

**Neural plasticity and the development of
intersensory functioning in bobwhite quail (Colinus virginianus).**

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NEURAL PLASTICITY AND THE DEVELOPMENT OF INTERSENSORY
FUNCTIONING IN BOBWHITE QUAIL (COLINUS VIRGINIANUS).

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(Abstract)

Previous research has demonstrated that augmented prenatal sensory stimulation can influence the emergence of normal or species-typical patterns of intersensory perception. For example, unusually early visual experience can produce a facilitative effect on subsequent postnatal perceptual responsiveness, while substantially augmented prenatal visual stimulation can interfere with early postnatal responsiveness. In constructing a link between early experience and neuronal plasticity, it has been established that unusual visual experience can produce measurable changes in post-synaptic structures, particularly dendritic morphology, in brain areas responsible for vision. In avian species, the brain area responsible for vision is the visual Wulst, thought to be analogous to the mammalian visual cortex.

This study examined the effects of differing amounts of augmented prenatal visual stimulation on the plasticity of neurons in the visual Wulst and on subsequent postnatal visual responsiveness to maternal cues in bobwhite quail chicks. Results revealed that the pattern of neuronal organization and postnatal behavior was influenced by the amount of prenatal visual experience subjects were provided. Specifically, chicks exposed to 240 min of prenatal visual stimulation during the last 24 hr prior to hatching had neurons with significantly fewer spines/10 μ m dendrite and displayed accelerated patterns of species-typical visual responsiveness. In contrast, chicks provided 900 min of prenatal visual stimulation had more complex neurons (including more spines, longer dendrites, and more branches) and failed to display normal species-specific visual responsiveness in the days following hatching. These results suggest that neuronal organization in the bobwhite Wulst proceeds in a selective fashion, molded by experience, and appears to influence early perceptual development and organization during the perinatal period.

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1.0 Intersensory functioning

1.1 The development of intersensory functioning.

How individual sensory modalities relate to one another and how their functions are integrated in the brain have been the subjects of increasing research attention over the last decade (Ettlinger & Wilson, 1990; Knudsen & Brainard, 1995; Lewkowicz & Lickliter, 1994; Smith & Katz, 1996; Stein & Meredith, 1993). From a developmental perspective, the sensory systems of birds and mammals begin to develop prenatally and in precocial species are structurally mature before birth (Bradley & Mistretta, 1975, Gottlieb, 1971). However, the onset of function within each modality does not occur simultaneously. To the contrary, empirical research on sensory system development indicates that the onset of function within the various sensory modalities proceeds in an invariant pattern (tactile - vestibular - chemical - auditory - visual, see Alberts, 1984; Gottlieb, 1968, 1971). The sequential nature of the onset of sensory functioning in birds and mammals raises the question of how the sensory systems and their respective stimulative histories might influence one another, especially during prenatal development.

It has been suggested by several theorists of early perceptual development that the relative immaturity of sensory systems during prenatal and early postnatal development and the consequent limitation of sensory input may be an important organizing feature in perceptual and behavioral development (Spear, 1984; Turkewitz & Kenny, 1982, 1985; Turkewitz & Mellon, 1989). For example, Turkewitz & Kenny (1985) argue that the timing of functional onset of the various systems in relation to each other is very important. For example, if an organism receives visual input before the other earlier developing sensory systems reach a high level of organization and differentiation, then perceptual development should potentially proceed differently than if visual input becomes available after other sensory systems have reached their appropriate level of organization. According to this view, sensory limitations are therefore adaptive to the developing organism, as they serve to reduce the amount and type of information the embryo has to deal with.

If this is the case, then the gradual and sequential onset of function within the modalities allows for the development of initial functioning in each sensory modality without competing stimulation from later developing systems. From this perspective, immature sensory systems are not handicaps that must be overcome but are adaptive and necessary for normal sensory development and perceptual learning (Turkewitz & Kenny, 1982; Turkewitz & Mellon, 1989). Since the appearance of this novel view of early perceptual development, researchers working with both altricial and precocial animal infants have provided a growing body of evidence in support of the importance of developmental

sensory limitations to early perceptual organization and behavioral development (Foreman & Altaha, 1991; Gottlieb, Tomlinson, & Radell, 1989; Kenny & Turkewitz, 1986; Lickliter, 1990a, 1990b, 1993; 1994; Lickliter & Banker, 1994; Lickliter & Hellewell, 1992; Radell & Gottlieb, 1992). This line of research has provided several advances in our understanding the nature of early perceptual development, including the importance of the amount, type, and timing of sensory experience provided during perinatal development (Kenny & Turkewitz, 1986; Sleight & Lickliter, 1996, 1998; Spear & McKinzie, 1994) and the strong intermodal linkages of the sensory modalities during perinatal development (Lickliter & Lewkowicz, 1995; Lickliter & Stoumbos, 1991; Radell & Gottlieb, 1992). For example, research has shown that premature visual stimulation can accelerate intersensory functioning in bobwhite quail chicks and can result in subsequent deficits in species-typical patterns of auditory responsiveness (Lickliter, 1990a,b; Lickliter & Hellewell, 1992).

1.2 The facilitative effect of prenatal visual experience on visual responsiveness.

Lickliter (1990a,b) demonstrated a facilitative influence of unusually early visual experience on visual responsiveness. In these experiments, bobwhite quail embryos were given augmented prenatal visual stimulation and then tested postnatally for their visual responsiveness to maternal cues. Although the precocial avian embryo is responsive to prenatal visual stimulation (Heaton, 1973; Oppenheim, 1968), the embryo does not ordinarily experience patterned visual stimulation until after hatching from the egg. Embryos were exposed to 24-36 hr of patterned light and then tested at 24 or 48 hr postnatally for their preference between a bobwhite maternal call paired with a stuffed bobwhite quail hen (species-typical) or a bobwhite maternal call paired with a stuffed scaled quail hen (species-atypical). In contrast to controls which do not make use of visual cues until after 48 hr, chicks which received the prenatal visual stimulation demonstrated a significant preference for the species-typical maternal audio/visual cues at 24 and 48 hr following hatching. In other words, chicks which had been exposed to the unusually early visual experience exhibited earlier use of species-specific visual cues (in conjunction with species-specific auditory cues) in directing their filial behavior than did normally hatched chicks.

These results suggest that chicks which receive unusually early visual experience are somehow more “visually oriented” than normally hatched chicks during the first 48 hours following hatching (Lickliter, 1990a). Presumably, the visual system of chicks receiving early visual stimulation becomes functionally organized at earlier ages than chicks receiving normally restricted and attenuated prenatal visual experience. That is, maturation of the bobwhite quail neonate’s visual system appears to be facilitated by premature visual

experience (although negative effects have been found with substantially large amounts of premature visual experience, see Sleigh & Lickliter, 1995). The logic of this hypothesis then suggests that premature visual experience during the later stages of prenatal development impacts the functional (and potentially morphological) development of the visual system, which in turn gives rise to earlier emerging visually directed behaviors. However, the relationship between prenatal visual stimulation and neuronal organization in the bobwhite quail visual system has not been empirically examined.

1.3 The interfering effect of substantially augmented prenatal visual stimulation on visual responsiveness.

As reviewed above, providing embryos with early visual experience can facilitate postnatal visual responsiveness, presumably because of increased organization of the visual system. Stimulation of the visual modality at an unusually early age enabled chicks to use visual cues to direct their filial preferences at earlier ages (24 and 48 hr following hatching) than normally hatched chicks, which fail to make use of visual cues until 72 hr following hatching (Lickliter & Virkar, 1989). However, recent evidence suggests that modified stimulation of an earlier developing system (for example, tactile and vestibular) can result in abnormalities in later developing systems (auditory, Radell & Gottlieb, 1992; auditory and visual, Carlsen & Lickliter, 1999). Rather than supporting a facilitative effect, substantially augmented tactile and vestibular stimulation appears to delay the emergence of species-typical patterns of auditory and visual responsiveness. Furthermore, substantially increased (e.g., Sleigh & Lickliter, 1995) or unusually early sensory stimulation in later developing modalities does not always lead to enhanced postnatal responsiveness. To the contrary, substantially large amounts of prenatal visual stimulation may *interfere* with normal perceptual development.

