

**The Influence of Enhanced Tactile and Vestibular Sensory Stimulation on Subsequent Auditory
and Visual Responsiveness: A Matter of Timing**

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Dissertation submitted to the Faculty of Virginia Polytechnic Institute and State University in partial
fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY
IN
PSYCHOLOGY

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May 3rd, 2002
Blacksburg, VA.

Keywords: Perceptual Development, Tactile and Vestibular Stimulation, Intersensory

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(Abstract)

The fact that sensory modalities do not become functional at the same time raises the question of how sensory systems and their particular experiential histories might influence one another. Few studies have addressed how modified stimulation to earlier-emerging modalities might influence the functioning of relatively later-developing modalities. Previous findings have shown that enhanced prenatal tactile and vestibular (proximal) stimulation extended normal patterns of auditory and delayed normal visual responsiveness to species-typical maternal cues in bobwhite quail. Although these results were attributed to the increased amount of sensory stimulation, they may be a function of when prenatal augmented proximal exposure took place. To address this issue the present study exposed groups of bobwhite quail embryos to equivalent amounts of augmented tactile and vestibular stimulation either at a time when a later-emerging modality (auditory or visual) was beginning to functionally emerge or when it had already functionally emerged. Results indicate that differences in the timing of augmented tactile and vestibular stimulation led to differences in subsequent auditory and visual responsiveness. Embryos were unable to learn a maternal call prior to hatching when enhanced proximal stimulation coincided with auditory functional emergence implicating a deficit in auditory functioning, but did learn a maternal call when enhanced proximal stimulation occurred after auditory functional emergence. Augmented proximal stimulation that coincided with visual functional emergence did not appear to influence normal visual responsiveness, but when proximal stimulation occurred after visual emergence, chicks displayed an accelerated approach response to species-typical visual cues. These findings support the view that the timing of enhanced stimulation to earlier-emerging modalities is important, and have meaningful implications for intersensory theory and research.

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Chapter 1

Introduction and Literature Review

Overview

In the study of developmental processes there has been a shift in attention from the notion of developmental *time* towards that of developmental *timing*. As discussed below, a theoretical framework based on developmental timing recognizes that *when* an experience occurs can be as causally important as *what* is experienced. The present study attempts to demonstrate the importance of timing in the area of sensory and perceptual development during the prenatal and early postnatal periods in bobwhite quail (*Colinus virginianus*). Timing is particularly important in these areas given that sensory systems become functional in a sequential fashion which has led researchers to ask how stimulation to one sensory modality influences the development of function in different modalities in light of the variations in their respective experiential histories. Findings and conceptual frameworks in intersensory research are discussed with special emphasis placed on a recent study by Carlsen and Lickliter (1999) that examined how enhanced stimulation to early-developing modalities influences relatively later-developing modalities. After reviewing this study and its conclusions, an alternative timing-based explanation is provided and empirically tested.

The Importance of Developmental Timing

Today development generally refers to structured, successive changes in living, functioning organisms and is characterized by the emergence of qualitatively new structures and functions (Lerner, 2002). However, during the formative years of developmental psychology, based on the observed regularities in skills and abilities across individuals, development was often characterized as a maturational process (e.g., Gessell, 1929). That is, the smooth and orderly sequence of developmental changes was thought to be under the strict control of a vital force, now identified as a genetic blueprint or template. From this point of view, the cause of development was the preexisting program. In the maturational approach, developmental time (or age) became an important tool used in organizing empirical observations. However, time referred to a causally uninformative marker for describing the developmental outcomes of maturational processes (Spear & Hyatt, 1993).

The role of time within this maturational approach is perhaps best exemplified in the notion of “critical periods”. The critical periods hypothesis was originally formulated by embryologists who advanced the idea that the various parts of the organism emerge in a fixed, maturationally-determined sequence, where each part was allotted a certain amount of time at a specific point in development to emerge (Lerner, 2002). That is, each part had a specific developmental critical period where the appropriate environmental stimulation could easily facilitate its development. In its strongest version, if the necessary environmental input during this critical period were impoverished or absent, the body part would not develop normally, if at all, and it would never have another chance to develop.

Critical periods hypotheses have come under close scrutiny over the last several decades. There is now a substantial body of evidence demonstrating that the onset and offset are not determined by a biological timetable, but are instead influenced by internal, external, and experiential factors (see Colombo, 1982 for review). Critical periods have also been criticized for ignoring the role of the organism as an active contributor to its own environment, which has resulted in an erroneous separation between the organism and its environment (Turkewitz & Devenny, 1994b). Such dichotomous, “either/or” thinking inevitably leads to conceptual dead ends (Turvey & Shaw, 1995).

Over the last several decades, it has become clear that ascribing ontogenetic changes to any single influence (genetic or environmental) undercharacterizes the richness and complexity of development, and avoids explaining *how* development is achieved. Likewise, attempts to reduce development to multiple, yet *independent* sources of information (e.g., genes plus environment) also fails for the same reasons (Anastasi, 1959; Gottlieb, Whalsten & Lickliter, 1998; Johnston, 1987; Lerner, 2002). Instead, modern developmental theory holds that the complexity of development is best captured by realizing that development is determined through the structured, bi-directional interactions among a large number of organismic and contextual influences (Gottlieb et al., 1998; Oyama, 1985). Control of any developmental outcome cannot be attributed to any individual component(s) but is made possible out of the dynamic relationships among relevant components within and between levels of organization (genetic, neural, behavioral, environmental). According to these assumptions, development does not result from preexisting or predetermined information. On the contrary, developmentally relevant information is not (assumed to be) stored somewhere in the structure of the organism or environment, but is itself a product of developmental interactions (Oyama, 1985). The skills and properties evident at one stage emerge from the interactions between the skills and properties of the immediately preceding stage and its changing context.

Modern developmental theory benefits from taking both time and timing seriously. By focusing on time, researchers can describe the normal sequence of development. This search for developmental norms is important for describing what skills and abilities are available and/or preferred at different points in development. Addressing these *what* and *when* questions is a crucial first step in conducting developmental studies. However, answers to these questions do not speak to *how* these skills and abilities are realized. Understanding the processes and mechanisms underlying change is also a central concern among developmentalists (Lickliter & Bahrick, 2001; Thelen & Smith, 1994; 1998).

By rejecting predeterminism and by recognizing that development is epigenetically constructed through a structured manifold of embedded, dynamic relationships, modern developmental theory focuses less on time (or age) and more on developmental *timing*. Timing, used here, refers to the interdependent, temporal relationships among events that bring about developmental change (Spear & Hyatt, 1993). From this definition it is clear that timing is a relational term, and therefore, researchers emphasize the relationships among developmental components, rather than reducing development to the separate contributions of individual factors (Gottlieb, 1991; Lerner, 1992; Spear & Hyatt, 1993). Schneirla (1959) captured the essence of a relational approach in his concept of “effective” stimulation, where the effectiveness of a particular stimulus depends not only on the physical characteristics of the stimulus but on a number of organismic factors as well including the organism’s general level of arousal, developmental state, and experiential history.

On this modern view, *when* an experience takes place is as potentially causally important as what is being encountered. In other words, because the organization of the organism may be qualitatively different at different points in ontogeny, an experience at one time can bring about a different set of consequences compared to when the experience occurs at an earlier or later point. For example, Hymovitch (1952, cited in Gottlieb, in press) reported a timing-based effect on problem solving skills in young rats. He reared one group of rats in an enriched environment followed by an impoverished environment (enriched → impoverished), and reared another group in an impoverished environment followed by an enriched environment (impoverished → enriched). Despite exposure to the same environments for equal amounts of time, those rats initially reared in the enriched environment performed significantly better during testing than did those initially reared in an impoverished environment, suggesting that the timing of exposure to an enriched environment is an important factor. Perhaps this idea of timing is best exemplified in teratological research where the perturbing effects of a toxin (if any) (e.g., thalidomide) depend on when exposure to the toxin takes place. In a similar vein, the influence (if

any) of prenatal maternal stress and depression on postnatal outcomes in their children varies according to when these stressful events occurred during pregnancy (Martin, Noyes, & Wisenbaker, 1999; Schneider, Roughton, Koehler, & Lubach, 1999).

