

An epigenetic theory of hemispheric specialization: The role of prenatal sensori-motor experience in the development of turning bias and spatial orientation in bobwhite quail (Colinus virginianus).

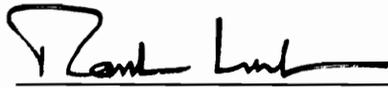
by

Michael Bernard Casey

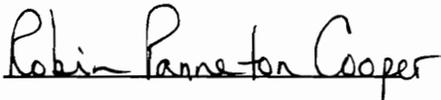
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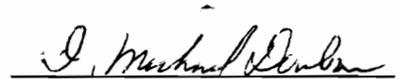
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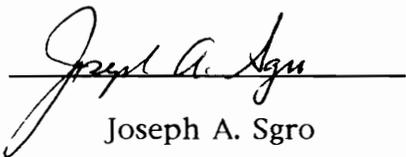
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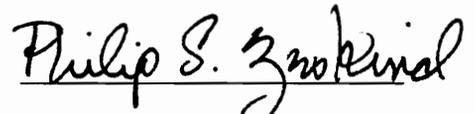
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AN EPIGENETIC THEORY OF HEMISPHERIC SPECIALIZATION: THE ROLE OF
PRENATAL SENSORI-MOTOR EXPERIENCE IN THE DEVELOPMENT OF TURNING BIAS
AND SPATIAL ORIENTATION IN BOBWHITE QUAIL (COLINUS VIRGINIANUS).

By

Michael Bernard Casey

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Psychology

(Abstract)

This study examined the effects of prenatal sensory and motor experience on the development of spatial orientation and turning bias in bobwhite quail. The theory presented here describes hemispheric specialization as the result of probabilistic events in the developing organism's prenatal environment; in particular, activity and experience in the final stages of prenatal development appear critical. Models and definitions of behavioral asymmetry, hemispheric specialization, and structural lateralization are reviewed. The results of Experiment 1 revealed a left-side turning bias in 85% of unmanipulated chicks. Experiments 2, 3, and 4 demonstrated that prenatal visual experience is a significant facilitator of population level left-side turning biases in bobwhite quail chicks. Experiment 5 investigated a potential underlying neurological basis for the bobwhite turning bias with unilateral injections of cycloheximide. The results of Experiment 5 suggest a left hemispheric specialization for the left-side turning bias. Furthermore, the results of Experiments 2 and 3 suggest that the asymmetrical hatching behaviors of the bobwhite quail are also a significant

canalizing influence on the development of turning bias. The findings of this study are discussed in terms of an epigenetic theory of the development of hemispheric specialization and questions are raised as to the efficacy of laterality indexes as a reliable quantification of degree of hemispheric lateralization.

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The fossil record suggests that behavioral asymmetries were present at least as long ago as 500 million years. This is evidenced by the concentrations of lateralized scars on the right side of fossilized trilobites (Babcock & Robison, 1989). Indeed as a testament to their pervasive nature, lateral asymmetries can be found in the behavior of fundamental particles (Mason, 1984), in the structure and function of organic molecules (Kondepudi, Kaufman, & Singh, 1990), in the asymmetries of flagella and cilia (Neville, 1976), in bacteria (Galloway, 1987), and even in creeping plants (Bradshaw & Rogers, 1993). It appears that the evolution of asymmetrical structure and function can be traced through nearly all the living and some extinct species. This realization has fueled a growing field of lateralization research.

To this end, the avian nervous system has several anatomical and developmental features which makes it an excellent model for studying laterality. One of the most significant anatomical features is that the avian optic nerves are completely decussated. Therefore, the primary visual connections project only to the contralateral side of the brain (Cowan, Adamson, & Powell, 1961). This structural feature allows monocular testing to achieve unilateral visual input to the bird's contralateral hemisphere, without the need for invasive surgical procedures. Complicated tachistoscopic presentation of stimuli placed in the extreme peripheral fields of vision is required for humans to achieve similar unilateral visual input. In this respect, the avian brain may be considered similar to a "split-chiasma" mammalian brain. In terms of developmental process, as the bird develops entirely within the egg, it provides a perfect "laboratory" for introducing experimental manipulations into the prenatal environment. In the following

experiments I examined the role of prenatal sensory and motor experience in the development of individual and population level turning bias in a precocial avian, the bobwhite quail (Colinus virginianus).

Specifically, the following experiments identified several interrelated mechanisms underlying the left-side turning bias that bobwhite quail demonstrate when responding to species-specific perceptual cues in a T-maze. Similar turning biases have been demonstrated in mice (Denenberg, 1977; Glick & Shapiro, 1985), dolphins (Ridgeway, 1986) and humans (Melekian, 1981). While such behavioral asymmetries have been extensively studied in rats (Denenberg, 1988; see Figure 1), they have never been investigated to any extent in birds. Thus, one of the unique aspects of this dissertation is that it identifies a population level turning bias in spatial orientation in a precocial avian species. Furthermore, this study examines prenatal sensory and motor influences that facilitate the development of turning biases in bobwhite quail neonates. Finally, this study investigated a potential neural basis for hemispheric specialization that underlies species-typical responding to species-specific maternal auditory and visual cues.

1.0 An Epigenetic Theory of Hemispheric Specialization.

Kuo (1967) argued that the principle determining factors that underlie behavioral development can be organized into five main categories: (1) morphological, (2) biophysical and biochemical physiology, (3) developmental history, (4) immediate stimulus array, and (5) environmental context. These five groups of determining factors are seen as interwoven, interrelated, and acting in unison. Therefore, every behavior is a functional product of the dynamic interrelationship of these five groups of determining factors. Kuo

(1967) used the terms "epigeneticism" and "epigenetics" in a far broader sense than they are typically used today. Kuo's epigenetics is not a simple rehashing of environmentalism applied to development. Kuo's use of the term epigenetics recognizes genetic influences on morphogenesis and biochemistry, but at the same time it stresses the importance of environmental constraints and neural plasticity in the development of the individual organism's behavioral repertoire.

The term "probabilistic epigenesis" was used by Gottlieb (1970) to designate the view that the behavioral development of individuals within a species does not follow an inevitable course, and more specifically that the sequence or outcome of individual behavioral development is probabilistic (with respect to species norms) rather than predetermined. This means that functional experience (exposure to stimulation and/or movement of musculo-skeletal activity) can potentially modify the development of the peripheral and central nervous system components that are involved in these events (Gottlieb, 1970). Probabilistic epigenesis assumes a bidirectional or reciprocal relationship between structural differentiation and function. Thus, an organism's structural development helps to determine function, while organismic behavioral functioning can alter the rate and direction of structural development (Gottlieb, 1983, 1992).

This system of transacting constraints and fluctuating degrees of freedom can be seen in the developmental relationship between hemispheric specialization and behavioral asymmetries. Following from the arguments of Previc (1991), Turkewitz (1988), Geschwind (1985), Corballis and Morgan (1978), and Collins (1977) that cerebral lateralization must be placed within a psychobiological context, a strong argument can be made that development of

hemispheric specialization is the result of environmental and organismic constraints reciprocally transacting from conception. Rather than being unique to higher order cognitive functioning in humans, physiological and behavioral asymmetry is found throughout the animal kingdom and is likely generated by a variety of prenatal influences and constraints.

The theory presented here embraces the general view that cortical development is largely driven by prenatal afferent input (Rakic, 1988; Von Der Marlsburg & Singer, 1988). In humans, it has been convincingly argued that higher order linguistic and visuo-spatial processing asymmetries derive from prenatal asymmetric lateral tendencies. Indeed, it has been argued that cerebral lateralization in humans is based in the asymmetric nature of the human intrauterine environment and its canalizing influence on the development of prenatal auditory and vestibular asymmetry (Previc, 1991). This dissertation presents evidence that the embryonic environment of avian species provides a similar system of canalizing influences that contribute to the development of functional asymmetries in the form of turning bias in bobwhite quail.

1.1 An epigenetic theory of hemispheric specialization: The role of the prenatal environment.

Patterns of hemispheric asymmetry are thought to be a product of the complex interplay of a number of genetic and environmental factors (Collins, 1977). The view presented here is that the basis for functional asymmetry is found principally in prenatal and early postnatal organism-environment transactions. It has been suggested that the development of functional asymmetries can be traced back to the ontogenetic formation of the first

neural structures, and perhaps even to asymmetries of the ovum and intrauterine environment (Bradshaw & Rogers, 1993; Previc, 1991; Turkewitz, 1988). From these early beginnings, functional asymmetries develop through the transaction of many organismic and environmental factors, beginning with the embryo and continuing well into the postnatal period. Few researchers have systematically studied the influence of a wide range of environmental factors on brain asymmetry (handling experiments and the effects of enriched environments on rats is the most notable exception). What little work that has been done has been on a limited number of species (see Figure 3). However, the work of Rogers (1991) and her colleagues on domestic chicks, as well as Denenberg (1981) and his associates' work on rats are clear examples which illustrate the critical importance of environmental factors as facilitating and inducing agents in the development of structural lateralization, hemispheric specialization, and behavioral asymmetry.

