amount of stimuli presented prenatally and during testing. Had subjects been tested with combined auditory/visual cues, they may have exhibited a preference for the combined auditory/visual cues. That is, if embryos that were exposed to patterned visual stimulation and a maternal call concurrently in Lickliter and Hellewell (1992) did not show a preference for the familiar call during testing due to an impoverished testing situation, then chicks exposed to the same concurrent prenatal auditory and visual stimulation should show a preference for the familiar call when tested with both auditory and visual cues presented concurrently.

Method

Twenty-five bobwhite quail, drawn from at least three separate hatches served as subjects. The embryos underwent the egg-opening procedure during the second half of day 21 and received 10 min/hr of exposure to a variant of the bobwhite maternal call ("Call B") during the 24 hr period prior to hatching. Subjects were also exposed to a 15-W light pulsed at three cycles per second (maximum flash energy

= 4-W/s) during the same 10 min/hr that the maternal call was played. In other words, subjects received concurrent prenatal auditory and visual stimulation. The call was played on a Marantz model PMD 221 portable cassette recorder and was presented at a uniform peak intensity of 65 db as measured by a Bruel & Kjaer model 2232 sound level meter. The temporally patterned light was located immediately above (4 cm) the plexiglass top of the portable incubator. Particular care was taken to insure that the presence of the light did not alter the ambient air temperature or relative humidity within the incubator.

Following hatching, chicks were placed in social groups containing 10-12 same-age chicks and were individually tested at 24 hr of age in a simultaneous choice test between the familiar bobwhite call (Call B) paired with a stuffed bobwhite hen replica and an unfamiliar variant of the maternal call (Call A) paired with a stuffed bobwhite hen replica. Pilot testing showed that normally hatched bobwhite chicks did not show a naive preference for either bobwhite hen. Choice and latency were scored as described in the General Method section.

If early visual stimulation accelerates chicks' audio/visual responsiveness (Lickliter, 1990a), then subjects that receive prenatal visual stimulation should require both auditory and visual stimuli to demonstrate preferential responding. In other words, chicks that receive concurrent

early visual stimulation should exhibit a preference for the familiar bobwhite maternal call when paired with a bobwhite hen replica. If subjects do not exhibit a preference for the familiar maternal call despite its being presented with visual cues, then it would appear that the concurrent presentation of the stimuli interfered with prenatal auditory learning.

Results and Discussion

The results of testing are shown in Table 7 and 8. Chicks tested at 24 hr did not exhibit a significant preference for the familiar bobwhite maternal call (Call "B") paired with a stuffed bobwhite hen over the unfamiliar bobwhite maternal call (Call "A") paired with a stuffed bobwhite hen (Table 7). Correspondingly there were no significant differences in subjects' latency or duration scores to either testing stimulus (Table 8).

These findings did not support the hypothesis that embryos exposed to concurrent auditory and visual stimulation simply require combined auditory/visual cues postnatally to direct their filial preferences during testing, in that the presence of species-specific visual stimuli paired with the familiar maternal call was not sufficient to facilitate preferential responsiveness. These results rule out the hypothesis that the results of Lickliter and Hellewell (1992) were due to an impoverished testing situation.

The present findings are consistent with those of Lickliter and Hellewell (1992) in that the concurrent presentation of prenatal auditory and visual stimulation appeared to interfere with prenatal auditory learning. As shown in Experiment 3, prenatal auditory and visual stimulation does accelerate visually guided responsiveness when the prenatal stimulation is presented non-concurrently. However, concurrent presentation of prenatal auditory and visual stimulation appears to interfere with subjects' typical pattern of perceptual responsiveness (see also Gottlieb, Tomlinson & Radell, 1989; Radell & Gottlieb, 1992). This result is consistent with the hypothesis that concurrent stimulation in two stimulus modalities may overload the developing embryo's attentional capacity during the prenatal period (Radell & Gottlieb, 1992) and lends further support to the role of overall amount of stimulation in the emergence of early perceptual preferences.

General Discussion

The results of this study indicate that the relationship between prenatal sensory stimulation and postnatal testing stimuli can play an important role in determining the apparent effects of prenatal sensory stimulation on postnatal perceptual functioning. Both the match between type of stimulation and amount of stimuli were shown to be involved

in determining quail chicks' postnatal perceptual preferences.