A focus on developmental timing provides a means to uncover developmental processes by leading researchers to focus on the present state and history of the organism and the surrounding context. In this sense, the timing (as opposed to the time) of developmental events can be assigned a formative role in development, influencing both the impact of these events and how the organism will come to subsequently respond to future events (Schneirla, 1957; Spear & Hyatt, 1993). Understanding the timing of developmental events provides a framework for integrating existing findings and for generating new understandings into the dynamic nature of developmental processes, without resorting to reductionistic strategies and explanations (Turkewitz & Devenny, 1993b).

The importance of understanding how timing influences development is underscored by the notion that developmental processes are best described as polyphasic (Gollin, 1981) or heterochronic (Turkewitz, 1993), wherein different structures or subsystems undergo different rates of change at different ontogenetic times. That is, tissue growth follows a non-linear course characterized by periods of relatively gradual growth interspersed with periods of relatively rapid growth (Gollin, 1981). However, when these growth spurts occur varies between regions resulting in different structural-functional relationships becoming organized and available at different times. For example, in humans the right hemisphere tends to develop more rapidly during early periods of prenatal development than does the left hemisphere (Previc, 1991). Thus, the organization of the organism can display qualitatively different configurations (understood to be the nature of relationships between subsystems of the organism as well as those between the organism and its context) during successive periods of ontogeny. Consequently, given the embeddedness and dynamic relationships among systems, the functioning and influence of any system at a particular point in time likely varies as a function of the current and historical configurational status of its surround (Gollin, 1981; Lerner, 1984; Oyama, 1985).

Given the causal contingency outlined above, it becomes the task of those interested in development to shift their focus of attention toward describing and explaining the nature of dynamic organization and how change is brought about and stabilized in polyphasic systems. A useful way to begin unpacking these relationships involves experimentally perturbing the system using various types and amounts of experiences at various points during ontogeny. In the case of behavioral development, this involves discerning not only those conditions under which a skill is realized, but also those conditions that fail to support the development of a particular behavior or skill (Rose & Ruff, 1987). With knowledge of these developmental contingencies in hand, it is possible (a) to draw inferences regarding the dynamic nature of the relationships among relevant components and the underlying processes which make them possible, and (b) to construct principles that accurately describe and predict the activity of these processes across domains and at different points in the life-cycle both within and across species.

Clearly, developmental timing is an important area of inquiry and deserves more theoretical and empirical attention. The current study was designed to contribute to our understanding of how differences in the timing of exposure to enhanced sensory stimulation can influence normal perceptual and behavioral responsiveness during the early postnatal period.

The Influence of Timing on Perceptual Development

The timing of experiential events appears to be a critical factor influencing normal patterns of early perceptual responsiveness. Differences in the timing of experience can be attributed in part to the heterochronous development of the various sensory systems. Sensory systems differ in when they

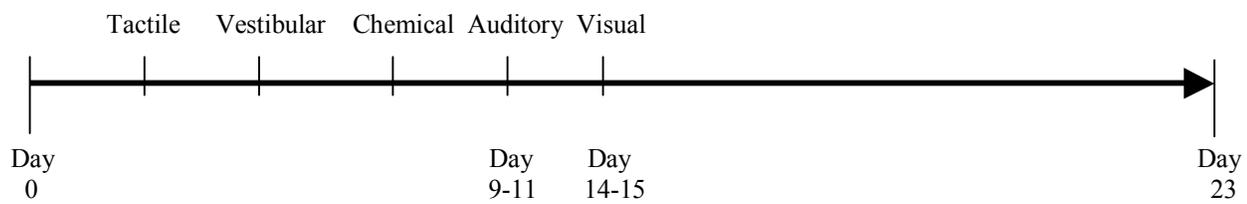
become functional during early ontogeny, showing an invariant and sequential (tactile → vestibular → chemical → auditory → visual) pattern across vertebrate species (see Figure 1 for the sequential onset in bobwhite quail) (Gottlieb, 1971). Gerald Turkewitz and his colleagues (Turkewitz & Kenny, 1982; 1985; Turkewitz & Mellon, 1989) have proposed a sensory limitations hypothesis (hereafter referred to as SLH) to show how this sequential onset of sensory functioning contributes to normal perceptual abilities and organization. According to the SLH, the limitations in early sensory functioning that arise from the sequential onset of sensory functioning are not deficits to be overcome, but instead provide an important source of structure and order which serves to organize normal patterns of perceptual responsiveness. Specifically, this structured pattern of sensory limitations is seen to regulate the timing of neural and attentional resources available to the emerging sensory modalities (Lickliter, 1993; Turkewitz & Kenny, 1982; 1985). In support of this notion of intersensory competition at the neural level, Turkewitz and Kenny (1982) described research demonstrating experience-dependent changes in neural structure (size and weight of various cortical and subcortical regions) and function (receptor fields, amount of activity) following altered sensory experience in one modality. Importantly, altered experience in one sensory modality effects changes in neural structure and function in neural areas associated with the altered modality as well as in areas associated with other sensory modalities. For example, more recent research on sensory maps in the superior-colliculus in the guinea pig indicates that the normal elaboration of auditory space depends on visual experience (Withington-Wray, Binns, & Keating, 1990). Given that the nature of neural structure and function is experience-dependent, then the different types, amounts, and timing of sensory stimulation that result from the sequential emergence of sensory functioning likely serves as an important source of structure influencing normal neural and perceptual organization and development. As a result, relatively earlier-developing sensory modalities (e.g., tactile or vestibular) typically emerge under conditions of reduced competition with other later-developing sensory modalities (e.g., auditory or visual). Moreover, under normal conditions, the earlier-developing modalities likely serve to regulate the onset of later-developing modalities and provide a basis by which the new input (from a later-developing modality) can be assimilated and accommodated (Ronca & Alberts, 1995; Turkewitz, 1994).

The fact that sensory systems do not become functional at the same time raises the question as to how the various sensory systems and their respective developmental histories influence one another during early ontogenetic periods. Such intersensory relationships, fueled in large part by issues raised by the SLH (see below), have constituted a burgeoning area of interest over the last two decades (Gottlieb, Tomlinson & Radell, 1989; Lickliter & Bahrick, 2000; Lewkowicz & Lickliter, 1994; Radell & Gottlieb, 1992; Stein & Meredith, 1993; Turkewitz & Mellon, 1989). This body of research provides converging evidence that altering the timing of sensory stimulation can have dramatic influences on early perceptual and behavioral organization.

The Influence of Timing on Intersensory Development

The SLH provides a framework to approach the study of early intersensory and perceptual organization and development. Predictions founded on the SLH stem from one of two related questions. The first question involves asking how unusually early (premature) stimulation to a later-developing sensory modality (e.g., visual stimulation), provided when this stimulation would normally not be available (e.g., prior to birth or eye-opening), influences the functioning of earlier-emerging modalities (olfaction and/or audition for example). According to the SLH, one should find deficits in the functioning of the earlier-emerging modalities because they are organizing themselves in a context of increased

Figure 1: A schematic diagram of sensory system emergence in bobwhite quail.



intersensory competition that would not be available under normal conditions (Turkewitz & Kenny, 1982). A second question involves addressing how enhanced stimulation in earlier-emerging modalities influences the concurrent or subsequent functioning in later-emerging modalities. In contrast to the former question, no specific predictions were made in regard to the latter question (e.g., Turkewitz & Kenny, 1982; Turkewitz & Mellon, 1989). To date the overwhelming majority of research has focused on addressing the first question, and so very little is known in regards to the second. Nevertheless, answering both these questions can potentially yield valuable information regarding the nature of early perceptual organization and development.

The Effects of Premature Stimulation to Later-Developing Modalities on the Functioning of Earlier-Developing Modalities

One of the earliest studies addressing the first question posed by the SLH was carried out by Celanza, Kenny, and Turkewitz (1984, cited in Lickliter, 1993). They provided visual stimulation to rat pups at a time when visual input would not normally be available, by surgically opening their eyelids 8 days before they would typically open. They found that unusually early visual experience (a later-developing modality) led to delays in responsiveness to olfactory cues (an earlier-developing modality). Specifically, rats whose eyelids were opened early failed to discriminate between familiar and unfamiliar shavings at a time when unmanipulated subjects could discriminate based on olfactory cues. This study clearly shows that providing premature input to a later-developing modality can lead to deficits in earlier-emerging modalities. An additional study by Kenny and Turkewitz (1986) also demonstrated that early eye-opening led rat pups to rely less on olfactory cues and more on visual cues to direct their homing behaviors. In a similar vein, it has been shown that when precocial avian embryos are given premature exposure to light during the days prior to hatching, auditory functioning can be disrupted (Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992). Specifically, avian embryos were able to learn an individual species-typical maternal call in the days prior to hatching, but not when the delivery of the call coincided with exposure to patterned visual input.