Specifically, it appears that the prenatal environment provides a highly structured, reliably consistent although not invariant, system of constraints that can canalize the developmental trajectory of brain lateralization. As seen in the development of the domestic chick embryo, extra-embryonic environmental stimulation (i.e., light) seems to determine the direction and degree of hemispheric specialization for a variety of seemingly unrelated behaviors (Rogers, 1991). In altricial rat pups, maternal hormonal conditions appear to be significant canalizing influences, but prenatal asymmetries are maintained and/or facilitated by postnatal environmental (including social interactions with conspecifics) conditions (Denenberg, 1981).

It has also been shown that there are a variety of asymmetric traits in non-human species which can be influenced by non-genetic factors, including cultural pressures (Levy, 1974), brain damage (Nagylaki & Levy, 1973), and instrumental conditioning (Collins, 1977). Morgan (1977) and Collins (1977) both argue that hemispheric specialization is not transmitted genetically, but emerges via asymmetry in the oocyte, which ultimately favors the left hemisphere in terms of developmental rate. These authors concur that only the degree and not the direction of asymmetry might be genetically determined. Morgan makes the claim that all organisms have a left-side developmental advantage and that such asymmetry is not encoded in the genome. Morgan (1977) argues that post-natal behavioral asymmetries may be ultimately attributed to asymmetries in maternal cytoplasmic conditions operative during ontogenesis. Indeed, there is some evidence that suggests that morphological asymmetries occurring in a variety of species tend to favor the left side in terms of developmental rate and degree of lateralization (Collins, 1969, 1970, 1975; Corballis & Beale, 1976). There is also evidence that the direction of many asymmetries is determined with reference to developmentally earlier asymmetries, possibly in the egg or sperm (Wolpert, 1969).

The human intrauterine environment is laterally asymmetric in several respects. Some lateralization appears to originate in the asymmetrical conditions and structure of maternal anatomy, whereas others appear to arise from the fetus itself (Previc, 1991). According to Previc (1991) one of the most important maternal asymmetries is found in the torsion of the uterus. Torsion of the uterus results in a large percentage of fetuses positioned with their head to the left side of the mothers midline and their right ear facing outward

(Taylor, 1976; Williams, 1926). Note the similarity to the right eye and ear of the chick embryo facing outward of the egg. Another important maternal asymmetry apparently relates to the placental site, most anterior placentas are located on the right side of the uterus and most posterior ones attached to the left (Hoogland & De Haan, 1980). Finally, asymmetric muscle contractions during labor appear to involve differentially active muscle fiber tracts of the left and right side of the uterus (Edmunds, 1954). The significance of this influence for fetal positioning remains unclear. However, Previc (1991) argues that given a leftward positioning during the final trimester, which prevails for about two-thirds of fetuses, and the many "natural" asymmetries that approximate a 2:1 ratio (typical human asymmetries such as handedness occur in a 2:1 ratio), it is conceivable that they emerge either directly or indirectly as the result of this influence during the final trimester.

Turkewitz (1988) suggests that (1) the human fetus is sensitive to its acoustic environment, (2) that there are systematic changes in the nature of this environment, (3) that there are differences in the rate of development of the two hemispheres, and (4) that the changes in the acoustic environment, developmental timing, and neurological structures interact to produce the hemispheric specialization that appears to characterize even very early stages of human development. For example, the right hemisphere is more developed than the left at a time when the fetal brain is exposed to various non-language sounds that are typically present in the prenatal environment (e.g., fetal heartbeat, mother's heartbeat, sounds of digestion, etc.). Turkewitz (1988) proposes that the more developmentally advanced right hemisphere has priority in dealing with classes of input for which there is not already an established hemispheric specialization. Thus, the more advanced right

hemisphere "learns" more from these prenatal noises than does the less advanced left hemisphere. This early experience is the foundation for later right-hemisphere dominance for processing a variety of non-language sounds.

Early appearing behavioral asymmetries are of importance within the present context because they are likely to have consequences for the subsequent development of other forms of behavioral functioning (see Hellige, 1995 for a discussion of the so-called "snowball effect.") In that early postnatal development tends to be a period of relatively rapid change, the timing of early asymmetries in relation to other developmental events can also shed light on the way in which temporal relationships between components developing at different rates can give rise to complex organizations and behaviors.

Taken together, the above suggests that the mammalian uterus and the avian egg share a common function in that they provide a highly structured environment for life to develop within. The theory presented here posits that hemispheric specialization is the result of probabilistic events in the developing organism's prenatal environment; in particular, the final stages of prenatal development appear critical. The environmental constraints of the prenatal environment exert a canalizing influence and structure on the development of hemispheric specialization that results in reliable postnatal perceptual and behavioral asymmetries.

1.2 Definitions and models of behavioral asymmetry, hemispheric specialization, and structural lateralization.

In any discussion of lateralization, it is necessary to make some clear distinctions in terminology. The field of hemispheric specialization has grown rapidly over that last 30 years and often the terminology has become blurred in meaning. To regularize commonly used terms, I make three principle distinctions in terminology. First, "behavioral asymmetry" refers to those perceptual and motor biases that are consistently of a left-right distinction. While such biases do suggest an underlying "structural lateralization," they do not necessarily represent a corresponding degree of isomorphism. For example, language is usually associated with the left hemisphere (Broca, 1865). However, significant components of language (such as prosody) are associated with the right hemisphere (Liberman, 1974). Indeed, given the complexity of behavior it would be prudent to recognize that even in simpler vertebrate brains, both hemispheres may participate to varying degrees in the production of complex behavior. Consequently, "hemispheric specialization" refers to any specific perceptual or motor function that is principally controlled (but not solely determined) by either the right or the left hemisphere. For example, right handedness and speech production in humans are specialized in the left hemisphere. "Structural lateralization" refers to those specific morphological differences that exist between an organism's left and right hemisphere. For example, lateralization of structure has been noted in the brains of cats, rabbits, and mice (Webster & Webster, 1975; Kolb, Sutherland, Nanneman, & Whishaw, 1982). Morphological lateralities have also been demonstrated in the rat (Diamond, Johnson, &

Ingham, 1975), in that male rat cortices are significantly thicker in several areas on the right side than on the left. Finally, "dominant" and "specialized" are used interchangeably to refer to the hemisphere most consistently responsible for a given behavior or pattern of behavior.

Given this terminology, the study of behavioral asymmetries typically involves a distinction between a left and right orientation in space. Gravity defines the vertical axis. Up and down, top and bottom are invariant contextual features of any terrestrial organism's environment. However, left and right, front and back are determined in relation to several contextually dependent factors: gravity's invariant vertical axis, an observed object with a potentially preferred orientation or direction of locomotion, and a relationship to an observer who also is asymmetrical. These factors must be kept in mind when constructing a research strategy that involves motor performance and perceptual biases in spatial orientation. As such, the left-right distinction is always determined from the organism's own perceptual and spatial orientation. With this terminology in mind, I will examine the conceptual framework and underlying principles that currently encompass and define most lateralization research.

a) Hellige's principles of lateralization

Hellige (1993) recently identified five principal themes in the study of behavioral asymmetries and structural lateralization that have consistently directed research with human and non-human species. His first principle states that hemispheric asymmetries exist and consequently influences behavior. Humans, for instance, have a number of cognitive (i.e., language) and behavioral asymmetries (i.e., handedness) which typically have been

attributed to structural brain lateralities. Virtually all higher vertebrates have two hemispheres that act synergistically to produce the perceptual and motoric abilities typically called behavior. Thus, Hellige's second principle states that, although hemispheric specialization is of critical significance to the functioning of the nervous system, the normal vertebrate brain ultimately functions most efficiently as an anatomical whole to produce unity of thought and action.