Furthermore, the results of the present study revealed a hierarchy among these two features of sensory stimulation. Much as Lickliter (in press) demonstrated a sensory dominance hierarchy in bobwhite chicks in which auditory cues are dominant over visual cues in directing chicks' early social behavior, there appears to be a similar hierarchy among the factors of type and amount of stimuli. Specifically, the match between the type of prenatal and postnatal stimuli appears dominant over the match between the amount of prenatal and postnatal stimuli in directing chicks perceptually guided behavior. In particular, the match between the type of auditory stimuli present prenatally and postnatally appears to be an important factor in influencing chicks' perceptual responsiveness. This finding is also consistent with Lickliter's (in press) reported early auditory dominance in bobwhite chicks during the days following hatching.

By way of review, Experiments 1 and 2 indicate that the match between the type of prenatal and postnatal stimulation was found to be more powerful in directing subjects' responsiveness than the match between the amount of prenatal and postnatal sensory stimuli. This preference for the familiar type of auditory stimulus appeared to outweigh the effects observed by Lickliter (1990a, 1990b) in which

subjects exposed to prenatal visual experience did not respond to maternal auditory cues presented alone, but rather required combined auditory and visual cues to direct their filial preferences. The preference for types of postnatal stimulus cues that match prenatal stimulation may help explain the apparently contradictory findings of Lickliter and Hellewell (1992), in which bobwhite chicks displayed a preference for familiar auditory cues presented alone despite having been exposed to prenatal visual stimulation.

Experiment 2 showed that accelerated responsiveness to auditory/visual cues depends upon the relationship between the type of prenatal and postnatal auditory stimuli employed. Subjects exposed to faster than normal embryonic calls displayed a preference for combined auditory visual cues when the maternal auditory cues were also faster than normal. It is important to point out that the postnatal auditory stimulation used in testing was neither identical to the prenatal stimulation (as was the case in Experiment 2), nor were the repetition rates of the two calls identical. In any case, subjects exposed to faster than normal prenatal auditory cues did display accelerated functioning when tested with faster than normal postnatal auditory cues. Thus, the previously reported findings of Lickliter and Stoumbos (1991) appear to be a function of the relationship between the prenatal stimuli and the postnatal stimuli used to test perceptual functioning. That is, when prenatal auditory

stimuli matched the testing stimuli subjects displayed accelerated responsiveness. When prenatal and postnatal auditory stimuli did not match (as in Lickliter & Stoumbos, 1991) subjects did not exhibit accelerated visual responsiveness. Thus, the "atypical" or faster prenatal auditory stimulation did accelerate auditory/visual responsiveness, but it was specific to the types of cues with which subjects were tested.

Taken together the results of Experiments 1 and 2 suggest that the experiential history of the embryo strongly influences its pattern of postnatal perceptual responsiveness. Specifically, subjects appear to respond preferentially to postnatal auditory stimuli that resemble their prenatal auditory experience. Furthermore, exhibition of accelerated auditory/visual responsiveness depends on the relationship between the type of auditory stimulus used in the prenatal manipulation and during postnatal testing.

In the more general sense, the results of this study provide some support for the intensity hypothesis which states that young organisms are sensitive to the overall amount of stimulation to which they are exposed (Lewkowicz & Turkewitz, 1980; Schneirla, 1965; Turkewitz et al., 1983). Across related studies, the amount of prenatal and postnatal stimulation has been found to be an important factor in affecting subjects' subsequent perceptual responsiveness. For example, subjects exposed to enhanced prenatal auditory

stimuli (Lickliter & Stoumbos, 1991), unusually early visual stimulation, (Lickliter 1990a), or as in the present study, combined auditory and visual stimuli, do consistently exhibit accelerated responsiveness to combined auditory and visual cues.