However, there are now a number of studies showing that unusually early sensory stimulation to a later-developing modality need not always interfere with the functioning of an earlier-developing modality. For example, in the Gottlieb et al. (1989) and Lickliter and Hellewell (1992) studies prenatal auditory learning did take place when the delivery of the light did not coincide with the delivery of the maternal call, despite premature exposure to visual stimulation. What appears to be the critical factor influencing learning in these experiments is the relational timing of the acoustic and visual events. Indeed, under certain conditions premature visual stimulation can *facilitate or enhance*, rather than disrupt, auditory functioning in avian embryos (Honeycutt & Lickliter, 2001a; Lickliter, Bahrick, & Honeycutt, 2002).

The discrepancies described above between the rodent and avian literatures (where premature exposure led to deficits in the former and could lead to facilitation in the latter) may be due to differences in precocity. In particular, functional emergence in the auditory and visual systems of altricial rats takes place postnatally, whereas in precocial avian embryos all the sensory systems are functional prior to hatching (see Figure 1). As a consequence, premature visual exposure was relatively *greater* (in terms of prematurity) for the altricial rats, whose visual systems were beginning to functionally emerge, compared to the level of prematurity in the precocial avian embryos, whose visual systems had functionally emerged several days prior to stimulus exposure. Thus, the facilitative effects found in the avian embryos during premature exposure procedures may reflect the operation of more mature (i.e., better organized) sensory systems, which are better equipped to deal with the augmented amounts of stimulation, and so may not be a fair comparison to the rodent findings. Thus, it is possible that support for the first prediction of the SLH (i.e., deficits in earlier-emerging modalities due to premature input to later-emerging modalities)

may be found by providing premature stimulation to avian embryos during earlier prenatal periods at the time when the particular modality in question is functionally emerging.

Despite the disparate findings regarding the first prediction made by the SLH, addressing the original question has brought invaluable insight into the mechanisms and organization of early intersensory responsiveness. The evidence from the studies described above emphasize that to explain any instance of responsiveness in a single modality one must take into account what is happening and what has happened in the other sensory modalities, the developmental state and level of organization of the organism, and the relationships between stimulus events. Collectively these studies suggest that the what and how of perception is a matter of contingency depending on a variety of internal and external conditions. It seems plausible, then, that addressing the second question posed by the SLH can yield just as important (if not more) information (like organismic and contextual contingencies) regarding the nature of early perceptual responsiveness.

The Influence of Augmented Stimulation to Earlier-Developing Modalities on the Functioning of Later-Developing Modalities

To date there are only a handful of studies that have assessed the influence of augmented stimulation to an earlier-developing modality on the functioning of later-developing modalities. This is somewhat unfortunate in that the earlier-developing modalities are thought to regulate the onset of functional emergence in later-developing modalities in addition to providing a foundation through which the new input can be assimilated and accommodated (Ronca & Alberts, 1995).

Lickliter and Stoumbos (1991) conducted one of the earliest studies that examined how enhanced stimulation to an earlier-developing modality can influence the functioning of a later-developing modality. They found an intersensory facilitative effect. Specifically, they provided bobwhite embryos with enhanced stimulation to conspecific contentment vocalizations during the day prior to hatching. During postnatal testing, these birds displayed patterns of visual responsiveness to bobwhite maternal cues at 24 hr not normally observed in controls until 72 hr after hatching. Thus, augmented exposure to an earlier-emerging modality was found to accelerate normal patterns of species-typical visual responsiveness. Similar accelerated patterns of visual responsiveness have been found following certain amounts (10 min/hr for 24 hr) of enhanced prenatal visual stimulation (Lickliter, 1990), which calls into question whether the developmental history of the modality (in terms of functional onset; early- vs. late-emerging) was an important factor. Using the prenatal auditory learning paradigm, Radell and Gottlieb (1992) demonstrated how exposure to patterned vestibular stimulation that coincides with the delivery of a maternal call can interfere with avian embryos' ability to learn the call. As previously described, similar interference effects on prenatal auditory learning have been obtained using concurrent visual stimulation (Gottlieb et al., 1989; Honeycutt & Lickliter, 2001a; Honeycutt & Lickliter, in press; Lickliter & Hellewell, 1992). In these cases, auditory interference was found using concurrent stimulation from a later-developing modality (vision) or from an earlier-developing modality (vestibular), which again calls into question whether the earlier vs. late-emerging distinction was a determining factor this particular task.

Thus, research addressing the SLH's second question, like the findings addressing the first question, converge to show that the timing of experiences can potentially influence the nature of early perceptual and behavioral organization. However, from these studies alone it remains unclear what these findings imply about the importance of taking into account the experiential histories of the sensory modalities to understand perceptual organization. In particular, nearly all of the studies (except Radell & Gottlieb, 1992) examining the perceptual consequences of altering the timing of sensory stimulation have assessed intersensory relationships using the auditory and visual modalities. Moreover, and potentially more importantly, *all* of the research using precocial avian embryos has focused on intersensory

relationships during the late prenatal period. To reiterate, delivery of stimulus events to these precocial organisms takes place at a time when all the sensory systems have emerged and have presumably had time to stabilize their internal and external organization. As of yet no study has assessed whether similar effects are found in altricial organisms. Thus, very little is known about the effects (if any) of experiencing altered sensory stimulation during earlier periods of prenatal development. And finally, there are few experimental observations concerning how stimulation to earlier-developing modalities influences later-developing ones. In fact, only one study (Carlsen & Lickliter, 1999) to date has assessed the impact on the functioning of later-developing modalities following exposure to enhanced sensory stimulation to earlier-developing modalities during earlier periods of prenatal development .

Thus, the Carlsen and Lickliter (1999) study is particularly noteworthy not only for (a) addressing the SLH's second question, and (b) providing sensory stimulation during earlier periods of prenatal development that are rarely studied, but also because it focused on sensory modalities that are rarely studied (tactile and vestibular). Again, these early-emerging modalities likely set the stage for the emergence of later-developing modalities. As a consequence, different patterns of responsiveness to stimulation in a later-developing modality may be found depending on the state of the earlier-developing systems (Turkewitz, 1994). In what follows, I outline the results and conclusions of this study, and suggest that the conclusions drawn by Carlsen and Lickliter (1999), although consistent with the data obtained, may have been premature.

A Timing-Based Alternative to the Findings of Carlsen and Lickliter (1999)

Carlsen and Lickliter (1999) provided bobwhite quail embryos with enhanced vestibular and tactile stimulation during the second week of incubation (Days 14-21 of the 23-Day incubation period) by augmenting the normal amount of egg-turning normally provided by the incubator. This enhanced stimulation was provided Relative to unmanipulated control subjects, embryos exposed to the enhanced vestibular and tactile stimulation showed atypical auditory and visual responsiveness. Specifically, they found that these subjects continued responding to species-typical auditory cues into later periods of postnatal development at a time when unmanipulated subjects no longer respond to species-typical auditory cues presented unimodally. However, their ability to learn a maternal call in the day prior to hatching was not impaired. Embryos given augmented vestibular and tactile stimulation also showed deficits in visual development. Whereas unmanipulated birds typically display a species-typical visual preference for bobwhite maternal features by 72 hrs of age, the subjects in the Carlsen and Lickliter (1999) study did not demonstrate a preference for the visual features at any age tested (72 hrs, 96 hrs, 120 hrs). These findings suggest that augmented vestibular exposure leads to significant delays in subsequent responsiveness to species-typical visual cues.

Collectively, these results demonstrate that augmented experience in an earlier-developing modality can have dramatic intersensory effects, altering the normal patterns of perceptual responsiveness in several later-developing modalities. Auditory responsiveness was intensified and temporally extended, whereas visual responsiveness was delayed.