Hellige's third principle recognizes that other species besides humans have asymmetries of structure and function. Animal models thus provide an excellent opportunity to investigate the development of asymmetry. Indeed, there are many reliable behavioral and biological asymmetries in non-human species, as demonstrated in work with birds (Nottebohm, 1971; Rogers 1980a), rats (Denenberg & Yutzey, 1985), cetaceans (Mathews, 1978), and several non-human primates (Stamm, Rosen, & Gadotti, 1977; Warren, 1980). Hellige's fourth lateralization principle recognizes that individuals differ in direction, degree, and kind of asymmetry. Specifically, individuals differ from each other in patterns of hemispheric asymmetry (for instance, right or left hemisphere dominance for handedness in humans or pawedness in mice) and in the ways that the two hemispheres interact (for instance, in producing attack or copulation behaviors in domestic chicks). Hellige's fifth principle of lateralization states that asymmetry develops both across an organism's lifetime and across the evolution of a species. Hemispheric asymmetries are shaped by the complex interactions of many biological and environmental factors. As such, various models have been developed to account for lateralization in terms of how the hemispheres function together and how such structure-function relationships develop.

b) Models of hemispheric specialization

Models of hemispheric specialization fall into two broad categories: unilateral models and bilateral models (Allen, 1983). Beginning with Broca (1865), the construct of unilateral specialization has been the most frequently invoked theoretical mechanism in the laterality literature. In its extreme form, the principle states that only one hemisphere performs a given behavioral process. Unilateral specialization implies an "all-or-nothing" functional difference between the hemispheres. That is to say, one hemisphere can do the processing, the other cannot. By way of contrast, a "functional unilateralization" model states that both hemispheres are capable of performing the task, but for one reason or another only one hemisphere actually does. Unilateral specialization models have been advanced in a number of areas. For example, manipulo-spatial functions (Gazzaniga & LeDoux, 1978; LeDoux, Wilson, & Gazzaniga, 1977), motor functions (Geschwind, 1975; Kumura & Archibald, 1974; Nottebohm, 1979), language (Broca, 1865), and visuo-spatial skills (Moscovitch, 1973; Seamon, 1974) have all been asserted as being under the control of a specific hemisphere.

The second general category of hemispheric specialization models are "bilateral." Bilateral models assume that both hemispheres have the capacity to perform a given function. Bilateralization means that both hemispheres have an equal capacity (equipotentiality) for a given behavior or neurochemical process. There are 4 principle types of bilateral models: allocation, parallel, negative interaction, and cooperative interaction.

Allocation models assert that both hemispheres have a specific behavioral capacity, but in typical situations only one hemisphere does the

actually processing. These models are thus bilateral, but not interactive or parallel in nature. Allocation models are often invoked in studies of attention (Levy, 1974; Moscovitch, 1979). Accordingly, the properties of the information to be processed are critical. In an allocation model of attention, preliminary analysis of the stimulus properties are performed either at the frontal lobe or brain stem, and the result is then used to direct the incoming information to the "appropriate" hemisphere, presumably the one specialized for the behavioral task (Moscovitch & Klein, 1980).

In contrast to allocation models, parallel models argue that the two hemispheres are operating simultaneously, but independently of each other. Such parallel models may be characterized as bilateral but not interactive, thus distinguishing them from the cooperative interaction and negative interaction models. Parallel models have been classified into two primary subtypes: those in which the hemispheres are both performing exactly the same function and those in which the hemispheres are performing qualitatively different functions. A typical model of hemispheric parallelism is that of Dimond (Dimond, 1972; Dimond & Beaumont, 1974). Dimond argued that both hemispheres in the human brain are "differentiated," meaning that even though both hemispheres concurrently perform the processing for a complex behavior pattern, they are independently processing different aspects of it.

The two models that describe a functional transactionalism between the two hemispheres are: negative interaction and cooperative interaction. In negative interaction models both hemispheres have the capacity to perform a given function (bilateralization) but that, under typical circumstances they inhibit each other's activity, either through the corpus callosum and the

cerebral commissures, or the brain stem, or both (see Denenberg, 1981 for an extensive review of negative interaction models of hemispheric specialization in rats). Two main types of negative interaction models have been suggested. The first of these postulates unidirectional inhibition in which one hemisphere inhibits the other, but not vice versa. For example, Rogers (1980b) argued that attack and copulation behaviors in domestic chicks are normally activated by the right hemisphere, but inhibited by the left hemisphere. The second model postulates a bidirectional inhibition capacity for both hemispheres either mutually or reciprocally inhibiting each other. The best known example of a bidirectional, negative interaction model is Kinsbourne's (1970, 1974a, 1974b) model of attention and orientation. To summarize very briefly, Kinsbourne's model states that, with regard to attention and orientation in space, the two hemispheres mutually inhibit each other simultaneously. Human gaze behavior is a possible example of this (Kinsbourne, 1978).

Cooperative interaction is the second transactional model and asserts a positive interaction between the hemispheres. Cooperative interaction models argue that both hemispheres are involved in performing a certain behavior simultaneously, and that they interact positively (i.e., non-inhibitory). In this view, overall hemispheric activity is conceived of as an integrated, conjoined, even synergistic functioning of the two hemispheres. In cooperative interactionist models two specific modes of interaction are possible. The first is that both hemispheres are doing approximately the same processing and that the overall performance of the given task is simply their interaction. The second is that the two hemispheres are performing distinctly different and necessary subprocesses of the given task, with overall performance dependent

on dynamic coordination of the subprocesses. The net result in either case is that normal performance is impossible or severely impaired without ongoing, cooperative interaction. Typically, cooperative interaction models are structured such that one hemisphere contributes more than the other. Luria (1966, 1973) has been one of the most outspoken advocates of cooperative interactional models especially with regard to the higher cortical functions in humans. Luria (1973) suggests that cooperative interaction may be a defining feature of hemispheric processing and that most types of human psychological activity conform to this model. Although empirical support for many of the bilateral models is impressive, the cooperative interactional position has continued to gather support over the last two decades. It has been argued to be the most accurate and theoretically useful model of hemispheric specialization (Broadbent, 1974; Chiarello, 1980; Marshall, 1973, 1981; Rogers, 1991).

With regard to this study, a cooperative interactional model is assumed to underlie species-typical perception. Indeed, pilot data suggested that species-typical recognition of maternal auditory and visual cues in bobwhite quail chicks is likely based on a cooperative interactional process, in that both hemispheres appear to be involved in behavioral responding. Bobwhite quail chicks are known to demonstrate a preference for the bobwhite maternal assembly call and/or a model of the bobwhite hen paired with the maternal call (Lickliter & Virkar, 1989). This preference for species-typical auditory and visual cues is demonstrated by chicks localizing the source, orienting toward it, and then approaching the source of stimulation. However, when either eye is occluded chicks do not demonstrate a preference for species-typical auditory and visual cues. In pilot studies, chicks were tested

monocularly with a simultaneous choice between a bobwhite quail model hen paired with the bobwhite maternal call and a scaled quail model hen paired with a bobwhite maternal call. Subjects preferred both stimulus configurations equally (see Table 1). This finding suggests that both hemispheres play essential, but potentially different roles in species-typical perception and responding. Therefore, a cooperative interaction model best describes the functional relationship between the right and left hemispheres in mediating species-typical perception.

c) Direction and degree of lateralization

Discussions of hemispheric specialization inevitably raise questions concerning the direction and degree of lateralization. Behavioral asymmetries have been likened to mathematical vectors in that they both possess a direction (left-right, clockwise/counter-clockwise) as well as a degree (strong/weak, tightly spiraled/loosely spiraled, etc.) (Allen, 1983; Denenberg, 1981). The direction of lateralization is used almost uniformly in the literature to describe either a right or a left response distinction that occurs beyond a 50-50 random distribution. This convention has been used in this dissertation. There is less consensus in the literature about the concept of "degree of laterality." Laterality investigators have used the term "degree of laterality" in at least two different senses: (1) to imply a bilateralization of function with both hemispheres functionally distinct; and (2) to refer to a distribution of unilaterally or bilaterally organized individuals within a population. This study followed the conventions used by such researchers as Denenberg (1981), Rogers (1991), and Andrew (1991a, 1991b). Degree of lateralization refers to the extent to which an individual organism or population of organisms

responds in an asymmetrical manner across multiple observations. In this study, degree of lateralization implies some form of bilateralization, demonstrated as a percentage of left-right responses across multiple testing situations, that may vary within a population and/or between populations. In this study both direction and degree of lateralization are quantified as a "laterality index." This index is based on a mathematical formula derived and modified by Denenberg (1981). This procedure is further explicated in the General Methods section.

d) Individual and population lateralization

In discussions of lateralization, a distinction must be drawn between the level of the individual animal and the level of a population of animals. If the population is lateralized, it can be concluded with some certainty that a majority of individuals within that population are lateralized in the same direction. However, it should be noted that the opposite is not necessarily true. Individual organisms may be lateralized with regard to a particular behavioral function, but not necessarily all members of the species will be lateralized in the same direction or to the same degree. For example, individual mice are either strongly right- or left-handed, but there are approximately equal numbers of each in the various populations studied (Collins, 1977). However, too often lateralization research will investigate population lateralization without first establishing that individual lateralization does exist. This dissertation argues that any sound lateralization research should first establish that individual lateralization does in fact exist, and then proceed to examine any potential population level lateralization.