The intensity hypothesis further posits that young infants respond to the overall amount of stimulation rather than to the specific nature of the stimulation (Schneirla, 1965; Turkewitz et al., 1983). If this were the case, then the amount of prenatal stimulation would be the primary factor that would affect young organism's postnatal perceptual preferences. While the present findings are in keeping with the notion that young animals are sensitive to the overall amount of stimulation, the results of this study and of previous research (Lickliter & Hellewell, 1992; Lickliter & Stoumbos, 1991) also indicate that neonates do not ignore the type of stimulation they are exposed to, as suggested by the intensity hypothesis. Rather, the specific nature of the auditory stimulation present prenatally and postnatally played a major role in determining whether or not subjects exhibited accelerated responsiveness in the days following hatching.

Taken together, the findings of this study suggest that overall amount of sensory stimulation is only one of several nested variables, including the types of prenatal and postnatal stimulation, the timing of presentation of stimuli,

the age and state of the organism, and the experiential history of the organism. A developing organism's perceptual preferences seem to be influenced by all of these variables. It is the interaction between both stimulus and organismic variables that determines the familiarity and the effective intensity of the stimulative experience. In this light, Turkewitz (in press) recently stated that "during the period when a young organism responds to unfamiliar stimuli additively it would not respond additively to an unfamiliar and a familiar stimulus nor two familiar stimuli. Therefore, transitions from intensity based to organizationally based responding is not age dependent, but is rather stimulus specific in relation to the experiential history of the individual involved."

Moreover, these variables may be hierarchically arranged. For example, in the present study, the match between the type of prenatal and postnatal auditory stimuli seemed to be a more influential factor than the amount of stimuli in directing chicks' postnatal perceptual preferences. Amount of stimulation was necessary but not sufficient to direct subjects perceptual preferences, in that subjects still required the appropriate type of auditory stimuli in order to exhibit accelerated responsiveness to combined auditory and visual cues.

The "appropriate type" of auditory stimuli used in testing was determined by the experiential history of the

organism, which of course determines what is familiar and novel to the organism. As demonstrated in the present study, this familiarity factor plays a significant role in determining subjects' perceptual preferences. Other studies have also demonstrated what Rheingold (1985) referred to as the "pull of the familiar". For example, rat pups exhibit preferences for tastes they experienced in utero over unfamiliar tastes (Smotherman, 1982). Similarly, mallard ducklings can be induced to prefer a chicken maternal call they experienced prenatally over their own species-specific maternal call (Gottlieb, 1987).

The results of this study raise the interesting question of how to define stimulus parameters which are actually familiar to an organism. For example, chicks in Experiment 2 were exposed to fast prenatal embryonic vocalizations and subsequently preferred a fast bobwhite maternal call. The prenatal and postnatal calls were not the same call. Both had increased repetition rates, but the repetition rates were not identical. If familiarity of type of stimulation is an important factor in determining perceptual functioning, it is then important to determine what exactly was "familiar" about the fast bobwhite call? Is there some definable "range of familiarity"?

Also, since familiarity is important in guiding perceptual functioning, future research should examine mechanisms underlying animals' preferences for familiar

events. It may be that once an animal has habituated to or become familiar with a stimulus, that now familiar stimulus affects the arousal level of the organism differently than a novel stimulus, which in turn may influence whether the animal will approach or withdraw from certain stimuli, or even whether the animal will attend to specific stimuli.

In sum, the results of this study indicate that future research aimed at examining the mechanisms underlying the effects of prenatal sensory manipulations on postnatal perceptual functioning must recognize the importance of the experiential history of the organism, the characteristics of the stimulation and the state of the organism (Figure 3). The investigation of early perceptual development, like other aspects of developmental science, will require the incorporation of ever more complex, dynamic, and hierarchically based notions about the processes and mechanisms associated with behavioral development.

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Table 1. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 1.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call B	Bobwhite Maternal Call A and Bobwhite Hen	No Preference
Prenatal Auditory/Visual Stimulation					
24	24	23	15*	4	4
Control					
24	20	18	6	7	5
72	20	17	0	16*	1

*p<.05 (chi-square test)

Table 2. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 1.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call B	Bobwhite Maternal Call A and Bobwhite Hen	Bobwhite Maternal Call B	Bobwhite Maternal Call A and Bobwhite Hen
Prenatal Auditory/Visual Stimulation					
24	24	75.3* (95.1)	169 (131)	107.6* (66.9)	61.1 (86.9)
Control					
24	20	130 (106)	95 (140)	58.3 (64.9)	75.9 (73.1)
72	20	238 (117)	34.9* (28.6)	5.4 (10.9)	120.4* (62.2)

*p<.05 (paired t-test)

Table 3. Preference of Chicks in Simultaneous Audio/Visual Choice Test in Experiment 2.