Interestingly, similar patterns of results have been found by providing increased amounts of sensory stimulation in other sensory modalities. For example, exposure to substantially augmented amounts of visual (Sleigh & Lickliter, 1995) or auditory (Sleigh & Lickliter, 1997) stimulation has been found to prolong auditory responsiveness to species-typical maternal cues and delay species-typical visual responsiveness to maternal visual cues. Because Carlsen and Lickliter (1999) provided bobwhite embryos with nearly ten times the normal amount of vestibular and tactile stimulation, they concluded that their findings reflected the consequences of exposure to substantially augmented amounts of prenatal sensory stimulation. However, their findings may reflect the influence of another factor beyond simply the overall amount of sensory stimulation encountered by embryos prenatally.

An alternative explanation points to the possibility of a timing effect, where the particular timing of vestibular and tactile exposure during prenatal development may have resulted in the observed patterns of auditory and visual responsiveness. In the Carlsen and Lickliter (1999) study, enhanced vestibular and tactile stimulation was provided at the time when the visual system was beginning to emerge. Heaton (1973) reported that the onset of visual functioning in bobwhite quail takes place following 65% - 67% of incubation (around Day 15 of incubation of the 23 Day incubation period). Carlsen and Lickliter (1999) began prenatal vestibular exposure on Day 14 of incubation. Hence, at the time of stimulus delivery the visual system was just starting to become functional. It could be that altered experience to the vestibular and tactile modalities *at this particular time during ontogeny* was responsible for the observed intersensory consequences, rather than the amount of enhanced sensory stimulation per se. According to the SLH, the sequential onset of sensory functioning (see Figure 1) is one source of structure during early periods of development, where the limitations in sensory functioning reduce the overall amount of intersensory competition between emerging modalities, thereby allowing for normal perceptual organization and development (Turkewitz & Kenny, 1982; 1985; Turkewitz & Mellon, 1989). It could be that altering the normal amount of sensory stimulation to a relatively mature modality at a time when a functionally immature modality is functionally emerging serves to delay the normal course of development in the latter because it is ill-equipped to compete for necessary neural and attentional resources at this sensitive stage of development.

On this view, altering when tactile and vestibular stimulation is experienced should lead to different developmental outcomes. In particular, by providing vestibular and tactile stimulation at a time when the visual system has already emerged should not disrupt visual responsiveness. Instead, visual responsiveness could be facilitated, wherein quail chicks would display a species-typical visual preference earlier in development. As described above, several studies have shown that enhanced unimodal stimulation in the auditory (Lickliter & Stoumbos, 1991) or visual (Lickliter, 1990) modalities during the late prenatal period can accelerate visual discrimination, with chicks showing a preference for conspecific visual features by 24 hr following hatching rather than 72 hr.

Indeed, the same pattern of timing-based intersensory disruption and facilitation should also hold for the effects of augmented vestibular and tactile stimulation on subsequent auditory functioning. Although the specific age at which auditory sensitivity first emerges has not been reported for bobwhite quail, studies using domestic fowl have found evoked potentials in cochlear nuclei as early as Day 11 of incubation (for review, see Freeman & Vince, 1974). Because Carlsen and Lickliter (1999) began vestibular and tactile stimulation on Day 14, the auditory system likely had emerged and developed enough to accommodate the enhanced activity in earlier-developing sensory systems, and therefore embryos did not show deficits in auditory learning abilities. However, altering the timing of vestibular stimulation where the onset of exposure begins on Day 9 of incubation, presumably a time when the auditory system is beginning to function, should lead to delays in normal auditory development, evident in embryos inability to learn a maternal call during the late prenatal period.

Clearly additional research is needed to gain a more complete understanding of the intersensory consequences of role enhanced stimulation to earlier-emerging modalities on the functioning of later-emerging systems. This is especially the case for the tactile and vestibular modalities, in that most intersensory research to date has focused on the auditory and visual modalities. Moreover, more research is needed to assess the intersensory impact of altered sensory experience during earlier periods of the prenatal period, when certain sensory systems are functionally emerging. It is possible that filling in these gaps could yield valuable information regarding the nature of perceptual organization during early development, especially in regards to the SLH. The present study is designed to address the intersensory impact on the development of function in later-developing modalities (visual and auditory) following

enhanced sensory stimulation at different times during earlier periods of prenatal development to early-developing sensory modalities (tactile and vestibular).

Chapter 2

Scope and Design of the Proposed Study

If the alternative timing-based explanation outlined above is accurate, then modifying when tactile and vestibular stimulation occurs should lead to different patterns of responsiveness in visual and auditory functioning. In particular, providing tactile and vestibular sensory stimulation during later prenatal periods (starting on Day 17 rather than Day 14 of incubation) should not disrupt subsequent visual functioning, because the visual system will have emerged in a context of reduced competition which is thought to facilitate normal visual responsiveness. Having reached a state of relative maturity, the impact of enhanced tactile and vestibular stimulation delivered at a later time may not be detrimental to visual development because the visual system will be better equipped to accommodate augmented tactile and vestibular stimulation. Likewise, providing vestibular and tactile stimulation at an earlier time (starting on Day 9 rather than Day 14) should disrupt auditory functioning, because the auditory system is beginning to emerge at this time, and may not be able to compete with the increased levels of intersensory competition.

To explore these questions, the current study was divided into two experiments. The first experiment was designed to assess the impact of enhanced vestibular and tactile stimulation on visual functioning, and how the effects (if any) may be modified by altering the timing of exposure. Three experimental groups were used. These groups differed in when (if at all) vestibular stimulation was experimentally provided. One group (Controls) did not receive any augmented vestibular stimulation. A second group (Early Vestibular) received augmented vestibular exposure from Day 14 of incubation to Day 19. Presumably, it is at this time (around Day 14) that the embryos' visual system is beginning to functionally emerge. Subjects in a third group (Late Vestibular) were also given exposure to enhanced vestibular experience, but differed from the latter group in terms of when exposure took place. For this group, vestibular stimulation was provided from Day 17 – Day 22 of incubation. Thus, Groups 2 and 3 differ only in terms of the *timing* of sensory stimulation, while holding other potentially important factors (type and amount of stimulation) constant.

In this first experiment, groups were tested for species-typical visual preferences at various ages following hatching. This test involved a choice between a bobwhite hen model versus a scaled-quail hen model. Specifically, subjects in each experimental condition were tested each day until a behavioral preference during testing (if any) was displayed. Different subjects were tested at different times within an experimental condition to discover the earliest age at which subjects in a particular condition would display a visually-based preference. Testing took place at 24, 48, 72, and 96 hr following hatching. Each group was tested at 24 hr, but not all groups were tested through 96 hr. If a group displayed a preference at 48 hr, this group was not tested at 72 or 96 hr because the earliest age of visual responsiveness had been identified. Thus, Experiment 1 sought to demonstrate normal patterns of perceptual responsiveness, and how the timing of enhanced vestibular exposure can influence these patterns.

The second experiment of the current study contained two experimental groups of bobwhite embryos and was designed to assess the impact of enhanced vestibular stimulation on auditory functioning. Groups differed according to when they were exposed to vestibular stimulation. One group (Early Vestibular Group) was given exposure at the time when the auditory system is beginning to functionally emerge (from Day 9 through Day 14), whereas the other group (Late Vestibular Group) was given exposure when the auditory system presumably had time to emerge and develop (from Day 14 through Day 19). Thus, as in Experiment 1, these two groups differ in terms of the timing of vestibular experience while holding other factors constant. During the 24 hr prior to hatching both groups were

exposed to an individual, species-typical maternal call. Testing took place 24 hr following hatching to determine whether subjects preferred the familiar call over a similar, but unfamiliar maternal call.

Chapter 3

Hypotheses and Predictions

Hypothesis 1

It is possible that the delays in visual responsiveness reported by Carlsen and Lickliter (1999) were not due solely to exposure to substantially augmented amounts of sensory stimulation prior to hatching. Instead, their findings may reflect the influence of timing based upon when augmented exposure to tactile and vestibular sensory stimulation began. In the present study, it was hypothesized that augmented stimulation to earlier-developing modalities will bring about different effects depending on when exposure takes place. Specifically, it was thought that the effects on visual functioning following exposure to enhanced tactile and vestibular stimulation would vary when the timing of enhanced stimulation to the latter was varied. If the onset of augmented stimulation to the earlier-developing modalities (tactile and vestibular) begins at a time when the later-developing modality (visual) is beginning to become functional, then one would expect to see delays in the responsiveness of the later-developing system, in that the latter is not able to adequately compete with the better organized earlier-developing modalities. On the other hand, if the onset of augmented stimulation to the earlier-developing modalities occurs at a time *following* the functional onset of the later-developing modality, then one should find evidence of facilitation in the later-developing modalities functioning.