Denenberg (1981) proposes that evidence of lateralization at the population level means that evolutionary processes have been at work. In his view, selection pressures must have been at work for a particular hemisphere to become specialized in the same manner in more than half the brains of the population. However, even if individual animals are lateralized for some behaviors, and the overall population is not, this may or may not have evolutionary significance. For example, Collins (1977) failed to find a heritable basis for handedness in mice. By way of contrast, one aspect of the ontogenetic argument posits that organisms are symmetrical at birth and events in the environment act to bias individuals one way or the other. Collins (1985) has called this process an "asymmetry lottery" and has demonstrated it in his studies of pawedness in mice. A second possibility is that organisms become lateralized through the agency of prenatal experience, but this functional asymmetry may not be revealed until later postnatal behaviors are manifested (Rogers, 1991). Indeed, the role of ontogeny as a basis of evolutionary change has been discussed in some detail in recent years (Gottlieb, 1991a; Johnston & Gottlieb, 1990; Oyama, 1985). It is possible that lateralization of behavioral abilities across species and throughout evolution is principally based on the role of experience in development. The work of Lesley Rogers (1980b, 1986, 1991) on the development of attack and copulation behaviors in the domestic chick supports the position that species-typical prenatal experiences facilitate, if not induce, the specialization of both hemispheres for specific behaviors at the individual and population levels.

Population asymmetries may have significant consequences for social behavior and species survival. Rogers (1989) points out that if "lateralization of brain function has a role in social behavior, whether or not most (or even

all) individuals in the social group or lateralized in the same direction may be influential (p. 20)". Rogers and Workman (1989) demonstrated that in groups of chicks the presence or absence of lateralization at the population level can alter the stability of the chicks' social hierarchy. Groups of highly lateralized chicks formed more stable and rigid hierarchies (as measured in terms of their competition for access to a food source) than groups with individual lateralization but no population lateralization. Indeed, the group structure of randomly lateralized chicks (50% right hemisphere specialized, 50% left hemisphere specialized) was found to be more variable from day to day and individual to individual. Rogers and Workman (1989) attributed this to less predictability between individuals within the social group structure.

Like the domestic chicken, the bobwhite quail is a very social bird, with a complex social hierarchy (Stoddard, 1931; Stokes, 1967). Bobwhite quail form tight social groups called "coveys." If there is a specific turning bias at the population level, quail would have a tendency to always turn in the same direction. Therefore, if the covey is suddenly flushed from cover by the approach of a predator, flying off in the same direction would help prevent collisions and ensure group cohesion (Denenberg, personal communication). Indeed, behavioral asymmetry for turning and other spatial orientation abilities would allow for more reliable predictability among covey members and potentially stronger, more stable group cohesion.

Questions of development and evolution are intimately tied to discussions of population and individual asymmetries. We generally think of evolution occurring at the level of populations, however, a growing trend in developmental and comparative psychology over the last 20 years argues that a role for individual development must be found before a complete theory of

evolution can be achieved (see Gottlieb, 1992 for a general review of this position). Recent attempts to develop a coherent theory for the development of hemispheric specialization across a range of species have placed a pronounced emphasis on the role of ontogeny (Andrew, 1991b; Collins, 1977; Corballis & Morgan, 1978; Denenberg, 1981, 1988; Previc, 1991; Rogers, 1982; 1991; Turkewitz, 1988).

1.3 Lateralization of species-typical perception.

The relationship between perception and spatial orientation is a fundamental one. Perception and action are synergistically tied together such that to perceive is to act, and to act requires an organism to spatially orient with regard to the perceived stimuli. J. J. and Eleanor Gibson proposed a theory of perceptual development that identifies the organism (human or otherwise) as an "active perceiver" and as "the perceiver as performer" (Gibson and Rader, 1979). In the general sense, their theory posits that organisms are active perceivers, that perceptual information is specified in stimulation, and that ecology is a critical consideration in understanding an organism's perceptual abilities. As active perceivers, organisms dynamically explore, attend to and extract information, and differentiate objects in their environment. Thus, perception involves active attention to relational information.

For the Gibsons, attention refers to activities that gather information. Thus, perceptual development is somewhat synonymous with attentional development. These activities of attention include exploratory activities, such as human infants looking back and forth between two faces, turning the head to facilitate locating a sound, or orienting the body in space towards or away

from a particular stimulus. Comparative examples from non-human species are also evident. For example, many precocial avian species (mallard ducklings, Gottlieb, 1985; bobwhite quail, Heaton & Galleher 1981; Lickliter, 1989; and domestic chicks, Falt, 1981) respond to their species-specific maternal assembly call by localizing the source (typically, the hen), orienting towards that source, and finally approaching the source of the call.

As such, in the perception of any particular stimulus an organism must accomplish at least three related activities: (1) localize the stimulus in relation to itself and its environmental context; (2) categorize the stimulus; (3) and, approach or withdraw from the source of the stimulus (Schneirla, 1959, 1965). These activities have been demonstrated to involve differing degrees of hemispheric specialization (Bradshaw & Rogers, 1993). For example, the right hemisphere in human and some non-human primates is typically specialized for spatial abilities, while the left hemisphere is thought to be more specific for visual discrimination and categorization (Rogers, 1991). In birds, however, although the right eye-system (henceforth, termed the RES as it includes the left hemisphere of the brain and the corresponding right eye visual pathways, see Andrew, Mench, & Rainey, 1982) is thought to play a role in assigning stimuli to categories and in the choice of the response appropriate to a stimulus, recent evidence suggests that the left eye-system (henceforth, termed the LES as it includes the right hemisphere of the brain and the corresponding left eye visual pathways, see Andrew, Mench, & Rainey, 1982) is important for the recognition of conspecifics in the domestic chick (Vallortigara, 1992). Vallortigara suggested that neural structures fed by the left eye (mainly located in the right hemisphere) are better at processing

and/or storing of visual information, which allows recognition of individual conspecifics.

Such work suggests that perception involves the cooperative interaction between the right and left hemispheres. Each hemisphere may perform different functions, but the functioning of both is essential to species-typical behavior. Pilot data for this proposal suggests that this is the case with regard to bobwhite chick's responsiveness to bobwhite maternal cues. Bobwhite quail chicks are known to demonstrate a preference for the bobwhite maternal assembly call and/or a model of the bobwhite hen paired with the maternal call (Lickliter & Virkar, 1989). This preference for species-typical auditory and visual cues is demonstrated by chicks localizing the source, orienting toward it, and then approaching the source of stimulation. However, when either eye-system is occluded (thus reducing the sensory input and activity of the contra-lateral hemisphere) bobwhite quail chicks do not demonstrate a preference for species-typical auditory and visual cues. For example, in pilot testing, chicks were presented with a simultaneous choice test between a bobwhite quail model hen paired with the bobwhite maternal call and a scaled quail model hen paired with a bobwhite maternal call. Subjects preferred both stimulus configurations equally (see Table 1). This finding suggests that both hemispheres play important roles in species-typical perception and responding, in that occlusion of either eye-system appears to interfere with species-typical preferences. An underlying hemispheric specialization is implied and assumed. Therefore, it is hypothesized that the right hemisphere of bobwhite quail chicks is specialized for processing spatial information and the left hemisphere is specialized for the categorization of stimuli. It is further hypothesized that this particular

ordering of hemispheric specialization results from contextual constraints and perceptual experience occurring during prenatal development. This hypothesis is consistent with other behavioral studies of the domestic chicken (*Gallus gallus*) (see Rogers, 1991, and Bradshaw & Rogers, 1993 for recent reviews).

1.4 Hemispheric specialization for spatial abilities and turning biases in mammals and birds.

An organism's spatial orientation typically refers to any adjustments made by the organism in response to the spatial aspects of a particular context (French, 1951; Guilford, 1947; Thrustone, 1950). However, opinion has differed over the years about what should be included within the scope of this concept. Loeb (1918) viewed all of an organism's movements as responses directed toward external stimuli. From Loeb's perspective, animal behavior consists primarily of orienting motions. Schone (1984) defined orientation as the ability of an organism to position its body (or parts of its body) in a particular way with respect to stimuli or to relate their locomotion in some way to them. Fraenkel and Gunn (1940) include both stationary and locomotor response in their definition of orientation. Adler (1970) argued that "orientation is a selective process in which certain stimuli in the environment elicit a response sequence that results in a non-random pattern of locomotion, direction of the body axis, or both." As such, the concept of orientation includes not only those responses which guide the organism into a species-typical stance or position, but also responses which guide the animal into its normal habitat or into other situations which are of importance to it (for example, proximity to mother or to conspecifics).