In a series of experiments by Sleigh and Lickliter (1995), bobwhite quail embryos were given a substantially large amount of visual experience during the last day of prenatal development and tested postnatally for their auditory and visual responsiveness. Embryos were exposed to 900 min (40 min/hr) of patterned light and then tested at 24, 48, 72, and 96 hr postnatally for their preference between a bobwhite maternal call paired with a stuffed bobwhite quail hen (species-typical) or a bobwhite maternal call paired with a stuffed scaled quail hen (species-atypical). In contrast to controls which normally make use of the visual cues by 72 hr of age, chicks which received the substantially large amount of prenatal visual stimulation failed to demonstrate a significant preference for the species-typical maternal audio/visual cues at all ages tested. In other words, chicks which had been exposed to the relatively large amount of early visual experience exhibited a failure to use species-specific

visual cues in directing their filial behavior at ages which normally-hatched chicks demonstrate these preferences.

The picture that emerges from this study is that providing embryos with a substantially large amount of early visual experience serves to delay the onset of visual responsiveness. In other words, large amounts of unusually early visual stimulation may have a detrimental affect on normal perceptual development. These chicks failed to make the shift in stimulation requirements controlling filial preferences (from auditory to an auditory-visual combination) by 72 hrs of age that is routinely demonstrated in normally hatched bobwhite quail chicks (Lickliter, 1990a,b; Lickliter, 1994; Lickliter & Virkar 1989).

It can be hypothesized then that the visual system of chicks given a substantially large amount of early visual stimulation is not functionally (or morphologically) mature by 72 hr of age. That is, maturation of the bobwhite quail neonate's visual system could be delayed by an substantial increase in the *amount* of prenatal visual experience during the period when the visual system is undergoing rapid development. This hypothesis is congruent with Turkewitz & Kenny's (1982) theory of sensory limitations and their adaptive significance for normal perceptual and behavioral development. In brief, the relative immaturity of sensory systems during early development and the organism's constrained developmental context may serve to reduce available stimulation and mediate the timing of the introduction of stimulation to the embryo (Turkewitz & Kenny, 1982, 1985). If this is the case, then one might expect an unusually early or large amount of stimulation to affect significant changes in subsequent perceptual development. Behavioral evidence for this effect is reviewed above. However, the relationship between substantially large amounts of visual stimulation and subsequent neuronal organization in the bobwhite quail visual system has not been empirically determined.

2.0 Neural Plasticity.

2.1. Experience and neural plasticity.

Neural plasticity, the property by which the nervous system changes in response to environmental conditions or experience during development, has received a considerable amount of attention in the past few decades (Hyson & Rubel, 1991). Although it has long been recognized that changes in behavior can be reflections of changes in the brain, it is not until recently that the relationship between brain changes and changes in behavior has been considered to be bidirectional. That is, experience is seen to influence chemical, structural, and functional changes in the brain, producing changes in behavior and affording altered experiences in a dynamic manner (Edelman, 1987; Globus, 1975; Gottlieb, 1976, 1991;

Greenough, 1986a, b; Greenough, Black, & Wallace, 1987; Knudsen & Brainard, 1995; Mistretta & Bradley, 1978; Movshon & van Sluysters, 1981; Rucci, Tononi, & Edelman, 1997; Sherman & Spear, 1982; Stein & Meredith, 1993).

To explore the biological mechanisms underlying experiential regulation of brain development, most studies typically alter the sensory information encountered by the organism during development. Alteration of sensory information can be accomplished by 1) manipulation of the peripheral receptor system, 2) isolation of the subject from some type of sensory information, or 3) enhancement of the sensory environment as compared to control subjects. Subsequently, the effects of these manipulations are then measured, following some intervening period, by various behavioral tasks or measure of neural structure or function. Using these methods, a growing body of data point to a dramatic influence of sensory experience on the development of brain and behavior.

The original impetus behind the study of neural plasticity was Hebb's (1949) report that home-reared pet rats were superior to laboratory rats on learning tasks. More controlled laboratory studies (e.g. Forgyays & Forgyays, 1952) demonstrated that maze performance of rats improved with the increasing complexity of the environment in which they were reared. Following this, two experimental programs emerged in the early 1960s that demonstrated that the brain could be altered by differential experience. First was the announcement that either formal training or informal experience in varied environments leads to measurable changes in the neurochemistry and neuroanatomy of the rodent brain (Bennett, Diamond, Krech, & Rosenzweig, 1964; Rosenzweig, Krech, & Bennett, 1961). At about the same time, Hubel and Wiesel (1965) showed that depriving light to one eye of a young kitten reduces the number of cortical cells responding to that eye (see also Wiesel & Hubel, 1965). While both programs differed in their manipulations and measurements, they both were able to empirically demonstrate the influence of experience upon brain and behavior.

Using the enriched environment paradigm (see Rozenzweig, Krech, Bennett, & Diamond, 1962), researchers made great headway in understanding the effects of experience on the brain. In this paradigm, subjects were typically reared in three different types of environments; a standard condition (standard laboratory cage with other animals), impoverished condition (standard laboratory cage in isolation), and an enriched condition (also called complex; a large cage with many animals and stimulus objects). Initial histological studies revealed that animals exposed to the enriched condition developed significantly thicker cerebral cortices than their standard or impoverished littermates (Diamond, 1967; Diamond, Krech, & Rosenzweig, 1964; Diamond et al., 1966). These demonstrations that the weight and thickness of the cerebral cortex could be reliably altered

by experience provided a solid foundation for a detailed quantitative neuroanatomical approach to the relationship among experience, brain structure, and behavior.

2.2 Neural plasticity and dendritic morphology.

Over the next few decades, investigations of neural plasticity became more sophisticated, noting specific experience-dependent changes in synapse size (e.g., Diamond et al., 1975), capillary density (Black, Sirevagg, & Greenough, 1987), and dendritic morphology (e.g., Coleman & Riesen, 1968; Fifkova, 1970; Greenough & Volkmar, 1973; Shapiro & Vukovich, 1970; Volkmar & Greenough, 1972). Most notably, the development of the dendritic spine has been shown to be particularly susceptible to experience. Dendritic spines are lateral extensions of dendrites and are recognized as representing specific postsynaptic receptive structures on the dendrites (Harris & Kater, 1994). According to Shapiro and Vukovich (1970), it is thought that afferent input during spine development increases regional blood flow to the maturing neuron field. This increased blood flow results in an enriched nutritional environment, which provides a competitive growth advantage to the relaying and receiving neurons and their spine processes. Therefore, differential development of dendritic spines and their interconnections are thought to occur in response to the localized blood flow and biochemical changes associated with the afferent input. The patterning of these interconnections may therefore be a foundation for later behavioral performance (Shapiro & Vukovich, 1970).

Indeed, the quality of rearing environment has been shown to influence dendritic morphology, such as dendritic spine frequency and dendritic length. Stellate cells of visual cortex in rats is more complex and dendritic surface area is increased following rearing in a complex (or enriched) environment (Greenough & Volkmar, 1973; Holloway, 1966; Volkmar & Greenough, 1972). Enriched environmental context also leads to an increase in dendritic branching (Greenough, Volkmar, & Juraska, 1973) and an increase in dendritic spine density (Globus, Rosenzweig, & Diamond, 1973). Furthermore, the structure of the dendritic spine seems also to be influenced by experience. For example, Comery et al. (1996) demonstrated an increase in multiple-head spines in visual cortex following rearing in a complex environment.

In addition to changes in dendritic morphology following differential rearing environments, other studies have looked at results of more direct sensory stimulation. While some research has focused on the auditory modality (e.g., Wallhauser & Scheich, 1987) and olfaction (e.g., see Frazier-Cierpial & Brunjes, 1989), the majority of studies concern an increase in or lack of early visual stimulation and their effects on dendritic pattern and structure. For example, animals reared in the dark or with monocular occlusions

show a decrease in dendritic spine density (Fifkova, 1970; Rothblat & Schwartz, 1979; Valverde, 1971), a decrease in dendritic branching (Coleman & Riesen, 1968; Valverde, 1971), and an increase in variability of dendritic length (Globus & Scheibel, 1967) in visual cortex. In contrast, animals receiving a combination of light and auditory stimulation or constant light at early ages show increases in dendritic spine density in visual cortex (Parnavelas, Globus, & Kaups, 1973; Shapiro & Vukovich, 1970). Thus, the structure of the visual cortex may reflect the degree of sensory input (or lack of it) during early development. These findings suggest that unusual visual experience, be it augmented, reduced, or qualitatively altered, can lead to measurable morphological changes in the cellular development of the visual cortex.