This hypothesis leads to several predictions (see Table 1). First, based on previous research (Lickliter, 1994; Lickliter & Virkar, 1989; McBride & Lickliter, 1993) it was predicted that bobwhite quail hatchlings given no unusual prenatal sensory stimulation (Control Group in Experiment 1) would not display a species-typical visual preference for a bobwhite hen model over a scaled-quail hen model until 72 hr following hatching. Second, it was predicted that bobwhite quail embryos given enhanced tactile and vestibular exposure beginning on Day 14 of incubation (Early Vestibular Group in Experiment 1) would show delays or deficits in visual responsiveness in the days following hatching compared to birds that did not receive this altered experience (Controls in Experiment 1). Specifically, it was proposed that these subjects would not demonstrate a preference for bobwhite maternal hen model over a scaled-quail hen model during testing at any age (24, 48, 76, or 96hr). Finally, it was predicted that bobwhite embryos given enhanced tactile and vestibular exposure beginning on Day 17 (Late Vestibular Group in Experiment 1) would not show delays in visual functioning, and would likely display accelerated species-typical visual responsiveness to bobwhite maternal cues relative to those who did not receive any altered prenatal experience (Controls in Experiment 1). This is despite receiving the same amount and type of stimulation as the Early Vestibular Group in Experiment 1. Previous research has shown that enhanced stimulation to an earlier-developing modality (e.g., audition) can accelerate the normal course of responsiveness in a later-developing modality (e.g., vision) such that hatchlings prefer a bobwhite hen model during testing by 24 hr following hatching (Lickliter, 1990; Lickliter & Stoumbos, 1991). Thus, it was thought that this group (Late-Vestibular) would likewise show a preference for the bobwhite hen model at 24 hr following hatching.

Hypothesis 2

It was hypothesized that the same pattern of timing effects of enhanced vestibular stimulation on visual functioning predicted in Experiments 1 also apply to auditory functioning. In general, it was predicted (see Table 1) that when the onset of vestibular exposure coincides with the emergence of auditory functioning, the organism will show deficits compared to when the onset of vestibular stimulation occurs after the auditory system has had a chance to emerge and develop. Specifically, it was thought (see Table 1) that bobwhite quail embryos given enhanced vestibular and tactile experience from Day 9 through Day 14 (Group 1, Experiment 2) will fail to learn a maternal call in the day prior to

Table 1: Predictions of the current study.

Experiment 1 (Visual Effects)

Testing involves a choice between a bobwhite hen and a scaled hen.

Control Condition

test at 24 hr

test at 48 hr

test at 72 hr

Prediction

No Preference

No Preference

Bobwhite Hen

Early Vestibular (Days 14-19)

test at 24 hr

test at 48 hr

test at 72 hr

Prediction

No Preference

No Preference

No Preference

Late Vestibular (Days 17-22)

test at 24 hr

Prediction

Bobwhite Hen

Experiment 2 (Auditory Effects)

Testing at 24 hr following hatching involving a choice between a familiar and unfamiliar bobwhite maternal call.

Early Vestibular (Days 9-14)

Late Vestibular (Days 14-19)

Prediction

No Preference

Familiar call

hatching because the emerging auditory system is not equipped to adjust to the enhanced intersensory competition. Likewise, it was thought that by changing the timing of tactile and vestibular onset augmented to a point when the auditory system has already emerged should not interfere with auditory functioning. That is, when the onset of enhanced tactile and vestibular stimulation began on Day 14 (Group 2, Experiment 2), bobwhite embryos should learn a maternal call, in that at this time the auditory system has emerged and presumably differentiated enough to compete with enhanced intersensory competition.

Chapter 4

General Method

Certain features of the experimental design were common to all experiments. In what follows, the shared features are described prior to presenting the particular details of each individual experiment.

Subjects

Subjects were 260 incubator-reared bobwhite quail embryos (*Colinus virginianus*). Fertile, unincubated eggs, received weekly from a commercial supplier, were set in a Petersime I incubator which maintained a temperature of 37.5°C and a relative humidity of 85-90%. This incubator was positioned in a sound and light attenuated room. After 22 days of the 23 day incubation period, eggs were transferred to a hatching tray located in the bottom of the Petersime Model I incubator which maintains equivalent temperature and humidity levels. To control for possible variations in developmental age, only those chicks that hatched on day 23 were used in this study. To control for possible between-batch variation, subjects for each experimental condition were selected from at least 3 different hatches (i.e., weeks) of eggs. The only sounds normally available to the incubating embryos were embryonic and postnatal vocalizations of broodmates in addition to the background low-frequency noise emitted by the fan and motor of the incubators. Following hatching, subjects were placed in large (45 x 25 x 15 cm) plastic tubs located in a sound-attenuated room that is illuminated by 100-W brooder lamps. These lamps were suspended above the plastic tubs and serve to maintain an ambient air temperature of 30°C. Food and water were continuously available throughout each experiment except during testing.

Tactile and Vestibular Stimulation Procedure

In the wild, precocial avian embryos receive recurrent tactile and vestibular stimulation several times a day as the hen intermittently moves or turns the eggs (Freeman & Vince, 1974). This movement or egg turning is required for normal embryonic development. As such the Petersime Model I incubator in which the quail eggs were incubated (see above) was set to turn the eggs once every 2 hours. Subjects who did not receive augmented tactile and vestibular exposure (Controls, Experiment 1) remained in this incubator through the duration of incubation. To experimentally augment this pattern of prenatal tactile and vestibular stimulation, some eggs were transferred to a Model RX2 Roll-X incubator located in a sound and light attenuated room. The eggs were placed on metal grid that gently slides forwards and backwards turning the eggs on their points in one coordinate plane from - 45 degrees to + 45 degrees. Each egg turned at a rate of one turn per 30 sec for 10 min every 4 hours for 5 days, resulting in 10 times the normal amount of tactile and vestibular stimulation during this period. Specifically, the total amount of stimulus exposure for unmanipulated eggs (Controls, Experiment 1) during these 5 days was 30 min, whereas the total amount of tactile and vestibular stimulation in the treatment groups (all other groups) was 300 min. At the end of the 5 days of stimulus exposure, the eggs were transferred from the Roll-X incubator to a hatching tray located at the bottom of the Petersime Model I incubator, where they remained until hatching.

Testing

The testing procedure took place in a circular arena, 160 cm in diameter, surrounded by a wall 24 cm in height. The walls of the apparatus were lined with foam to attenuate echoes and covered by an opaque black curtain to shield the observer from the subject's view. The floor of the arena was painted black. Two rectangular approach areas (32 x 15 cm) on opposite sides of the arena were demarcated by green stripes painted on the floor. These approach areas represent 5% of the total area of the arena. Mid range dome-radiator speakers were hidden behind the curtain in each of the two approach areas. Each speaker received input from a Tascam Model 122-B cassette tape player located on a control table which

allowed for the presentation of maternal auditory cues during the test trials. The auditory cues were recordings of bobwhite maternal calls. Depending on the specific experiment, each speaker independently emitted either an identical bobwhite maternal call (Call B; Experiment 1) or one of two similar bobwhite maternal calls (Call A and Call B; Experiment 2) (see Heaton, Miller & Goodwin, 1978, for acoustical details).

Testing involved placing each subject in the arena equidistant from the two approach areas. All birds were given an individual 5-min simultaneous choice test between the testing stimuli. The sound intensity of each call was adjusted to peak at 65 dB (using a Bruel & Kjaer Model 2232 sound level meter, fast response), measured at the point where the chicks were introduced in the arena. The locations of the two hen models were counterbalanced across individual trials to prevent possible side-bias.

Each subject was tested only once. Subjects were scored on both the latency of approach and the duration spent in each of the two approach areas. An observer sat at a table located several feet away from the testing arena, and observed the each subject's activity through a large mirror positioned above the arena. A system of handheld stopwatches were used to score the latency and duration of response to the test stimuli. Latency was defined as the amount of time (in seconds) that elapsed from the onset of the trial until the subject entered an approach area. Duration was defined as the cumulative amount of time (in seconds) the subject remained in an approach area. A chick that did not enter either approach area will receive a score of 300 s for latency (i.e., the length of the trial) and 0 s for duration, and will be considered a non-responder. A "preference" for a given stimulus was scored if a chick that stayed in an approach area for at least 10 s, and at least twice the time spent in the opposing approach area. "No preference" for a stimulus was scored if a chick approached both areas during a trial without showing a preference for either. These measures of preference constituted the primary dependent variable.