With regard to underlying hemispheric specialization, Kosslyn (1987) has speculated that the impetus for right-hemispheric specialization of spatial abilities was the need for unilateral control over spatial attention. Like speech, spatial attention involves bilateral operations but often requires complex functioning, so that control is more likely coordinated in a single hemisphere. In humans, the right hemisphere is superior to the left for extracting visuo-spatial information (Corballis, 1989). In humans and other primates, there is a longstanding belief that the hemispheres are also asymmetrical in their ability to localize a visual stimulus in space (Corballis, 1982, 1991). The predominant view has been that the right hemisphere in primates and other mammals is superior for virtually all aspects of identifying spatial relations among objects (Corballis & Beale, 1983).

Spatial orientation biases, also known as rotatory bias or turning tendencies, are a form of motor asymmetry wherein the organism typically turns all or part of its body toward one side (left or right) in responding to stimuli. These biases have been examined in invertebrates (Chapple, 1977a, 1977b), rats (Denenberg, Garbanati, Sherman, Yutzey, & Kaplan, 1978), monkeys (Warren, 1958), and humans (Bradshaw & Bradshaw, 1988). The reason for the importance of spatial orientation biases is that they appear to be a phylogenetically old and pervasive lateral synergism with which many other asymmetries of interest may be coupled. This means that other lateralized nervous system activities may trigger turning (usually contralateral to the dominant hemisphere) and conversely, turning may facilitate other asymmetric activities. For example, bobwhite quail typically respond to the bobwhite maternal assembly call by orienting towards the

source and initiating approach behaviors (Lickliter, 1989; Stokes, 1967). Thus, perception of the stimulus is bound to the resultant approach behavior.

Starting as apparently random, non-functional rotatory asymmetries in invertebrates, spatial orientation biases can become coupled to progressively more elaborate structural lateralization in mammals. In rats, for example, their underlying neural mechanism is thought to be a complex network of pre- and post-synaptic asymmetries in dopamine and other neurotransmitter systems in the basal ganglia (Glick, Jerussi, & Zimmerberg, 1977). These asymmetries appear to be regulated by an inter-caudate pathway in the ventral callosum (Denenberg, Gall, Berrebi, & Yutzey, 1986). Behaviorally, they are thought to underlie spatial preferences and interact with paw preferences in influencing learning proficiency (Warren, 1958). In general, turning and/or spatial orientation has been empirically studied in a limited number of other species (see Figure 3). However, naturalistic observations have revealed a turning preference in some cetacean species. Dolphins demonstrate a marked directional swimming preference, leftward in confined aquariums and rightward in open sea (Ridgeway, 1986). In either case, the direction of turning is consistently biased within the population. Some species of baleen whales, although they appear to have no structural lateralization, show behavioral side preferences at a population level (Warren, 1980). From distributions of barnacle encrustation and direct observation, it has been suggested that some species of whales swim on their sides near the bottom of the ocean with their right side downward (Mathews, 1978).

In work with terrestrial mammals such as ungulates, Jarmon (1972) examined the harvested skins of impalas (*Aepyceros melampus*) shot in the Serengeti National Park. He reported the presence of significantly more scars

on the right side of the forequarters than the left. The asymmetry in distribution of the scars diverged significantly from a random distribution. This may indicate that there may be a preference for turning leftward into the attack or a preference for turning leftward away from it, possibly reflecting right hemisphere mediation of emotional responses during encounters with predators (Denenberg, 1981).

a) Asymmetries of spatial orientation in humans.

In humans, exploration is one characteristic of the more general phenomenon of spatial orientation and perception which is thought to have a right hemispheric specialization (Geschwind, 1985). A right hemisphere advantage in spatial analysis is generally accepted in humans, and has been shown to affect ability to orient by and recognize topographical features, as well as other tasks involving spatial relations (DeRenzi, 1982). Recent demonstrations of left visual field advantage in analysis of stimuli affected by optical blurring (Michimoto & Hellige, 1987), which are comparable with asymmetries at a relatively peripheral level, appear to be superimposed upon a right hemisphere advantage in higher level processing of visuo-spatial stimuli (Chiarello, Senehi, & Soulier, 1986).

Bradshaw and Bradshaw (1988) have argued for a potential analog between human rotational and turning tendencies and spatial orientation biases in rats. Left- and right-handed humans were tested in an experimental free-field observational study paradigm which had previously demonstrated rotation (turning) biases in rats. When required to rotate 360 degrees clockwise (rightwards) or counterclockwise (leftwards) with reduced sensory input, right-handed humans demonstrated a rightwards bias and left-handed

humans a leftwards bias. When attempting to walk blindfolded in a straight line, all subjects tended to deviate to the right. These lateral biases may relate to dopamine asymmetries in the basal ganglia (Bradshaw & Bradshaw, 1988). Such dopamine asymmetries have been demonstrated in other mammalian species (Bracha, Seitz, Otemaa, & Glick, 1987; Castellano, Diaz-Palarea, Rodriguez & Barroso, 1987; Glick & Shapiro, 1984, 1985; Robinson, Becker, & Camp, 1983), and are thought to underlie many observed spatial-motor biases (Zimmerberg, Glick, & Jerussi, 1974). It has been suggested that future research might address the common informal observation that passengers promenading around the decks of ships or ferries, or visitors to museums in large halls, tend to prefer a counterclockwise (i.e., leftwards) progression (Collins, 1985).

b) Asymmetries of spatial orientation in rats.

There are numerous examples of asymmetry in rats and mice (Yoshioka, 1928; Dashiell & Bayroll, 1931; see Figure 1). Some of these asymmetries are present in individuals, but without a consistent bias in the population (for example, preference of forelimb use in feeding, or "pawedness," and direction preference for turning or rotating, Denenberg, 1988). Other asymmetries occur in individuals and, because the majority of individuals show the same direction of asymmetry, there is also asymmetry in the population as a whole. Asymmetries present at the population level in rats have been described for a range of behaviors (i.e., maze running, exploratory behaviors, etc.) and for neurochemical and structural parameters as well (Corballis & Morgan, 1978; Morgan & Corballis, 1978; Denenberg, 1981). Denenberg (1977) has demonstrated that lateralized differences in spatial exploration abilities are exaggerated if animals are given handling stimulation in infancy. In

addition, lateralized behaviors can be found in handled animals which are not seen in non-handled controls, thereby leading to the conclusion that handling in infancy can induce laterality (Denenberg & Yutzey, 1985).

Apart from the need to document these asymmetries, perhaps the most notable finding to arise from the studies on rats and mice is that many forms of spatial asymmetry depend on prenatal and/or early postnatal experience and hormonal conditions. The studies of Denenberg and his co-workers (see Denenberg and Yutzey, 1985) have shown that early experiences can generate laterality in the brain or enhance laterality that is already present, and that the effect of early postnatal experience can be modified by the prenatal hormonal condition of the pups in utero. In the context of lateralization, the rat brain displays a remarkable degree of neural and behavioral plasticity (Denenberg, et al 1978; Sherman, Garbanati, Rosen, Yutzey, & Denenberg, 1980). In fact, studies using rats have shown that brain plasticity is not entirely lost in adulthood. Even adult rats show changes in the thickness of the cortex and changes in laterality in response to being raised either in enriched and or impoverished environments (Diamond, 1985).

With regard to motor behavior, it has been shown that the direction rats move off from a starting position in an open field is lateralized at the population level and influenced by handling (Sherman, Garbanati, Rosen, Yutzey, & Denenberg, 1980). Sherman has demonstrated that non-handled rats with only their left hemisphere intact show a preference to move off toward their right side. In contrast, non-handled rats with only the right hemisphere intact consistently demonstrated a preference to move off toward their left side. In either experimental condition, the rats moved off from their initial starting location toward the ablated hemisphere's side. Interestingly,

the directional preference of intact right hemisphere rats was more pronounced than that of rats with only the left hemisphere intact. Thus, there appears to be asymmetry for this motor behavior, with the right hemisphere having the more dominant influence. Hemispherically intact, non-handled rats demonstrate no directional preference, whereas intact handled rats showed a significant bias to move off toward the left. Population bias in rats appears as moving off toward the left, implying a dominant right hemisphere. Handling, therefore, appears to "unmask" dominance of the right hemisphere for this particular motor behavior. These data confirm earlier reports of the specialization of the right hemisphere (left eye system) for spatial performance (Denenberg, et al, 1978). Indeed, in this respect the development of asymmetry or lateralization in rodents is similar to that of birds. The direction and degree that lateralization takes in individuals and/or populations (rat or bird) appears to be determined by the interaction of genetic, environmental, and hormonal factors (Rogers, 1991).

c) Asymmetries of spatial orientation in birds.

Empirical research on spatial orientation abilities in birds has typically focused on visually guided behaviors. The left eye-system (right hemisphere) is more responsive to the spatial position of stimuli than is the right eye-system (left hemisphere). For example, habituation of pecking at an illuminated violet bead following repeated presentations of the bead to the left eye is dishabituated when the position of the stimulus is changed, but similar dishabituation does not occur when the position of the stimulus presented to the right eye is changed (Andrew, 1983). In similar tests using color discrimination as a cue for a food source, chicks demonstrated greater

evidence of learning when the color cue was placed on their right side than on the left (Vallortigara, 1989). This result may be consistent with right eye superiority (left hemisphere specialization) for categorization of non-topographical stimuli.