2.3 Vision in avian species: the visual Wulst.

In avian species, the brain structure analogous to the mammalian visual cortex is the visual Wulst. The avian Wulst, a telencephalon structure, is strikingly similar to the mammalian visual cortex with respect not only to the fiber connections but in the morphological configurations of the visual receptive neurons and their synaptic relations (Watanabe, Ito, & Masai, 1983). Furthermore, the general morphology of the Wulst is similar across avian species, including pigeons and owls (Karten & Hodos, 1967; Karten, Hodos, Nauda, & Revzin, 1973), finches (Rollenhagen & Bischof, 1991), and quail (Watanabe, Ito, & Masai, 1983).

Similar to results found in mammalian species, modified visual experience influences changes in the morphology of dendrites in avian Wulst. For example, diffuse retinal illumination produces a marked increase in responsiveness of cells in the Wulst of domestic chicks (Brown & Horn, 1979; Jones & Horn, 1978). Additionally, domestic chicks exposed to patterned light also have measurable differences in dendritic structure in the Wulst when compared to dark reared birds (Bradley & Horn, 1979).

The Wulst of the quail consists primarily of three layers of stellate neurons; (a) the hyperstriatum dorsale (HD), a deep lying layer composed of small round cells (6-11 μm in diameter); (b) the nucleus intercalatus hyperstriatum accessorium (IHA), an intermediate layer of small round cells (6-14 μm in diameter) which are distributed in linear arrangement perpendicular to the layer; and (c) the hyperstriatum accessorium (HA), an overlying layer consisting of small to medium-sized, round cells (6-17 μm in diameter; Watanabe, Ito, & Masai, 1983). Using the Fink-Heimer (1967) method and electron microscopy, Watanabe, Ito, and Masai (1983) described a visual pathway in quail which is comparable to the geniculocortical system in mammals. According to these researchers, retinal fibers terminate in the nucleus dorsolateralis anterior thalami (DLL). This nucleus then projects to

the visual Wulst, and more specifically in quail, the IHA. It is the IHA in quail which corresponds to the mammalian visual cortex.

Using the rapid-Golgi technique of tissue staining (Valverde, 1970), three classifications of neurons were found to inhabit the IHA. Of these three, the Type II and Type IV neurons were most predominant (Watanabe, Ito, and Masai., 1983). Type II neurons have a medium-sized somata (10-15 μm in diameter) with wide-ranging dendrites. A most notable feature of the Type II neuron is its extremely dense covering of spines. Type IV neurons are smaller in diameter (7-12 μm in diameter) and have several primary dendrites extending in all directions. Spines on these neurons are irregular in shape, but very dense. The spiny nature of these two neuron types make them prime candidates for measuring dendritic spine density as a function of early afferent experience.

3.0 Hypotheses.

A review of the preceding discussion reveals that (1.1) early or unusual amounts of sensory stimulation can influence the emergence of normal intersensory perception. Furthermore, (1.2) some prenatal visual experience can produce a facilitative effect on the emergence of visually directed behavior, while (1.3) a substantially large amount of prenatal visual stimulation can produce a retarding effect. Studies of neural plasticity have revealed that experience can have a profound effect upon the brain and, in particular, (2.2) influences changes in dendritic structure, spine density, and function. The studies reviewed provide a reasonable argument that changes in dendritic morphology are good indicators of neural plasticity. Several studies have also revealed that (2.3) the Wulst of avian species in general, and the IHA of quail in particular, is the brain area primarily responsible for vision, analogous to the mammalian visual cortex. This site is a likely candidate for demonstrations of neural plasticity following sensory stimulation.

It therefore seems reasonable to conclude that dendritic complexity and spine density may provide useful measures of the morphological basis for behavioral results obtained in previous intersensory studies with bobwhite quail (e.g., Lickliter, 1990a,b; Sleigh & Lickliter, 1995). Given that visual responsiveness is enhanced following unusually early visual experience (Lickliter, 1990a,b), it can be hypothesized that unusually early visual stimulation increases the complexity of dendrites and the number of dendritic spines in the visual Wulst (quail IHA), enhancing the functionality of the visual system and thereby facilitating unusually early visually directed behavior.

Additionally, visual responsiveness is delayed by providing embryos with a substantially large amount of prenatal visual stimulation. This effect can also be hypothesized as the result of changes in the dendritic fields of the chick's visual system.

More specifically, a substantially large amount of visual stimulation could serve to interfere with normal neuronal organization of the Wulst. Consequently, visual responsiveness is delayed compared to normally hatched chicks.

The present study was designed to investigate the effect of unusually early visual experience on the maturation of the dendritic fields of the bobwhite quail's visual Wulst. It is hypothesized that there is a dynamic relationship between early experience, neuronal organization, and behavioral development in bobwhite quail. As such, the following specific hypotheses were made:

(1) Unusually early visual stimulation will increase spine frequency in the cells of the bobwhite quail Wulst (Experiment 1, replication of Lickliter 1990a,b; 24 hr group only). Consequently, chicks will demonstrate visually directed behavior at earlier ages than normally reared chicks.

(2) A substantially large amount of prenatal visual stimulation will decrease dendritic spine frequency in the cells of the bobwhite quail Wulst (Experiment 2, replication of Sleigh & Lickliter, 1995; 96 hr group only). Consequently, chicks will demonstrate a delay in visually directed behavior when compared to normally reared chicks.

4.0 Design and methods.

4.1 Subjects.

120 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%-85% relative humidity. To control for variations in developmental age, only those birds which hatched during Day 23 of incubation were used in these experiments (by convention, Day 23 of incubation begins at 23 day, 0 hours and ends at 23 day, 23 hours, with the first day of incubation being Day 0). The possible influence of between-hatch variation in behavior was controlled by drawing subjects for each experiment from at least three different weeks of eggs. Following hatching, chicks were housed in large (45 x 25 x 15 cm) plastic tubs placed under heat lamps which maintained a brooding temperature of approximately 30 °C. Each rearing tub contained 10 to 12 same-aged chicks to mimic natural brood conditions (Stokes, 1967).

4.2 Prenatal visual stimulation procedure.

During the second half of the 21st day of incubation (Day 21, 1200-1600 hr) a portion of the shell (approximately 1.5 cm in diameter) and the inner shell membrane over the air space of the egg of each subject was removed to provide the embryos unusually early visual stimulation. The embryo's bill penetrates the air space of the upper portion of the egg early on Day 21, and the embryo begins to respire and vocalize at this time (Freeman & Vince, 1974). Exposing the embryo's head in this manner does not interfere with incubation, survival, or subsequent species-typical behavior (Lickliter, 1990a,b; Lickliter & Stoumbos, 1991; Banker & Lickliter, 1993).

Following this procedure, the opened eggs were placed in a portable Hovibator incubator and exposed to a 15-W light pulsed at 3 cycles per second. In experiment 1, embryos were exposed to the light for 10 min/hr during the last 24 hr prior to hatching. In other words, embryos received approximately 240 min of exposure to temporally patterned light. In experiment 2, embryos were exposed to the light for 40 min/hr during the last 24 hr prior to hatching, resulting in approximately 900 min of exposure to temporally patterned light. In both experiments the light was placed directly above the plexiglas top of the incubator and care was taken to ensure that the presence of the light did not alter the ambient air temperature or the relative humidity within the incubator. After hatching, the chicks were placed in rearing tubs with 10-12 same-aged chicks (as described above) until testing.