Data Analysis

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

Chapter 5

Experiment 1

As a first step in assessing whether the timing of enhanced tactile and vestibular stimulation influences visual functioning, it was necessary to chart the normal course of responsiveness to species-typical visual cues in incubator reared, maternally-naïve bobwhite quail. With this in hand, it was possible to determine whether enhanced tactile and vestibular stimulation provided at two different points during the prenatal period would accelerate, decelerate, or have no effect on the normal trajectory of visually guided social preferences.

The current experiment included three experimental groups or conditions. One group of embryos did not receive any unusual (i.e., experimentally provided) sensory stimulation before or after hatching (Control Group). A second group was exposed to substantially augmented tactile and vestibular sensory stimulation for 10 min every 4 hr for 5 days beginning on Day 14 of the 23 Day incubation period (Early Vestibular Group). A third group received the same type and amount of augmented tactile and vestibular stimulation, but for this group exposure took place between Days 17 – 22 of incubation (Late Vestibular Group). Thus, any differences observed between the Early and Late Vestibular groups could reasonably be attributed to a timing-based effect.

Subjects in each group were given a test between a bobwhite hen model and a scaled-quail hen model. Testing began 24 hr following hatching. If no preference was shown at 24 hr, then testing took place again (using different subjects) at 48 hr. This pattern of testing continued up through 96 hr.

Method

220 bobwhite quail embryos divided into the three experimental conditions outlined above, served as subjects. Testing involved a choice between a bobwhite hen model located in one approach area in the testing arena and a scaled-quail hen model placed in a different approach area. The two models were alternated across subjects to control for possible side-biases. In addition, identical bobwhite maternal calls (Call B) were emitted from a speaker hidden behind each approach area. Previous research has shown that bobwhite quail will not approach static hen models in the absence of auditory stimuli (Lickliter & Virkar, 1989). It is important to note that because identical maternal calls were used during testing, the only differences available between testing stimuli were the visual features of the hen models. Testing took place every 24 hr following hatching until a significant preference was displayed or until the final test at 96 hr. For each testing period (e.g., at 24 hr), each experimental condition contained 20 subjects. If subjects in a condition showed no preference for either model during testing, a different group of 20 subjects was then tested 24 hr later (at 48 hr), and so on until 96 hr.

Results and Discussion

Preference scores are shown in Table 2. Latency and duration scores are shown in Table 3. Subjects given no unusual sensory stimulation (Control group) did not display a preference for either hen model during testing at 24 hr ($\chi^2 = .421$, ns), 48 hr ($\chi^2 = .105$, ns), 72 hr ($\chi^2 = .875$, ns), or 96 hr ($\chi^2 = .118$, ns). Analyses of latency ($z = -.604$, ns; $z = -.564$, ns; $z = -.052$, ns; $z = -.402$, ns at 24, 48, 72 and 96 hr respectively) and duration ($z = -.201$, ns; $z = -.242$, ns; $z = -.341$, ns; $z = -.454$, ns at 24, 48, 72 and 96 hr respectively) scores support this finding in that no significant differences were found. Subjects in the Early Vestibular group who were given augmented tactile and vestibular stimulation beginning on Day 14 of incubation also failed to display a preference for either hen model at 24 hr ($\chi^2 = 1.368$, ns), 48 hr ($\chi^2 = .118$, ns), 72 hr ($\chi^2 = .824$, ns), or 96 hr ($\chi^2 = 1.53$, ns). No significant differences were found in latency ($z = -.201$, ns; $z = -.497$, ns; $z = -.024$, ns; $z = -.355$, ns at 24, 48, 72 and 96 hr respectively) and duration

Table 2: Preference Scores of Chicks in Experiment 1

Control Group

Age (in hr)	n	<i>n</i> Responding	Bobwhite Call Bobwhite Hen	Bobwhite Call Scaled Quail Hen	Both
24	20	19	7	5	7
48	20	19	6	6	7
72	20	16	5	7	4
96	20	17	6	6	5

Early Vestibular (Days 14-19) Group

Age (in hr)	n	<i>n</i> Responding	Bobwhite Call Bobwhite Hen	Bobwhite Call Scaled Quail Hen	Both
24	20	19	7	4	8
48	20	17	6	5	6
72	20	17	7	6	4
96	20	17	4	8	5

Late Vestibular (Days 19-22) Group

Age (in hr)	n	<i>n</i> Responding	Bobwhite Call Bobwhite Hen	Bobwhite Call Scaled Quail Hen	Both
24	20	19	8	9	2
48	20	20	11	4	5
72	20	17	12*	2	3

* $p < .05$ (Chi-Square Test)

Table 3: Latency and Duration Scores of Chicks in Experiment 1

Control Group

Age (in hr)	Latency (in sec.)		Duration (in sec.)	
	Bobwhite Hen	Scaled Quail Hen	Bobwhite Hen	Scaled Quail Hen
24	83.5 (36-200) (100)	41.5 (17-148) (105)	62.5 (31-140) (70)	76.0 (27-107) (66)
48	66.5 (21-67) (79)	85.5 (27-181) (103)	52.0 (13-125) (70)	40.0 (13-106) (49)
72	117.0 (40-300) (129)	94.0 (60-300) (120)	20.5 (0-94) (69)	47.5 (0-91) (67)
96	138.5 (15-300) (125)	131.5 (68-300) (115)	27.5 (0-53) (55)	38.5 (0-90) (61)

Early Vestibular Group

Age (in hr)	Latency (in sec.)		Duration (in sec.)	
	Bobwhite Hen	Scaled Quail Hen	Bobwhite Hen	Scaled Quail Hen
24	51.5 (21-152) (95)	54.5 (22-269) (117)	76.5 (27-167) (81)	28.0 (4-90) (61)
48	89.5 (47-300) (114)	56.5 (26-265) (116)	61.0 (0-95) (52)	49.0 (0-116) (73)
72	146.0 (45-300) (117)	151.0 (45-300) (119)	24.0 (0-90) (73)	28.5 (0-69) (64)
96	72.5 (17-300)	71.0 (27-300)	18.5 (0-54)	44.0 (0-140)

Late Vestibular Group

Age	Latency (in sec.)		Duration (in sec.)	
	Bobwhite Hen	Scaled Quail Hen	Bobwhite Hen	Scaled Quail Hen
24	61.0 (23-249) (116)	54.5 (19-171) (103)	50.0 (2-114) (69)	80.0 (14-185) (83)
48	59.5 (17-217) (111)	111.5 (17-60) (114)	103.0* (44-181) (80)	37.0 (0-71) (57)
72	62.0* (55-134) (90)	200.5 (31-300) (129)	87.5* (24-176) (83)	7.5 (0-64) (54)

Median Scores are shown in table. Inter-quartile ranges shown in parentheses to side, standard deviations below.

* p < .05 (Wilcoxin Test)

($z = -1.307$, ns; $z = 0$, ns; $z = -.024$, ns, $z = -1.183$, ns at 24, 48, 72, and 96 hr respectively) scores. Subjects in the Late Vestibular group who received augmented tactile and vestibular exposure between Day 17-22 of incubation did not show a significant preference at 24 hr ($\chi^2 = 4.526$, ns) or 48 hr ($\chi^2 = 4.3$, ns), but did show a significant preference at 72 hr ($\chi^2 = 10.706$, $p = .005$). Analyses of duration scores support and extend this finding in that differences in duration of approach were statistically significant at 72 hr ($z = -2.374$, $p = .018$) and 48 hr ($z = -2.222$, $p = .026$), but not at 24 hr ($z = -.684$, ns). No significant differences in latency of approach were found ($z = -.241$, ns; $z = -1.045$, ns; $z = -1.895$, ns at 24, 48, and 72 hr respectively).