Left eye superiority for spatial orientation has also been demonstrated in a task requiring chicks to search for food using cues from large, relatively distant objects (Andrew, 1988; Rashid & Andrew, 1989). Binocularly trained, but monocularly tested, chicks were allowed to find food buried in sawdust in one corner of an arena. From day 9 of testing, chicks using their left eye showed a superior searching strategy. Specifically, left-eyed chicks appeared to use both the distant and proximal cues to specify the food source. Chicks using their right eye searched inefficiently over the entire arena. The left-eye system (and thus the right hemisphere) appears to be the one that attends to information about the spatial position of stimuli. Andrew (1988) suggests that the left-eye system (right hemisphere) is better suited to building up a description of the spatial organization of the environment because it examines the relationships between stimuli and encodes their unique characteristics rather than assigning them to categories, as the right-eye system (left hemisphere) apparently does.

Furthermore, Rashid and Andrew (1989) report a left eye (right hemisphere) advantage in orientation by topographical features in the young domestic chick. Decussation at the optic chiasma is virtually complete in birds, and it is likely that during independent scanning by the two eyes the input from the left eye is confined to structures of the right hemisphere and right brain stem (the "left-eye system" LES). Rashid and Andrew (1989) found that when chicks have to choose whether to orient by distant or proximal cues,

chicks using the left eye (and so the right hemisphere) orient more quickly and make more use of distant cues than do right-eyed (left hemisphere) chicks. They argue that when both eyes are in use, the left-eye system (right hemisphere) is mainly responsible for spatial orientation, whereas the right-eye system (left hemisphere) may concentrate on identifying and categorizing food.

1.5 Developmental processes and contextual constraints underlying hemispheric specialization in birds.

Rogers and Anson (1979) suggested that lateralized forebrain function in birds may result from asymmetric perceptual input during prenatal development. During most stages of embryonic development, with the latter stages being particularly important, the left eye is shielded by either the yolk sac or the left side of the body, while the right eye is exposed to light entering the egg. The left ear is also occluded, and thus, it too may receive relatively less auditory stimulation than the right ear. Rogers (1991) suggested that this lateralized auditory and visual input may determine the direction of lateralization in the forebrain, in part because light received by the right eye may speed development of the contralateral, left hemisphere. This initial bias conferred on the hemispheres may then be elaborated upon during subsequent postnatal experience (Denenberg, 1988).

a) Lateralization of avian brain structure

The avian brain has clear asymmetry or lateralization of function at several levels of neural organization (Benowitz, 1980) ranging from lateralized perceptual input (Andrew, 1991a) through processing of higher-

order information (Andrew, 1983) to lateralized control of motor output (Brooks & Stoney, 1971; Mench & Andrew, 1986). In addition, lateralization has been demonstrated for a range of visual functions (see Figure 2). For instance, Rogers and Anson (1979) found that in the domestic chicken (Gallus gallus) there is lateralized control by the forebrain hemispheres of a number of visually guided behaviors, including food search and pecking for food.

In many avian species the visual field is almost entirely monocular (Horn, 1985). Thus, most stimuli are initially perceived by only one eye, and the visual input is processed to a large extent by the side of the brain contralateral to that eye. Avian species which have been studied in any detail have been found to frequently use independent movements of the two eyes in order to scan the environment (Walls, 1942; Wallman & Pettigrew, 1985). As such, each eye typically examines different visual environments and stimuli even in the "binocular" field. In other words, each eye system acts as a relatively independent unit. Consequently, the presence of hemispheric specialization in birds may be important to prevent conflicting responses elicited by stimuli perceived by the left and right eyes (Bradshaw & Rogers, 1993). Conflicts between hemispheres may be avoided by one hemisphere taking a dominant role in the control of some behaviors.

Andrew (1988) reviewed the extensive literature regarding the development of visual lateralization in domestic chicks. He argues that the requirements of visual perception may have been a major impetus to the evolution of lateralization of brain function in some avian species. This may have occurred as a consequence of laterally placed eyes, which clearly predates the evolution of birds. However, avian species have highly developed visual abilities (Andrew, 1988), thus visual processing and lateralization may

have reached an advanced form achieved by developmental mechanisms somewhat different from those seen in mammals (Bradshaw & Rogers, 1993). More important to this study, birds are excellent subjects to test for lateralization of visual function because the optic nerves of the bird cross over almost completely in the optic chiasma (Cowan, Adamson, & Powell, 1961; Weidner, Reperant, Miceli, Haby, & Rio, 1985). By restricting visual input to one eye or the other, it is possible to relay visual information directly to the contralateral hemisphere of the brain (see Bradshaw & Rogers, 1993 for details). As such, lateralization of visual functions may be investigated by testing birds monocularly.

The avian brain also lacks the large corpus callosum found in the typical mammalian brain (Arnold & Bottjer, 1985). However, a number of small commissures are present in the avian brain (the pallial, anterior, posterior, and tectal commissures, Cuenod, 1974; Horn, 1985). Also, left-right connections of non-homologous brain regions occur via the supraoptic decussation. As such, information can be transferred from one side of the avian brain to the other, as interocular transfer of some tasks demonstrates (e.g., visual discrimination learning, Goodale & Graves, 1982; Gaston, 1984; Watanabe, 1986; Zappia & Rogers, 1987). Generally speaking, however, the avian brain has fewer significant neural pathways that connect the left and right hemispheres, particularly at higher levels of processing in the forebrain, than are found in mammalian brains (Benowitz, 1980).

Even though inter-hemispheric transactions occur in the avian brain (Watanabe, Hodos, & Bessette, 1984), relative to the more complex mammalian brain, avians appear to have much less left-right information transfer (Bradshaw & Rogers, 1993). As such, large amounts of information are

processed unilaterally or uni-hemispherically (i.e., in the hemisphere contralateral to the open eye in monocularly tested birds). This may limit the kinds of functions that can be lateralized, but such lateralization could potentially prevent hemispheric competition and eliminate redundancy of neural capacity.

b) Invariant developmental position of the embryo.

It is fairly well established that the avian brain is structurally and functionally lateralized (Bradshaw & Rogers, 1993). The processes whereby the avian brain becomes lateralized have also been investigated. Some arguments have been made that avian and mammalian brain lateralization results from coded instructions in the genome (Gazzangia & LeDoux, 1978; Levy, 1974; Warren, 1977). However, Morgan (1977) and Collins (1977) have provided evidence that genes may play little or no significant role in determining the direction and degree of lateralization. For example, the direction of structural lateralization in the visual system of the domestic chicken brain is facilitated by light exposure of the embryo prior to hatching (Freeman & Vince, 1974; Sedlacek, 1972; Thanos & Bonhoeffer, 1987). This result appears due to the invariant posture of the embryo in the egg. During the last several days before hatching, the embryo is oriented in the egg with its left eye and ear occluded by the yolk sac and the embryo's body, while the right eye and ear remain exposed to light entering the egg via the shell and membranes of the air space (Rogers, 1986). This posture of the body occurs at the stage in incubation at which the central visual connections in the forebrain are becoming functional and when light stimulation can evoke motor responses in the embryo (Freeman & Vince, 1974). The eye itself opens

and closes during this period; yet, even when closed it is covered by transparent eye-lids which allow light to pass through them (Gottlieb, 1968).

Interestingly, chickens hatched from eggs incubated in darkness during the last 3 days of incubation do not show functional lateralization at the population level (Zappia & Rogers, 1983, 1987). Rather, each individual chick hatched from an egg incubated in darkness retains lateralization of brain function, but half of the chicks so incubated have the lateralization in one direction and half in the other. As such, it appears that light exposure synchronizes or aligns the direction of lateralization so that all individuals are lateralized in the same direction. It has been suggested that prenatal light exposure of the right eye may enhance the development of visual projections from that eye, increase blood flow to the contralateral hemisphere (Bondy & Morelos, 1971) and thereby stimulate a number of developmental processes in that hemisphere. In so doing it may advance the development of the left hemisphere relative to the right, as has been demonstrated by unilateral treatment of the hemispheres with the drug cycloheximide (Rogers, 1991).