4.3 Behavioral testing apparatus and stimuli.

Testing was conducted postnatally in a test apparatus located in a sound-attenuated room that was maintained at approximately 25 °C throughout the study. The test apparatus consisted of a large circular arena, 160 cm in diameter, surrounded by a black curtain that shielded the observer from the subject's view. The walls of the apparatus were lined with foam to attenuate echoes, and the floor was painted flat black. Two rectangular approach areas (32 x 15 cm) were delineated on opposite sides of the arena by green lines painted on the floor. A midrange dome radiator speaker was positioned behind the curtain in each of the approach areas, equidistant from the point at which subjects were placed in the apparatus. Each speaker was connected to a cassette tape recorder located at a control table, and allowed for the presentation of maternal auditory cues during the test trial. A taxidermically prepared natural model of a quail hen was placed in each of the two approach areas. One model was an adult bobwhite hen and the other a scaled quail hen, a species whose habitat range overlaps that of the bobwhite quail (Johnsgrad, 1973; for a photo of the two hens, see Lickliter & Virkar, 1989). The observer sat at the control table and observed

each subject's activity through a large mirror positioned above the arena. A system of hand-operated stopwatches was used to score the latency and duration of response.

4.4 Behavioral testing procedure and measures.

One simultaneous choice test, 5 min in length, was given to each subject. Presentation of the test 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 stimuli was scored as follows: As the chick entered each approach area, its choice and the latency (amount of time elapsed in seconds from the onset of the trial to the chick's entering the approach area) and duration (the cumulative amount of time in seconds the bird remained in the approach area during the course of the trial) of response was recorded. When over the course of the 5-min test, a chick remained in one approach area for more than twice the time it spent in the opposing area, a preference was registered. If a chick entered both approach areas during a test without showing a preference for either one, the behavior was scored as "no preference". If a subject did not enter either approach area, it was considered a "nonresponder" and received a score of 300 s for latency (the length of the trial) and 0 s for duration for both test stimuli.

4.5 Behavioral data analysis

Before performing any statistical analyses, testing duration scores that totaled less than 10 s were replaced with a score of zero, in order to avoid scoring accidental responses as subjects moved about the arena. The corresponding latency score was replaced with a score of 300 s (the length of the testing trial). As such, these subjects were considered "nonresponders" and were not included in the analyses.

The primary data of interest in this study were measures of preference for the stimuli presented during the test trials. Three such measures of preference were analyzed: (a) Differences in the latency to approach and (b) duration of time spent near each stimulus by a subject in a group were evaluated by the Wilcoxon matched-pairs signed-ranks test, and (c) an individual preference, assigned to any subject that stays near one stimulus for more than twice as long as the other, was evaluated by the chi-square test. In all tests an α of 0.05 was used to evaluate the results.

4.6 Histology and quantitative procedures.

Subjects were euthanized with carbon monoxide, and their brains excised and stored in Golgi-Cox solution (1% HgCl₂, 1.5% K₂Cr₂O₇, 1.2% KCrO₄; see Appendix 1, Protocol

for Golgi-Cox stain). All tissue was stained by a variant of the Van Der Loos (1956) modification of the Golgi-Cox technique. Comparable tissue from subjects of the same hatch was stained concurrently and tested regularly to determine optimal impregnation. Optimal impregnation was determined to occur at 32 days. After 32 days, the tissue was removed from the stain, dehydrated, embedded in celloidin, sectioned on a microtome in the coronal plane (see Figure 1) at 120 μm , washed, darkened in ammonia, fixed in Kodak Rapid fix, dehydrated, and mounted with DPX mounting medium and a coverslip (see Appendix 2 for processing protocol). All tissue was coded prior to sectioning to avoid experimenter bias in all facets of the quantification procedure.

For each subject, 10 individual cells were drawn at 500 \times with the use of a camera lucida. Cells were selected as follows: using the stereotaxic atlas of the brain of the one-day-old Japanese quail (Peczely, Forgo, & Kovach, unpublished manuscript) and stereotaxic topography developed by Bayle, Ramade, and Oliver (1974), sections of the visual Wulst were scanned in a rostral to caudal direction until the IHA layer was identified (in the nomenclature of Peczely et al., area IHA is called hyperstriatum intercalatus superior; Joseph Kovach, personal communication). Subsequently, cells in the IHA (see Figure 2) which exhibited complete staining and which were primarily contained within the section were isolated. One cell (Type IV; Wantanabe, Ito, & Masai, 1983) was drawn from each section.

Two measures were obtained for each cell. First, the number of dendritic spines were counted and the number of spines/10 μm dendrite were computed. Statistical comparisons were made between groups in the average number of spines/10 μm dendrite using the Wilcoxon's rank-sum test (due to an inability to meet the assumptions of the independent-samples t-test).

Second, projected dendritic length and dendritic complexity were analyzed in the following manner. The branches originating from the cell body were designated the first order or 'primary' branch; after a bifurcation, each resulting branch was termed second order, etc.. Overall dendritic length and mean length at each dendritic order was subsequently calculated and statistical comparisons were made between groups on these measures using an independent-samples t-test.

4.7 Experiment 1: Assessment of intersensory functioning and dendritic spine frequency in visual Wulst following unusually early exposure to visual stimulation.

Lickliter (1990a,b) demonstrated that early exposure to visual experience can facilitate the early emergence of visual responsiveness in bobwhite quail chicks. Presumably this is due to an acceleration of development in the visual system, which is presumed to be supported by enhanced functional organization of the neural systems governing visual preferences. However, the relationship between early visual experience and subsequent neural organization in bobwhite quail chicks has not been examined. Other studies (Globus Rosenzweig, & Diamond, 1973; Greenough & Volkmar, 1973; Parnavelas, Globus, & Kaups, 1973; Holloway, 1966; Shapiro & Vukovich, 1970; Volkmar & Greenough, 1972) suggest that early visual experience produces an increase in the number of dendritic spines in a variety of mammalian visual brain areas. The Wulst of avian species is analogous to the mammalian visual cortex (Wantanabe, Ito, & Masai, 1983) and changes in dendritic structure in this area have also been associated with visual sensory experience (Bradley & Horn, 1979; Brown & Horn, 1979; Jones & Horn, 1978). The present experiment was designed to assess the impact of early visual experience upon the dendritic fields of the bobwhite quail Wulst area IHA, as well as the timing of emergence of postnatal visual preferences. It was hypothesized that early visual experience would enhance development of dendrites in the bobwhite quail Wulst, thereby facilitating the previously observed early emergence of visually directed behaviors.

Method

Forty bobwhite quail chicks were drawn from three separate hatches. The egg shells of all experimental subjects (n=20) were opened and the embryos were exposed to 240 min of patterned light prenatally during the 24 hr period prior to hatching (see Prenatal Visual Stimulation Procedure section for details). Control subjects (n=20) were given the same egg-opening procedure, but did not receive exposure to the patterned light. After hatching, the chicks were placed in social groups and reared in tubs under heat lamps.

At 24 hr following hatching, chicks were tested in a simultaneous choice test between a bobwhite maternal call paired with either a taxidermically prepared natural model of a bobwhite quail hen (species-typical) or a scaled quail hen (species-atypical). In other words, during testing both hen models were emitting the same species-typical bobwhite maternal call, requiring subjects to direct their social preference on the basis of available visual cues. Choice, latency, and duration of response were scored as described in the Behavioral Testing Procedure and Measures section.

Immediately after testing, a sample of ten chicks from each group was chosen for histological analysis. From the experimental group, subjects demonstrating a species-typical preference were selected for the analysis. From the control group, subjects failing to

make a species-typical preference were selected for the analysis. All subjects selected for the histological analysis were sacrificed, their brains extracted, stained, and examined as described in the Histology section. Unfortunately, a blind recording error prior to the data analysis resulted in the loss of data for several subjects. Therefore, the histological analysis contained a total sample of 10 subjects. Statistical comparisons between groups in the average number of spines/10 μ m dendrite were made using Wilcoxon's rank-sum test (due to an inability to meet the assumptions of the parametric test), and comparisons between groups in dendritic length and complexity were made using an independent-samples t-test.