Age (in hrs)	n	n responding	Preference		
			Fast Bobwhite Maternal Call and Bobwhite Hen	Fast Bobwhite Maternal Call and Scaled Hen	No Preference
24	21	18	13*	3	2

* $p < .05$, chi-square test

Table 4. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 2.

Age (in hrs)	n	Latency		Duration	
		Fast Bobwhite Maternal Call and Bobwhite Hen	Fast Bobwhite Maternal Call and Scaled Hen	Fast Bobwhite Maternal Call and Bobwhite Hen	Fast Bobwhite Maternal Call and Scaled Hen
24	24	88* (105)	177 (130)	112.2* (78.1)	30.8 (51.5)

*p<.05 (paired t-test)

Table 5. Preference of Chicks in Simultaneous Auditory-Visual Choice Tests at 24 hr in Experiment 3.

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call B	Bobwhite Maternal Call B and Bobwhite Hen	No Preference
Prenatal Auditory/Visual Stimulation					
24	20	20	4	13*	3
Control					
24	20	18	5	6	7
72	20	10	0	10*	0

*p<.05 (chi-square test)

Table 6. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 3.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call B	Bobwhite Maternal Call B and Bobwhite Hen	Bobwhite Maternal Call B	Bobwhite Maternal Call B and Bobwhite Hen
Prenatal Auditory/Visual Stimulation					
24	24	137 (120)	73* (100)	52.7 (69.4)	112.2* (79.4)
Control					
24	20	116 (135)	101 (125)	54.2 (54.8)	50.9 (48.3)
72	20	202 (132)	66* (52.9)	1.2 (3.79)	111.0* (76.1)

*p<.05 (paired t-test)

Table 7. Preference of Chicks in Simultaneous
Auditory/Visual Choice Tests in Experiment 4

Age (in hrs)	n	n responding	Preference		
			Bobwhite Maternal Call A/ Bobwhite Hen	Bobwhite Maternal Call B/ Bobwhite Hen	No Preference
24	25	23	8	14	1

Table 8. Means and Standard Deviations of Latency and Duration Scores of Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 4.

Age (in hrs)	n	Latency		Duration	
		Bobwhite Maternal Call A/ Bobwhite Hen	Bobwhite Maternal Call B/ Bobwhite Hen	Bobwhite Maternal Call A/ Bobwhite Hen	Bobwhite Maternal Call B/ Bobwhite Hen
24	24	149 (137)	99 (124)	44.4 (60.6)	63.7 (58.0)

Figure 1: Summary of previous research on the effects of various prenatal sensory manipulations on auditory and visual responsiveness in bobwhite quail chicks.

Normal Unstimulated
Controls



Early Visual
Experience



Augmented Auditory
Experience



24

48

72

Hour Posthatching



No Preference for Species
Specific Auditory cues



Preference for Species
Specific Auditory cues



No Preference for Species-
Specific Visual Cues



Preference for Combined
Auditory/Visual Cues

Figure 2: Repetition Rates of altered and unaltered bobwhite vocalizations during prenatal exposure and postnatal testing.

	Rep. Rate of Prenatal Emroyonic Vocalization Exposure		Rep. Rate of Bobwhite Maternal Call Employed in Testing
Altered Auditory Cues	4.5	>	3.2
Unaltered Auditory cues	2.6	>	1.4

Figure 3: Proposed hierarchical relationship between stimulus and organism variables that may influence perceptual development

STIMULUS

< = = >

ORGANISM

Level 1:

TYPE OF
STIMULUS

< FAMILIARITY >

EXPERIENTIAL
HISTORY

Level 2:

AMOUNT OF
STIMULATION

EFFECTIVE
< INTENSITY >

STATE OF
ORGANISM

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