While domestic chickens hatched from eggs incubated in a lighted incubator show lateralization for attack and copulation behavior (Howard, Rogers, & Boura, 1980), recent experiments have shown these behaviors are not lateralized at the population level in chicks hatched from eggs incubated in darkness, even though there still appears to be lateralization for these behaviors at the level of the individual (Rogers, 1991). The embryo must receive light input (48 hr is usually sufficient) just before it pips the eggshell if the direction of lateralization for attack and copulation is to be synchronized in the population (Rogers & Workman, 1989). While genetic factors may play a role in determining synchrony of lateralization in chicks, in that they may

act to determine orientation of the embryo in the egg, they do not appear to act at the level of the brain itself (Geschwind & Galaburda, 1984). While the brains of individuals may have to be lateralized for these behaviors, the left-right directionality for this may simply be a by-product of body orientation during development. Thus, a consistent developmental constraint (i.e., the invariant position of the embryo in the egg, particularly during the last 96 hr of incubation) may underlie asymmetry at the population level.

As previously discussed, the left and right hemispheres of the domestic chick are thought to control different behavioral functions, the right hemisphere for analyzing the position of stimuli in space and the left hemisphere for categorizing stimuli (Andrew, 1991b). It can be argued that both spatial relations and unique intrinsic properties are a special concern of the LES (Horn, 1990). A system specialized in this way has a variety of potential uses, including topographical learning and estimation of degree of novelty. Rapid estimation of novelty is a critical skill if an animal is to decide quickly what to avoid and what to approach (Sanberg, Faulks, Anson, & Mark, 1982; Schneirla, 1965). Taken together, the foregoing presents a basic argument for using precocial bird species' (in this case the bobwhite quail) to investigate the development of lateralization.

1.6 The Hypotheses

Pilot data suggests that bobwhite quail demonstrate a spatial turning bias. Specifically, when chicks were tested to simultaneous presentations of two pairings of the BW call/BW hen model (at opposite ends of the T-maze), 70% of chicks demonstrated a strong left turning bias (see Table 2). Taken

together with the empirical and theoretical material previously reviewed, pilot data suggested the following hypotheses:

a. Hypothesis #1: Based on pilot data, it is hypothesized that bobwhite quail chicks will demonstrate a left side turning bias when responding to species-specific maternal auditory and visual cues.

-Experiment 1 will test the above hypothesis. Experiment 1 will determine if there is indeed a specific turning bias in bobwhite quail chicks.

b. Hypothesis #2: Previous research suggests that hemispheric specialization in the avian brain is facilitated by the invariant position of the developing embryo and the resulting differential amounts of visual stimulation that the left hemisphere receives (Rogers, 1991). However, it has also been demonstrated that chicks incubated in complete darkness may develop specialization in either hemisphere (Zappia & Rogers, 1983). Therefore, it is hypothesized that there exists a hemispheric "equipotentiality" for specialization of a given behavior. Specifically, each hemisphere should be capable of becoming specialized for the same behavior. This phenomenon is usually referred to as "functional plasticity" or the "equipotentiality of the hemispheres" (Hellige, 1993). If this is indeed the case, then exposure of the left eye system to prenatal light stimulation, while occluding the right eye system (a species-atypical pattern), should shift the species-typical left side turning bias to a right side turning bias.

-Experiment 2 will test the hypothesis that there exists an equipotentiality for both hemispheres to become specialized for a turning bias (presumably demonstrated in Experiment 1). Further, it will test the

hypothesis that the invariant developmental position of the embryo and the consequent differential hemispheric sensory experience facilitates the direction of the turning bias.

c. Hypothesis #3: If a turning bias is present from hatching, it is hypothesized that this postnatal behavioral asymmetry results from prenatal sensory experience (potentially demonstrated by Experiment 2). However, several potential influences are present in the prenatal environment, including auditory and visual sensory experience. If behavioral asymmetries are affected by prenatal sensory experience, then the type of stimulation (visual or auditory) may be differentially effective in facilitating the development of a left-right lateralization (Corballis & Morgan, 1978; Zappia & Rogers, 1983).

-Experiment 3 will test the hypothesis that specific type of sensory stimulation may be an important facilitating influence on the development of hemispheric specialization.

d. Hypothesis #4: If prenatal visual experience is the critical factor in the development of hemispheric specialization, then it is important to determine the role of overall amount of visual stimulation necessary to be effective. Differential prenatal visual stimulation has been shown to facilitate the development of a left-right lateralization gradient in domestic chicks (Rogers, 1991). Therefore, it is hypothesized that enhanced amounts of visual stimulation will result in higher degrees of laterality at both the individual and population levels when compared to controls. It is also hypothesized that

attenuated visual stimulation (i.e., incubation in darkness until hatch) will result in random population level lateralization.

-Experiment 4 will test the hypothesis that overall amount of prenatal visual stimulation is a critical factor in facilitating high levels of individual and population lateralization.

e. Hypothesis #5: Based on what is known about the structure of the avian brain it is hypothesized that the chicks' right hemisphere will be specialized for this behavior. If there is a right turning bias, it is hypothesized that the left hemisphere is specialized for this behavior. If there is no population bias for turning, than neither hemisphere should be specialized.

-Following from this, Experiment 5 will test whether the turning bias is associated with a morphological component of unilateral hemispheric specialization.

2.0 General Methods

2.1 Subjects

Maternally naive, incubator-reared bobwhite quail chicks (*Colinus virginianus*) served as subjects. Fertile, unincubated eggs were received weekly from a commercial supplier and set in a Petersime Model I incubator, maintained at 37.5° C and 80-85% humidity. After 20 days of incubation, the eggs were transferred to a hatching tray located in the bottom of the incubator. Only those birds that hatched between the second half of day 22

and the first half of day 23 of incubation were used as subjects (by convention, Day 23 of incubation begins at 23 day, 0 hr and ends at 23 day, 23 hr). This constraint controlled for the possible effects of variations in developmental age. The possible influence of between-hatch variation in behavior was controlled, by drawing subjects for each experiment from at least three different batches of eggs. Specific manipulations and changes to this procedure are detailed in each experiments methods section.

Following hatching, each chick was labeled with a small numbered, colored dot, which was adhered to the top of chick's head. Chicks were then placed in large plastic tubs (45x25x15 cm) which contained 12-18 same-aged chicks. This group size was chosen to mimic naturally occurring brood conditions (Stokes, 1967). The room in which the hatchlings were kept was illuminated by a 100-W brooder lamp suspended above the plastic rearing tubs. This arrangement maintained an ambient temperature of approximately 30° C. Food and water were continuously available throughout the course of the experiments.

Sex differences

Although sex differences in some behavioral asymmetries have been demonstrated in the domestic chick (Andrew & Brennan, 1983; Vallortigara, 1989; Zappia & Rogers, 1987), potential sex differences in responding to species-specific maternal cues are unlikely. Bobwhite quail chick responding to the maternal assembly call is highly consistent and reliable across groups of chicks (Heaton, Miller, & Goodwin, 1978; Lickliter & Virkar, 1989), therefore no differences in responding are likely due to gender. Additionally, Rogers

(1989) points out that there are no sex differences in the effect of unilateral injection of the chick forebrain with glutamate or cycloheximide (see Experiment 5). Unilateral treatment by injection of either the right or left forebrain reveals the same lateralization for visual discrimination learning in both males and females (Rogers, 1986).

2.2 Testing Apparatus and Stimuli

Apparatus

The testing apparatus consisted of a large T-maze (30 cm high x 7 cm wide) painted flat black (see Figure 4). The stem was 65 cm and the arms were 80 cm each (160 cm from end to end). The walls were 30 cm high and 8 cm apart. The maze was located in a sound-attenuated room and within a larger 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. A mid-range dome radiator speaker was positioned behind the curtain at each end of the T-maze crossway and directly opposite each other. The speakers were equidistant from the point at which each subject was placed in the apparatus and at opposite ends of the T-maze crossway. These speakers allowed for the simultaneous presentation of maternal auditory cues during the test trial. Each speaker was connected to a Tascam model 122-B cassette tape recorder located at a control table. The observer sat at this table and observed each subject's activity (recording the chicks latency to approach and turning direction) through a large mirror positioned above the arena. The visual stimuli (bobwhite quail hen models) was located immediately in front of the

speakers. The testing room was maintained at approximately 26° C throughout the study.

Stimuli

A combination of species-typical auditory and visual maternal cues were used throughout the following experiments. The auditory stimuli used in this study were two identical recordings of a bobwhite quail maternal call (see Heaton, Miller, & Goodwin, 1978 for acoustical details). The auditory stimulus tapes were looped to repeat continuously during the test trial. The sound level was calibrated with a General Radio Model 1933 sound level meter to a peak amplitude of 65 dB, measured at the cross point of the T-maze. This ensured that subject responding was not due to differential sound levels of either speaker. Two taxidermically prepared natural models of bobwhite quail hens served as the visual stimuli in the simultaneous choice test. Previous pilot work has demonstrated that the two bobwhite hens are visually equivalent, in that neither hen evokes differential responding from bobwhite chicks during the days following hatching. That is, chicks do not prefer one hen over the other in simultaneous choice tests (see Lickliter, 1990; Lickliter & Virkar, 1989; McBride & Lickliter, 1993 for examples of this testing procedure). To avoid any potential confounds due to non-obvious differences in stimulus combinations, hen model and tape pairings were rotated between testing times across individuals. Thus, since there were 8 testing sessions and 4 possible combinations of auditory and visual stimuli pairings, chicks were exposed to each combination twice.