Results and Discussion

The results of the behavioral testing are shown in Table 1. Embryos exposed to 240 min of augmented prenatal visual stimulation during the last 24 hr of incubation demonstrated a significant preference for the bobwhite hen model paired with the bobwhite maternal call over the the species atypical combination [$\chi^2(2)=9.1$, $p<.05$]. In contrast, control chicks failed to demonstrate a significant preference for either test stimulus combination. This finding is consistent with those of Lickliter (1990a,b), demonstrating that early exposure to visual experience can facilitate the early emergence of visual responsiveness. Although chicks in the experimental condition demonstrated a trend toward shorter latencies and longer durations in the response to the species typical combination, the analysis of latency and duration of response by the Wilcoxon test revealed no statistically significant differences between responses to test stimuli in either condition.

As indicated in the General Methods section, all brains were coded prior to the histological analysis. This permitted blind measurements throughout all aspects of the quantification procedure. Individual cells were examined under a microscope (see Figure 3 for a photomicrograph of a sample neuron) and drawn with a camera lucida. The results of the histological analysis are presented in Table 2. Two independent spine counts (for an sample cameral lucida drawing used to conduct the spine counts, see Figure 4) were conducted for all cells in the analysis and found to be reliable ($r=0.94$, $p<.05$). The mean for the two counts was then computed for each cell and this average was used in the analysis. Since there were no significant differences in spine frequency between animals within each group, values of the animals in a group were pooled (for a similar analysis, see Wallhausser & Scheich, 1987). Although there were no significant differences in total dendritic spines and total dendritic length between experimental and control animals, neurons of chicks which received 240 min augmented prenatal visual stimulation had significantly fewer spines/10 μ m dendrite than did the cells of control subjects ($W=1486.0$, $p<.05$). That is, taking into account the size of the cell (total dendritic length), chicks which

received the early visual experience had fewer dendritic spines (17.8% fewer) than normally incubated chicks.

In addition to an analysis of dendritic spines, the mean dendritic length was also computed for each branching order of each cell (see the histology section of the General Methods). The mean dendritic length of each branching order across cells was then computed, and comparisons of these means were made between experimental and control subjects. Cells were found to contain branches in six orders. No significant differences in dendritic length for each order were found, except in the fourth order, where chicks which received 240 min augmented prenatal visual stimulation had significantly longer dendritic branches [$t(98)=2.5$, $p<0.05$] and significantly more branches per cell [$t(98)=2.4$, $p<0.05$]. It should be noted that most cells in this analysis had four or fewer than four orders of branches. This suggests that there were more outer branches of cells in the visual Wulst of experimental subjects and these branches were longer than those in normally incubated chicks.

The results of this experiment indicate that unusually early visual stimulation may serve to *reduce* the number of dendritic spines, thereby facilitating the early emergence of visual responsiveness. That is, those subjects receiving 240 min augmented prenatal visual stimulation had neurons with fewer dendritic spines (taking into account dendritic length) and demonstrated visual preferences not seen in normally incubated chicks until later ages. This suggests that the visual system of bobwhite embryos is organized in such a way to permit the selective reduction of dendritic spines through experience, retaining only those spines necessary for normal visual functioning. By experimentally subjecting embryos to visual stimulation earlier than normally incubated chicks, the visual Wulst was reorganized by the selective reduction of unnecessary dendritic spines, a process which would normally occur later in life with normal visual experience.

If the normal process of neuronal organization in the bobwhite visual Wulst is indeed influenced by early visual experience, then it should be possible to demonstrate both a facilitative effect as well as a detrimental effect of early visual experience on this process. In other words, it may be possible to disrupt normal neuronal organization in such a way that chicks will fail to demonstrate a timely emergence of visual responsiveness. While the *timing* of visual experience seems to be influential in neuronal organization, this process may also be sensitive to the overall *amount* of stimulation the sensory system receives. Therefore, by providing the organism with a substantially large amount of early visual stimulation, it may be possible to disrupt normal neuronal organization, thereby delaying the normal emergence of intersensory perception. The next experiment was designed to test this idea by examining the effects of substantially increasing the amount of augmented

prenatal visual stimulation utilized in this experiment on the neuronal organization and subsequent behavior of bobwhite quail chicks.

4.8 Experiment 2: Assessment of intersensory functioning and dendritic spine frequency in visual Wulst following substantially augmented prenatal visual stimulation.

While early visual experience may enhance or facilitate postnatal visual responsiveness, other studies suggest that substantially increased auditory or visual experience (Sleigh & Lickliter, 1995; 1996) or tactile and vestibular experience (Carlsen & Lickliter, 1999) may have a retarding effect upon the emergence of visual preferences. These results suggest that the overall amount (e.g., substantially augmented) of sensory stimulation influences the development of intersensory functioning. The specific mechanisms underlying this effect are as yet undiscovered.

The present experiment was designed to assess the relationship between substantially augmented prenatal visual stimulation, functional changes in the nervous system, and the subsequent visually guided behavior of bobwhite quail chicks. It was hypothesized that a substantially large amount of prenatal visual stimulation would retard normal development of dendrites in the bobwhite quail Wulst area IHA, thereby serving to delay the emergence of visually guided preferences.

Method

As in Experiment 1, forty bobwhite quail chicks were drawn from three separate hatches. The egg shells of all experimental subjects (n=20) were opened and the embryos were exposed to 900 min of patterned light prenatally during the 24 hr period prior to hatching (see Prenatal Visual Stimulation Procedure section for details). Control subjects (n=20) were given the same egg-opening procedure, but did not receive exposure to the patterned light. After hatching, the chicks were placed in social groups and reared in tubs under heat lamps.

At 96 hr following hatching, chicks were tested in a simultaneous choice test between a bobwhite maternal call paired with either a taxidermically prepared natural model of a bobwhite quail hen (species-typical) or a scaled quail hen (species-atypical). In other words, during testing both hen models were emitting the same species-typical bobwhite maternal call, requiring subjects to direct their social preference on the basis of available visual cues. Choice, latency, and duration of response were scored as described in the Behavioral Testing Procedure and Measures section.

Immediately after testing, 10 subjects were chosen as a sample from each group for histological analysis. From the experimental group, subjects failing to demonstrate a species-typical preference were selected for the analysis. From the control group, subjects making a species-typical preference were selected for the analysis. All subjects selected for the histological analysis were sacrificed, their brains extracted, stained, and examined as described in the Histology section. Unfortunately, a blind recording error prior to the data analysis resulted in the loss of data for several subjects (the same error discussed in Experiment 1). Therefore, the histological analysis contained a total sample of 15 subjects. Statistical comparisons between groups in the average number of spines/10 μm dendrite were made using Wilcoxon's rank-sum test, and comparisons between groups in dendritic length and complexity were made using an independent-samples t-test.

Results and Discussion

The results of the behavioral testing are shown in Table 3. Embryos exposed to 900 min of augmented prenatal visual stimulation during the last 24 hr of incubation did not show a significant preference for either the bobwhite hen model paired with the bobwhite maternal call or the scaled hen paired with the maternal call. This finding is consistent with those of Sleigh and Lickliter (1995), in which a substantially augmented amount of prenatal visual stimulation delayed the normal emergence of species-typical visual responsiveness. However, unlike the Sleigh and Lickliter (1995) findings, control subjects in the present experiment *also* failed to demonstrate a strong preference for either test stimulus combination. An analysis of latencies and durations with the Wilcoxon test further supported these findings.

As indicated in the General Methods section, all brains were coded prior to the histological analysis. This permitted blind measurements throughout all aspects of the quantification procedure. The results of the histological analysis are presented in Table 4. As in Experiment 1, two spine counts were independently conducted and found to be reliable ($r=0.94$, $p<.05$). The mean for the two counts was then computed for each cell and this average was used in the analysis. As in Experiment 1, there were no significant differences in spine frequency between animals within each group and values of the animals in a group were pooled. Neurons of chicks which received 900 min of augmented prenatal visual stimulation during the last 24 hr of incubation had significantly more dendritic spines ($W=4517.0$, $p<.05$), longer total dendritic length ($W=4697.0$, $p<.05$), and more spines/10 μm dendrite (8.7%; $W=4701.0$, $p<.05$) than did the cells of control subjects.