The patterns of behavior observed in subjects in the Control condition were not expected and represent a failure to replicate previous findings (Lickliter, 1994; Lickliter & Virkar, 1989; Lickliter, Lewkowicz, & Columbus, 1996; McBride & Lickliter, 1993, but see Honeycutt & Lickliter, 2001b). Previous studies showed that unmanipulated subjects reared in standard laboratory conditions demonstrate a visual preference for species-typical visual cues at 72 hr following hatching. In the current experiment, subjects reared under similar conditions showed no preference between a bobwhite hen model and a scaled-quail hen model at any age tested (24, 48, 72, and 96 hr).

Consistent with the predictions made by Hypothesis 1, subjects in the Early Vestibular condition also failed to demonstrate a preference for bobwhite visual features at any age tested. However, these findings can not serve to support Hypothesis 1. Given the failure of the Control group to display a visually-based preference at any age, one cannot claim that exposure to enhanced tactile and vestibular stimulation at a time that coincides with the functional emergence of the visual system disrupts or delays the normal trajectory of visual responsiveness. What is clear is that tactile and vestibular stimulation provided at this time (between Day 14-19 of incubation) does not accelerate or promote (or necessarily delay) subjects' visual discrimination of static species-typical cues. The findings from this Early Vestibular group call into question Carlsen and Lickliter's (1999) conclusion that augmented tactile and vestibular stimulation leads to delays in visual responsiveness. Because Carlsen and Lickliter (1999) did not include a control group, it is not possible to say that enhanced tactile and vestibular stimulation led to delays in visual responsiveness, especially given the failure of control subjects in the current experiment.

The patterns of behavior found in those subjects given exposure to tactile and vestibular stimulation between Days 14-22 of incubation also failed to support Hypothesis 1. However, these results suggest that when augmented tactile and vestibular stimulation occurred at a time after the visual system has functionally emerged, the normal course of visual responsiveness was different from subjects in the Early Vestibular and Control groups. These differences emerged in subjects' (a) significant preference for the bobwhite hen during testing at 72 hr, and (b) longer duration of approach towards the bobwhite hen during testing at 48 hr.

Although the results from the Early Vestibular group parallels those reported by Carlsen and Lickliter (1999) (i.e., failure to show a preference at any age tested), the results from the Late Vestibular group suggest that their conclusion (that the overall amount of stimulation was the critical factor influencing visual responsiveness) may have been premature. Because the Late Vestibular group differed from the Early Vestibular only in terms of when enhanced exposure took place while holding the type and amount of stimulation constant, the failure of subjects in the Carlsen and Lickliter (1999) study to display a preference for the bobwhite hen was likely due in part to the timing of stimulation.

Collectively, these findings support the notion that augmented experience in earlier-developing modalities can influence the functioning of a later-developing modality, and that this influence is in part a matter of timing. However, given the failure of Control subjects to display a preference at any age tested,

it is impossible to say with certainty that augmented stimulation to earlier-developing modalities accelerates or delays the functioning of a later-developing modality.

Chapter 6

Experiment 2

This experiment sought to determine whether the timing of augmented tactile and vestibular exposure can influence subsequent auditory responsiveness. As in the previous experiment subjects were exposed to augmented tactile and vestibular stimulation either at the time when the auditory system is beginning to functionally emerge (Day 9) or when the auditory system has already emerged and has had time to stabilize its organization (Day 14). Thus, two groups of bobwhite quail embryos were used in this study. One group received enhanced tactile and vestibular exposure between Days 9-14 of incubation (Early Vestibular group), whereas a second group received the same type and amount of augmented exposure between Days 14-19 of incubation (Late Vestibular group). Both groups were given exposure to an individual species-typical maternal call during the day prior to hatching. Testing for both groups took place 24 hr after hatching, and involved a choice between the familiar maternal call (i.e., the one encountered prenatally) versus a similar, but unfamiliar maternal call.

Method

40 bobwhite quail embryos, divided equally into 2 groups ($n = 20$) served as subjects. Groups differed according to when they receive exposure to vestibular and tactile stimulation. One group was given vestibular experience from Day 9 through Day 14 of incubation. A second group received this exposure from Day 14 – Day 19 of incubation. Both groups were then exposed to one of two variants of an individual maternal call (Call A or Call B) for 10 min/hr during the 24 hr prior to hatching (240 total min). In each group, approximately 1/3 of the subjects were given exposure to Call A while remaining subjects were given exposure to Call B. Specifically, on Day 22 of incubation the eggs in these groups were placed in a Hovi-bator portable incubator which permitted the delivery of auditory stimuli. The intensity of the maternal calls was adjusted to 65 dB measured at the point where the eggs were placed in the incubator. After hatching, chicks were relocated to the large plastic tubs described in the General Method section. Testing involved a choice between the familiar variant of the bobwhite maternal call and an unfamiliar variant of the same maternal call. The two calls were counterbalanced during testing to control for possible positional bias-effects. Testing for both groups took place 24 hr after hatching.

Results and Discussion

Results are shown in Tables 4 and 5. Subjects given tactile and vestibular stimulation between Days 9-14 of incubation failed to demonstrate a significant preference ($\chi^2 = .4$, $p = .819$) for the familiar call during testing. This group also did not show significant differences in their latency ($z = -1.027$, ns) or duration ($z = -.523$, ns) of approach between the two maternal calls. However, subjects given the same type and amount of tactile and vestibular stimulation at a later time (Days 14-19) did display a significant preference for the familiar call during testing ($\chi^2 = 12.1$, $p = .002$). The latter group showed significant differences in their latency ($z = -2.8$, $p = .005$) of approach and duration ($z = -2.352$, $p = .019$) of time spent near the familiar call.

These results are consistent with the predictions of Hypothesis 2, and suggest that the timing of enhanced tactile and vestibular experience can influence subsequent auditory responsiveness. Previous research has shown that bobwhite embryos are able to learn an individual species-typical maternal call in the day prior to hatching and will prefer this familiar call over a similar, but unfamiliar call in the day following hatching (Carlsen & Lickliter, 1999; Honeycutt & Lickliter, 2001 a; in press; Lickliter & Hellewell, 1992; Lickliter et al., 2002). The findings from the current experiment indicate that the delivery of enhanced tactile and vestibular stimulation which coincides with the onset of auditory

Table 4: Preference Scores of Chicks in Experiment 2 tested at 24 hr.

Early Vestibular (Days 9-14) Group

n	<i>n</i> Responding	Familiar Call	Unfamiliar Call	Both
20	20	6	6	8

Late Vestibular (Days 14-19) Group

n	<i>n</i> Responding	Familiar Call	Unfamiliar Call	Both
20	20	14*	3	3

* $p < .05$ (Chi-Square test)

Table 5: Latency and Duration Scores of Subjects in Experiment 2

Condition	Latency (in sec)		Duration (in sec)	
	Familiar Call	Unfamiliar Call	Familiar Call	Unfamiliar Call
Early Vestib.	56.5 (28–224) (110)	46.5 (19-145) (96)	67.5 (22-149) (76)	65.0 (8-98) (62)
Late Vestib.	23.5* (17–38) (67)	75.5 (51-258) (109)	110.0* (58-147) (74)	24.5 (1-60) (66)

Median Scores are shown in table. Inter-quartile ranges shown in parentheses to side, standard deviations below.

* $p < .05$ (Wilcoxin test)

functioning results in delays or deficits in subsequent auditory responsiveness (Early Vestibular group). On the other hand, when enhanced exposure takes place after the auditory system has functionally emerged, no delays in auditory responsiveness are apparent (Late Vestibular group).

These findings stand in contrast to Carlsen and Lickliter's (1999) conclusion that moderately enhanced tactile and vestibular stimulation facilitates auditory responsiveness. Whether or not tactile and vestibular stimulation facilitates auditory responsiveness is in part a matter of timing, as the findings from the current experiment show. Under certain timing conditions, auditory responsiveness can be delayed (Early Vestibular group).

Chapter 7

General Discussion

The present study underscores the necessity of considering the timing of sensory stimulation in our attempts to understand early perceptual development. By recognizing that organismic structures and functions develop in a heterochronous manner, altering sensory experience at various points during early ontogeny can yield valuable information concerning the nature and dynamics of early perceptual organization and responsiveness. For instance, the results from this study show that the relationships between early and later-developing modalities are not fixed and become re-organized with experience. Overall, this study provides a relatively novel contribution to the growing body of empirical and theoretical work on early intersensory relationships. The uniqueness of this contribution lies in this study's (1) assessment of how augmented stimulation to earlier-emerging modalities effects on the functioning of later-developing modalities, and its (2) focus on sensory modalities that are rarely examined (tactile and vestibular) during (3) periods of prenatal development rarely studied.