As in Experiment 1, the mean dendritic length of each branching order across cells was also computed, and comparisons of these means were made between experimental and

control subjects. Cells were found to contain branches in five orders. Although there were no significant differences in the mean lengths of each branching order across conditions, there were significantly more dendritic branches in the cells of experimental subjects for the first order [$t(148)=2.6, p<.05$], second order [$t(148)=3.4, p<.05$], and third order [$t(148)=2.2, p<.05$] when compared to controls. Therefore, the neurons of chicks which received a substantially augmented amount of prenatal visual stimulation were more complex than those of normally incubated chicks, as indicated by more dendritic branches in the first, second, and third orders.

The results of this experiment indicate that a substantial amount of augmented prenatal visual stimulation may serve to prevent normal neuronal organization in the bobwhite visual Wulst, thereby delaying the emergence of intersensory functioning. Subjects which received a substantial amount of unusually early visual experience (900 min) had more complex neurons, including more spines, longer dendrites, and significantly more branches, than their normally-incubated counterparts. While it is clear from Experiment 1 that sensory stimulation which falls in some optimal range may facilitate normal patterns of perceptual development (e.g., less complex neurons and an accelerated emergence of visual responsiveness), the results of the present experiment provide evidence that stimulation beyond the range of the species' norm may result in intersensory interference (more complex neurons and the delay of normal patterns of visual responsiveness).

5.0 General discussion.

The experiments of this study examined the effects of augmented prenatal visual stimulation on the plasticity of neurons in the visual Wulst and subsequent postnatal visual responsiveness to maternal cues in bobwhite quail chicks. Results revealed that the pattern of neuronal organization and postnatal behavior was influenced by the amount of prenatal visual experience subjects were given. Specifically, chicks provided a relatively small amount of prenatal visual stimulation (240 min) had neurons with fewer spines/10 μm dendrite and displayed early patterns of visual responsiveness (Experiment 1), while chicks provided a substantially larger amount of prenatal visual stimulation (900 min) had more complex neurons (including more spines, longer dendrites, and more branches) and failed to display normal species-specific visual responsiveness (Experiment 2).

Previous findings regarding intersensory development have indicated that normal patterns of perceptual development can be modified by unusually early experience and that this effect is mediated by the overall amount of stimulation a sensory system receives. While normally reared quail chicks respond preferentially to species-specific maternal visual cues (in combination with auditory cues) at 72 hr of age, chicks given 240 min

augmented prenatal visual stimulation during the final day before hatching demonstrate the same preference as early as 24 hr of age (Lickliter 1990a, b). However, when chicks are given a substantially larger amount of prenatal visual stimulation (900 min), they fail to demonstrate normal species-specific visual preferences at 72 hr and as late as 96 hr postnatally (Sleigh & Lickliter, 1995). Taken together, these studies suggest that there is an optimal range of sensory stimulation which an organism needs for normal perceptual development (see Carlsen & Lickliter, 1999; Gottlieb, Tomlinson, & Radell, 1989; Lickliter & Hellewell, 1992; Lickliter & Lewkowicz, 1995 for other examples further supporting the existence of some optimal range of prenatal sensory stimulation necessary for species-typical perceptual development). Amounts of stimulation inside this range can maintain or facilitate normal perceptual development, but amounts outside the optimal range may produce intersensory interference.

What has remained unclear until now is the mechanism by which these behavioral effects are achieved. Neural plasticity, the ability of the brain to be shaped by experience, and in turn, for this newly reconstructed brain to facilitate the emergence of new experiences, may be such a mechanism. Indeed, several decades of work in this area have revealed that many of the brain's systems are malleable and plastic, in particular the visual system (for a review, see Boothe, Vassdal, & Schneck, 1986). It is important to note that neural plasticity may be both adaptive and maladaptive for the organism. That is, "right" experiences can have beneficial effects on the brain whereas "wrong" experiences can have deleterious effects on the developing brain and early behavior (Nelson, 1999).

The present study revealed that the bobwhite quail visual Wulst is plastic and can be molded by experience. Specifically, neurons in area IHA of the visual Wulst were modified by early visual experience and these experience-dependent modifications were related to the postnatal behavioral patterns of bobwhite chicks. In Experiment 1, neural plasticity seemed to be adaptive. An unusually early and relatively small amount of visual stimulation modified neurons of the Wulst and facilitated the early emergence of visual responsiveness. On the other hand, Experiment 2 revealed that neural plasticity in the Wulst can also be deleterious to the organism. A substantially larger amount of early visual stimulation modified cell morphology and normal intersensory functioning was delayed.

These findings can be seen to reflect a common developmental phenomenon; namely, the nervous system is "streamlined" by experience to do more with less. That is, in early neural development there is an initial overproduction of synapses followed by selective retention of a subset of them (Boothe, Vassdal, & Schneck, 1986). Although it is unclear whether the mechanism of synapse loss is an active process of elimination or if it is the result of their passive withdrawal due to the absence of sufficient levels of neural activity

(Greenough, 1986a), it is clear that the functional consequence is the connections appropriate to the past experiences of and potential future demands upon the system are typically preserved. Cast in this light, a relatively small amount of unusually early visual stimulation (Experiment 1) appeared to initiate the early reduction of dendritic spines, selecting the efficient and functional circuits necessary for the demands of normal intersensory functioning, and enabling chicks to demonstrate visually-guided maternal preferences at an earlier age than normally-reared chicks. These findings are similar to those reported for the domestic fowl, in which neurons in an auditory area of the forebrain of chicks imprinted to an auditory stimulus contained fewer spines/10 μm dendrite when compared to the cells of control chicks (Wallhauser & Scheich, 1987). Thus, it appears that the early emergence of normal patterns of neuronal organization can be facilitated by early experience.

In contrast, a substantially larger amount of unusually early visual experience (Experiment 2) appeared to interfere with the normal process of neural selection, allowing the retention of dendritic spines, and chicks failed to demonstrate species-specific maternal preferences at ages which normally-reared chicks show this preference (e.g., Carlsen & Lickliter, 1999; Lickliter & Virkar, 1989; Stoumbos & Lickliter, 1995). The effects of such overstimulation have also been observed in rodents. For example, constant lighting has been reported to increase spine frequency on neurons in the rat lateral geniculate nucleus (Parnavelas, Globus, & Kaups, 1973) and also in the visual cortex (Parnavelas & Globus, 1976). Similar disruptions of normal cell organization and cell death have also been documented in the domestic chick. For example, Oppenheim, Pittman, Bray, and Manderdrut (1978) demonstrated that cell death was slowed down or inhibited by a lack of movement and activity following neuromuscular blocking by curare. However, once the blocking agent was removed, cell death resumed its normal course.

While it is becoming increasingly clear that more sensory stimulation during early development is not necessarily better (and as noted above, may in fact be detrimental), at present little is known about what constitutes appropriate ranges or thresholds of stimulation for the developing embryo or fetus of any avian or mammalian species. In other words, little is known about the boundaries associated with the type, amount, and timing of stimulation that is optimal for the developing nervous system. Additionally, it is unclear how unusual patterns of sensory stimulation may differentially influence diurnal and nocturnal species, or influence early development differently than latter development (see Greenough, 1986b for a discussion of plasticity in early and late development). Research suggests however, that prior to birth or hatching, the embryo or fetus appears to be particularly sensitive to the *amount* of overall stimulation present in its immediate

environment. Nevertheless, the normal or typical amount of sensory stimulation is regulated both by the limited sensory capacities of the young organism and the constrained developmental context (i.e., egg or uterus) in which the organism is developing (Lickliter, 1995; Turkewitz & Kenny, 1982, 1985). Thus, stable and reliable perceptual outcomes within a species are routinely achieved by the interplay of internal and external factors of the developmental system (Oyama, 1985). The results of this and other related studies (Carlsen & Lickliter, 1999; Radell & Gottlieb, 1992; Sleigh & Lickliter, 1995, 1997) suggest the emergence of normal perceptual functioning is influenced by the relative amounts of sensory stimulation available to the young organism.