Results from the first experiment revealed that bobwhite embryos given no unusual sensory stimulation (Control group), and those given enhanced exposure to tactile and vestibular stimulation between Days 14-19 of incubation (Early Vestibular group) do not prefer visual features of a bobwhite hen model through 96 hr following hatching. In contrast, subjects given the same type and amount of vestibular stimulation between Days 17-22 of incubation (Late Vestibular group) spend significantly longer amounts of time near the bobwhite during testing at 48 hr and display a significant preference for the bobwhite hen by 72 hr. Results from Experiment 2 indicate that early exposure to enhanced tactile and vestibular stimulation between Days 9-14 (Early Vestibular group) of incubation leads to an impairment in embryos' ability to subsequently learn a maternal call on Day 22 of incubation, whereas embryos given the same type and amount of augmented tactile and vestibular exposure (between Days 14-19) display evidence of prenatal auditory learning.

These findings underscore the idea that when sensory experiences occur can be as important as what is being experienced. Consistent with the hypotheses outlined earlier, when augmented stimulation from early-emerging modalities coincides with the emergence of a later-developing system, the latter showed delays in its normal developmental trajectory. Although the findings from the first experiment fail to address this issue clearly (and so fail to support Hypothesis 1) in that both the Control and Early Vestibular groups did not display any preferences, the findings from the second experiment speak more clearly to this issue. Given that previous studies have shown that bobwhite embryos can learn an individual maternal call in the days prior to hatching and will prefer this call 24 hr after hatching (e.g., Honeycutt & Lickliter, 2001; in press), subjects in Experiment 2 who received tactile and vestibular stimulation at the time when the auditory system was presumably coming online clearly showed deficits in normal auditory skills.

Because timing matters, changes in the timing of stimulus onset were hypothesized to lead to different patterns of responsiveness in the target modality. Specifically, it was hypothesized that experiencing enhanced stimulation to earlier-developing modalities at a time after the functional onset of a later-developing modality, would either not disrupt or accelerate the normal developmental trajectory of the later-developing modality. As mentioned earlier, the results from the first experiment do not speak to this issue, but do support the notion that differences in timing can lead to differences in patterns of responsiveness. However, embryos in Experiment 2 exposed to tactile and vestibular stimulation after the auditory system had emerged did not show deficits in their ability to learn and recognize a species-typical maternal call. These findings (from Experiment 2) indicate that when stimulation to earlier-developing

modalities occurred after the functional emergence of a later-developing system, the normal course of responsiveness associated with the later-developing system was promoted rather than disturbed.

That subjects reared under standard laboratory conditions and given no unusual sensory stimulation failed to display a preference for the visual features of the bobwhite hen during testing was surprising. Previous research has shown that these hatchlings display a preference for the bobwhite hen model by 72 hr (Lickliter, 1994; Lickliter & Virkar, 1989; Lickliter, Lewkowicz, & Columbus, 1996; McBride & Lickliter, 1993). Recently, Honeycutt and Lickliter (2001b) also failed to replicate this finding. Although the specific reasons for these discrepant findings in control subjects are unknown, two possibilities come to mind. On the one hand, in the current study and in the other study that failed to replicate this finding (Honeycutt & Lickliter, 2001 b) the particular bobwhite and scaled-quail hen models used during testing were intentionally selected because they shared certain overt similarities including body posture and head orientation. The only differences available (to the experimenter's eyes) were the species-typical color markings and a size difference (the scaled hen is slightly taller and wider than the bobwhite hen). It could be that earlier studies did not intentionally choose these two models, opting instead to use more distinct quail models. In this light, it is not known which models were used in the earlier studies including Carlsen and Lickliter (1999). On the other hand, because the hen models used in the present study are approximately 14-years-old, it could be that the models used during testing in the current study and Honeycutt and Lickliter (2002b) have impoverished visual features compared to earlier studies due to time-related deterioration. In either case, one can assume that the visual tests used in the current study were (in some unknown way) more difficult than those used in earlier studies.

It is important to note that although Honeycutt and Lickliter (2001 b) failed to replicate a preference for bobwhite visual features in standard controls at 72 hr, they did show that hatchlings learn species-typical visual features in the days following hatching. Specifically, they found subjects discriminated between and preferred the bobwhite hen model over the scaled quail model at 48 hr when (otherwise unmanipulated) hatchlings were reared with slightly older (1 week-old) siblings. This preference was then eliminated by rearing similar hatchlings with slightly older siblings whose species-typical visual markings were reduced (by dyeing their feathers black). Collectively, these findings suggest that quail hatchlings were noticing and were influenced by the species-typical visual markings of the older birds. The findings of Honeycutt and Lickliter (2001 b) provide some support for the notion that subjects in the Late Vestibular group in Experiment 1 were displaying a promotion (and perhaps an acceleration) in responsiveness to visual cues.

The findings from the current study have important implications for the sensory limitations hypothesis (SLH; Turkewitz & Kenny, 1982; 1985; Turkewitz & Mellon, 1989), despite the fact that it made no specific predictions concerning how augmented stimulation to earlier-developing modalities might influence later-developing modalities. The results of this study indicate that augmented experience in early-developing modalities can facilitate or disrupt the normal functioning of later-developing modalities, and that facilitation or disruption can be predicted through reference to the sequential onset of sensory functioning, and can be understood within the primary metaphor of intersensory competition. When enhanced stimulation to an earlier-emerging modality coincides with the onset of functioning of a later-emerging modality, the latter appears ill-equipped to compete for neural and attentional resources necessary for normal development. However, when the augmented stimulation to an earlier-emerging modality occurs at a time after the later-developing system has functionally emerged, the latter appears able to compete with or accommodate the unusually enhanced stimulation and shows acceleration in the normal development of responsiveness. Further, the findings from this study (and the take-home message from the SLH) suggest that when one seeks to understand perceptual development (especially using perturbation procedures), one must at the very least take into account the experiential histories and

relationships between sensory modalities, the current state and developmental status of the organism, the affordances of the context, and the objective features of the available sensory stimulation.

In addition, the findings from this study warrants a reexamination of conclusions that stem from providing precocial avian embryos unusual types and amounts of sensory stimulation during the late prenatal period. By the day prior to hatching (which is typically when enhanced stimulation is provided), all the sensory systems have functionally emerged and have had at least 8 days to reach a stable level of organization. With this in mind, it comes as no surprise that tests of the SLH using precocial organisms have not been fully supported. More appropriate tests of the SLH may come from providing precocial embryos with enhanced stimulation during earlier periods of prenatal development when sensory systems are beginning to come “online”. The current study is a step in this direction, and demonstrates the importance that the timing of stimulus delivery can have. Thus, future research using precocial organisms should address how premature sensory stimulation to later-developing modalities influences the functioning of an earlier-developing modality (the first question of the SLH) during earlier ontogenetic periods.

Although the timing of sensory stimulation has been primarily emphasized throughout this study, timing in and of itself holds no meaning. The timing of what? Timing is a relational term, and can never be separated from its referents. In this study, the type and amount of sensory stimulation was held constant and the timing altered so that the impact of timing could be assessed. The results clearly demonstrate that timing matters, but so too does the type and amount. To a certain extent the type of stimulation was also emphasized throughout this study. For instance, that the augmented stimulation used was provided to earlier-developing modalities seems to be an important type of stimulation. Whether the same patterns of observations would be found using a different method of stimulation to the tactile and vestibular modalities (delivery (e.g., water-bed stimulation rather than egg-turning) is an interesting question that future research should address. As there is no when (timing) without a what (type), so too is there no what (type) without an how much (amount). Future research should also address whether changes in the amount of enhanced sensory stimulation would also lead to different patterns of results. For instance, would 5 (instead of 10) times the normal amount of tactile and vestibular stimulation bring about a different set of findings and conclusions? At this point, the most likely answer to all of these questions begins with “it depends”, and it depends on no less than all the factors listed earlier. Causation is a matter of current and historical contingency, and the challenge facing developmentalists involves mapping out the dynamic nature of these contingencies.

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Lickliter, R. & Honeycutt, H. (in preparation). Social experience facilitates species-typical visual discrimination in bobwhite quail chicks.

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