Although this study provides useful insight into the mechanisms underlying plasticity and perceptual development, it is not clear at present how the various modalities interact at the neural level to bring about normal patterns of intersensory development. For example, while the present study empirically addresses the relationship between early or unusual amounts of visual stimulation and visual functioning, the effect of stimulation in one modality upon brain plasticity in other developing modalities remains unclear. Further descriptive and empirical studies are needed to better understand the processes whereby specific sensory experience at particular times maintain, facilitate, or interfere with the normal course of neural organization and early perceptual and behavioral development.

6.0 References.

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Appendix 1
Protocol for Golgi Cox Stain

best for fresh, unfixed tissue
test blocks determine staining time

How to make solutions:

Three solutions (A, B, and C) are prepared separately and mixed with 1500 mls more water in a brown jug. Makes almost a gallon.

- A. 37.5 grams $K_2Cr_2O_7$ and 750 ml warm distilled water (Mix and then warm mixture) (This is 5%)
- B. 37.5 grams $HgCl_2$ and 750 ml hot distilled water (Mix and heat almost till boiling) (also 5%)
- C. 30 grams K_2CrO_4 and 600 ml cold distilled water (This is also a 5% solution)

After these three solutions are combined with 1500 ml of water, let mixture stand in brown jug out of light for 5 days and then filter.

Generally, a small tissue block is placed in a jar with 50-100 ml of staining solution with a small piece of gauze. Fresh solution after 24 hours. Test slices after 12 days.

When tissue is completely stained, rapid dehydration and celloidon embedding is often used before cutting and processing.

Appendix 2
Protocol for Processing Golgi-stained Tissue

1. Slice tissue on microtome and place in 70% ethyl alcohol.
2. Rehydrate: 70%, 50%, 2x water (2 min each).
3. Rinse: water, 3x30 sec.
4. Fix: (used or new Kodafix solution), 10 min.
5. Rinse: water, 2x30 sec.
6. Dehydrate: 50%, 70%, 80%, 95%, 100% (2 min each).
7. Clear: xylenes, 2 min each.
8. Mount: layer DPX, place sections on DPX (straightened out), another layer DPX over sections, coverslip very carefully.

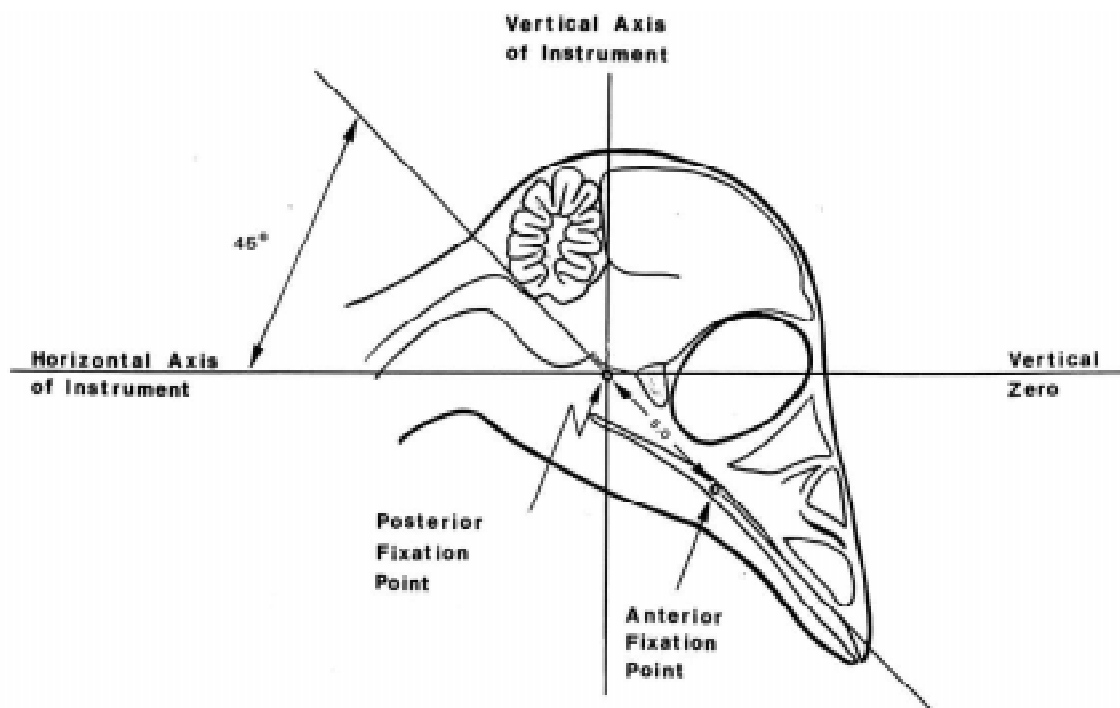


Figure 1: Sagittal view and diagram of the one-day-old Japanese quail (*Coturnix japonica*) brain indicating horizontal and vertical axes. Reproduced from Peczely, Forgo, & Kovach (unpublished manuscript).

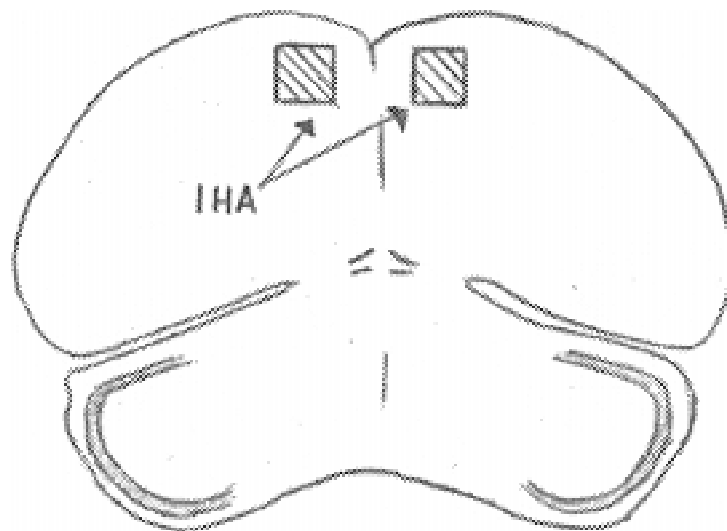


Figure 2: Diagram of coronal section of bobwhite quail brain used to select cells in area IHA (drawn from Wantanabe, Ito, & Masai, 1983).

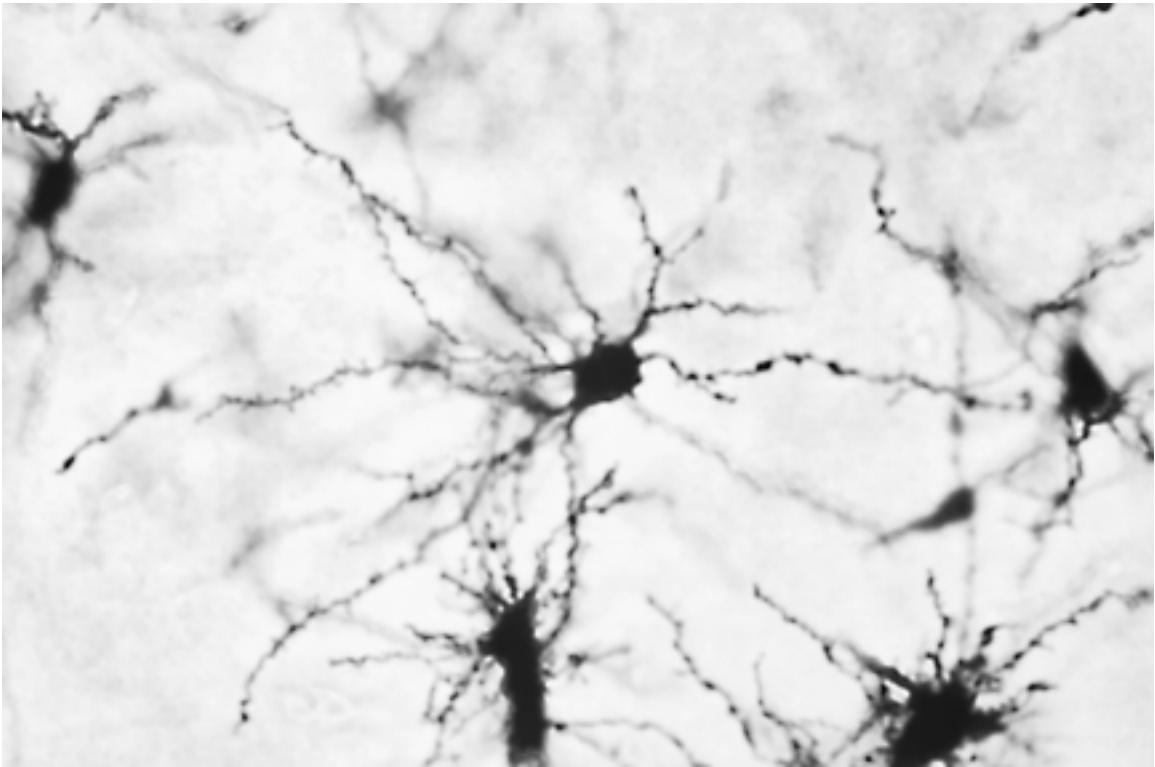


Figure 3: Photomicrograph of a Type IV neuron of the bobwhite quail visual Wulst (area IHA).

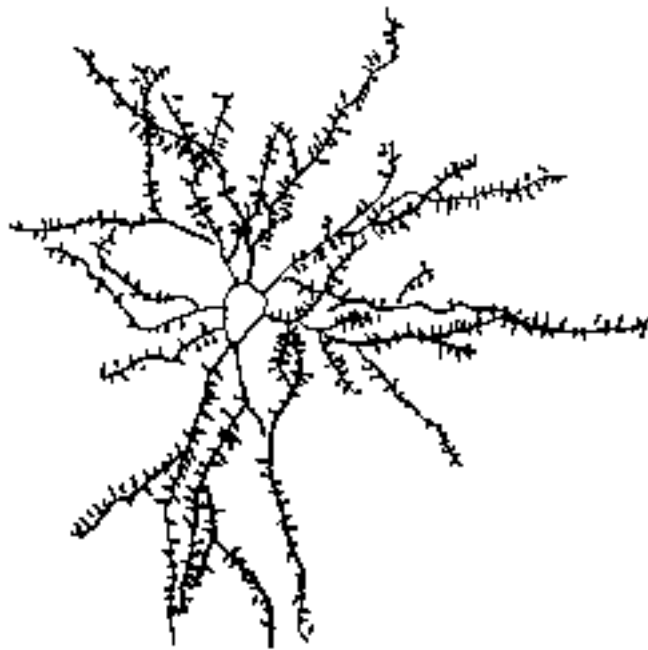


Figure 4: Sample camera lucida drawing of a Type IV neuron in area IHA of the bobwhite visual Wulst.

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

Condition	<i>n</i>	<i>n</i> responding	Preference		
			Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	Both
240 min visual stim	23	20	13*	3	4
Control	27	20	9	7	4

* $p < .05$ (chi-square test)

Table 2
Histological Measures for Cells in Experiment 1

Condition	<i>n</i>	Mean Spines	Mean Total Dendritic Length (in μm)	Mean Spines/10 μm Dendrite
240 min visual stim	40	159.4	650.0	2.45*
Control	60	185.4	621.6	2.98

* $p < .05$ (Wilcoxon's rank sum test)

Table 3

Preference of Bobwhite Quail Chicks in Simultaneous Auditory-Visual Choice Tests in Experiment 2

Condition	<i>n</i>	<i>n</i> responding	Preference		
			Bobwhite Hen with Bobwhite Maternal Call	Scaled Hen with Bobwhite Maternal Call	Both
900 min visual stim	28	20	10	7	3
Control	28	20	10	8	2

Table 4
Histological Measures for Cells in Experiment 2

Condition	<i>n</i>	Mean Spines	Mean Total Dendritic Length (in μm)	Mean Spines/10 μm Dendrite
900 min visual stim	80	218.7*	637.2*	3.43*
Control	70	176.5	563.3	3.13

* $p < .05$ (Wilcoxon's rank sum test)

CURRICULUM VITA

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Degrees:

- Ph.D. Virginia Polytechnic Institute and State University (1999)
 Psychological Sciences
- M.A. East Carolina University (1995)
 Academic/Experimental Psychology
- B.S. Averett College (1992)
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Computer Literacy:

HTML web publishing, including professional site development and course web sites.

Macintosh O/S; Windows 3.1; Windows '95; Netscape Navigator; Adobe Photoshop;
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Professional Experience:

- 1999- **Assistant Professor**
 Department of Psychology
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- 1998-1999 **Adjunct Faculty**
Department of Psychology
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Courses: Psychology as a Natural Science, Psychology as a Social Science,
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- 1997-1998 **Graduate Teaching Assistant**
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- 1997-1998 **Investigator**
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- 1996-1997 **Introductory Psychology Coordinator**
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Journal Articles:

Carlsen, R. & Lickliter, R. (1999). Augmented prenatal tactile and vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail chicks. Developmental Psychobiology, *35*, 215-225.

Invited Addresses:

Carlsen, R. (1998). Successful course web sites. Talk given at the 6th Eastern Conference on the Teaching of Psychology, James Madison University, Harrisonburg, VA. Sponsored by The Society for the Teaching of Psychology (APA Division 2).

Carlsen, R. (1998). Course web sites: beyond homepages. In S. Kronheim (Chair), Cyberpsychology III. Symposium conducted at the annual meeting of the Eastern Psychological Association, Boston, MA.

Workshops Conducted:

Carlsen, R. (1998). Building and managing web sites. Workshop given during Faculty Development Day, Averett College, Danville, VA.

Presentations at Professional Meetings:

- Carlsen, R. (1999). Building course web sites. Electronic poster presented at the BEA Miniconvention on Education and Technology during the annual meeting of the American Psychological Association, Boston, MA.
- Carlsen, R. & Lickliter, R. (1998). Effects of augmented prenatal vestibular stimulation on postnatal perception of bobwhite quail chicks. Poster session presented at the annual meeting of the Eastern Psychological Association, Boston, MA.
- Roberts, J., Bell, M.A., Carlsen, R. (1998). Sex differences on a computerized mental rotation task disappear with computer familiarization. Poster session presented at the annual meeting of the American Psychological Society, Washington D.C.
- Carlsen, R.M. & Lickliter, R. (1997). Augmented prenatal vestibular stimulation alters postnatal auditory and visual responsiveness in bobwhite quail. Poster presented at The Society for Developmental Psychobiology annual meeting, New Orleans, LA.
- Carlsen, R.M., Mumford, S.P., Graham, R.B, & Means, L.W. (1995). Prefrontal and parietal cortical lesions fail to disrupt performance by rats on tasks requiring allocentric and egocentric spatial working and reference memory. International Behavioral Neuroscience Society Abstracts, 4, 57. Presented in Santiago de Compostelo, Spain.
- Hatten, J., Hatten, A., Lumpkins, H., & Carlsen, R. (1992). The effect of pretraining on control by elaborate instructions. Paper presented at The Association for Behavior Analysis annual meeting, San Francisco, CA.
- Carlsen, R., Parnell, A., & Hatten, J. (1991). Changes in contingency control as a function of type of pretraining and type of instruction. Poster presented at The South Eastern Association for Behavior Analysis annual meeting, Charleston, SC.

Attendance at Professional Workshops:

Building and Managing Course Web Sites. 1998 workshop sponsored by the Virginia Tech Faculty Development Initiative.

Higher Education: Critical Issues for Virginia's Next Generation. 1997 meeting sponsored by the Faculty Senate of Virginia.

Training the Future Professorate '97. Workshop sponsored by Virginia Tech's Research and Graduate Studies.

Awards and Honors:

Nominated, Center for Innovation in Learning XCaliber Award (1999)
Award for exceptional, high caliber contributions to courseware development
Virginia Polytechnic Institute and State University

First Place, Graduate Student Research Symposium (1998)
Virtual Poster Category
Virginia Polytechnic Institute and State University

Graduate Student Assembly Research Travel Award (1998)
Virginia Polytechnic Institute and State University

Membership in Professional Organizations:

American Psychological Association

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International Society for Developmental Psychobiology

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