2.3 Procedure and measures

Testing procedure

Subjects were individually placed in the stem of the T-maze. A lab assistant simultaneously began the two tapes of the bobwhite maternal assembly call. A stop watch was used to record the time it took the chick to reach either the left or the right approach area containing the bobwhite hen models. A lab assistant recorded the time of approach (i.e., latency score) and noted the side first approached (i.e., turning side bias) on a special data sheet (see Appendix A). The trial was terminated when the chick reached the end of a T-maze arm or at 3 min (180 sec), whichever occurred first. Chicks that did not complete the maze were removed from consideration.

Each chick was tested at 24, 30, 48, 54, 72, 78, 96, and 102 hr following hatch. These times allowed for two testing trials per day over the course of the first four days following hatching. Multiple testing times were necessary to establish the presence or absence of individual lateralization. This testing pattern is typical of lateralization research in rats (Denenberg, 1988), chicks (Bradshaw & Rogers, 1993), monkeys (Warren, 1977), and other avian and mammalian species (see Glick, 1985 for extensive reviews). The particular times of testing were essentially arbitrary (although they allowed at least two test per day for the first 4 days following hatching). The possible occurrence of a temporally-based shift in population bias was evaluated with a repeated measure ANOVA procedure. Specifically, the number of left turns made at each of the 8 testing times were compared in Experiments 1. Differences between number of left turns made at each of the 8 testing times were found to be not significant ($F > 1$). The occurrence of temporally based shifts in

lateralization is a questionable idea (Colbourn, 1977). It is certainly confounded by the problems inherent in the idea of "degree" of lateralization. Any observed shift in behavioral responding across time may be the result of factors unrelated to a supposed shift in hemispheric specialization. Because of these problems the temporal measure was discarded from this study.

Repeated testing of individuals might introduce confounds into the experimental design. In this proposal, the possibility existed that lateralization might result from post-natal experience in the T-maze (i.e., as a learned preference). However, previous studies have found limited support for this position. For example, Collins (1975) found that rearing left-pawed mice in a spatially biased right-sided environment resulted in a slight shift in paw preference from left to right. However, Collins findings could be attributed to asymmetrical reinforcement that was inherent in the testing and/or rearing context employed. In the present study, the chicks were not given any obvious, or consistent asymmetrical reinforcement. Left and right turning chicks were removed from the T-maze under the same conditions and in the same manner. Additionally, subjects were tested in alternating entry positions into the T-maze. This meant that the orientation of the T-maze within the testing arena was alternated between testing sessions (see Figure 4). On the first testing trial, the T-maze stem (starting position) faced away from the observer (facing the top of the testing arena, see Figure 4 "A"). During the second testing session, the T-maze stem faced toward the observer (see Figure 4 "B"). This pattern of alternating entry positions was used throughout the 8 testing trials. Thus, chicks were tested 4 times in starting position "A" and 4 times in starting position "B". This should have reduced any potential confounds due to spatially based testing environment cues. Additionally, pilot

testing revealed that chicks turning bias was maintained in both T-maze configurations. Finally, chicks were reared in a relatively symmetrical, "un-enriched" (although not socially impoverished) environment (i.e., rectangular plastic rearing tubs) to prevent any rearing-testing situational confounds.

Behavioral measures

The measures of primary interest in the original proposal were the direction and degree of individual turning biases and overall population biases in turning response. Individual turning bias indexes were derived using a formula developed by Denenberg (1981, see also Catellano, Diaz-Palarea, Rodriguez, & Barroso, 1987; and Corballis, 1991 for a similar "laterality quotient" in human handedness, pp. 82-83). In essence, the formula produces a quantitative index for the direction and degree of side preference or turning bias: $(R-L) / \text{SQR}(R + L)$. The numerator is the number of right side responses (by an individual chick at each of the eight trials) minus the number of left side responses. The denominator is the square root of the total number of responses made by that chick (i.e., 8). A positive score indicates a right-side bias, a negative score reflects a left bias, with zero indicating no lateral bias.

Laterality indices in this study can be quantified as follows:

$$(+/-) 2.83 = 100\%-0\%$$

$$(+/-) 2.14 = 90\%-10\%$$

$$(+/-) 1.41 = 75\%-25\%$$

$$(+/-) 0.71 = 60\%-40\%$$

$$0 = 50\%-50\%$$

Population level turning bias was evaluated by summing the total number of right and left turns made by each subject and using a matched sample t-test for correlated measures for statistical analysis.

Latency scores

In the proposal for this study, latency scores were to be examined. Subsequent analysis revealed no significant differences in latency scores across experimental groups. Indeed, there was a very high consistency across all experimental groups and subjects in the average latency scores. The average individual latency score for all experimental conditions was 21.4 seconds.

2.4 Data analysis

The data of primary interest are: (1) the individual chick's laterality index (direction and degree), and (2) the overall population bias. The procedures for determining individual laterality indices and population lateral biases are detailed above. A one-way ANOVA was used to evaluate differences in degree of individual laterality indexes across experimental conditions. As the ANOVA tested variability in "degree" of lateralization as opposed to "direction," absolute values for laterality indexes were used. A matched-paired t-test was used to determine population differences. The total number of individual right turns were compared with total number of left turns. Significance levels of $p < .05$ were used to evaluate the data.

Issues to be determined by data analysis:

1. Direction of Lateralization: Laterality indexes were used to determine the existence and overall direction of individual turning bias across experimental conditions. T-tests were used to examine population level differences in direction of lateralization.
2. Degree of Lateralization: A one-way ANOVA was used to examine the variability of degree of lateralization. Specifically, variability in subjects' individual degree of laterality across experimental groups was examined.
3. As the data became available, it became clear that differences in left-side population bias percentages across experimental groups was, in some instances, of significant interest. Such differences were examined with a z-score.

2.5 Experiment 1: Assessment of Turning Bias in Naive Chicks (Control Group)

Turning biases in spatial orientation have been demonstrated in a variety of species, including rats, mice, and birds (Denenberg, 1981; Rogers, 1991). Additionally, side biases in a T-maze have been demonstrated in rats (Zimmerberg, Glick, Jerussi, 1974; Castellano, Diaz-Palarea, Rodriguez, & Barroso, 1987; Diaz-Palarea, Gonzalez, & Rodriguez, 1987). However, such turning biases have not been examined in any avian species, even though birds appear to be as lateralized, if not more so, than many mammalian species. This experiment will examine whether bobwhite quail chicks demonstrate a

side bias in orienting to maternal auditory and visual cues during the first few days following hatching. Since each side of the T-maze presented the subjects with identical auditory/visual stimuli, subjects were not expected to show a preference for one side or the other based on the combined maternal cues presented during testing. Therefore, it could be concluded that any turning bias was the result of some organismic variable rather than some aspect of the testing situation.

Method

Twenty bobwhite quail chicks drawn from three separate hatches were tested in a T-maze at 24, 30, 48, 54, 72, 78, 96, and 102 hr following hatch. Chicks were exposed to a simultaneous choice test between a left and right pairing of the bobwhite maternal assembly call paired with a model of the bobwhite hen (see General Methods section for details).

Results

Naive bobwhite quail chicks were found to demonstrate individual and population level turning biases. Eighty-five percent of subjects demonstrated a left-side bias, 10% of subjects a right-side bias, and 5% were found to be unbiased (see Table 3). Chicks demonstrated a population level left-side turning bias, $t(19) = -6.19, p < .001$, (Mean left turns = 5.9, SD = 1.37; Mean right turns = 2.1, SD = 1.95). Thus, bobwhite quail chicks demonstrate a clear individual and population level bias for left turning in a T-maze when responding to species-typical maternal auditory and visual cues. The average individual latency score was 22.36 sec.

Discussion

Although turning biases have not been investigated in other terrestrial avian species, the motor bias observed in this experiment may serve several purposes, both for the individual and for the population. At the population level, a high degree of lateralization would help promote social cohesion. For example, when quail are flushed from the bush by a predator having a population bias that would initially synchronize the direction of escape would prevent many birds from flying into each other. Thus, turning biases might facilitate escape from predation. At the individual level, strongly lateralized chicks are more predictable chicks. This may impact their standing within the covey.

Regardless of what purpose a turning bias may serve at the individual and population levels, the development of such a bias must be explained. As the bias appears to be present from hatch, it seems prudent to begin the search for turning bias origins during the prenatal period. Postnatal behavioral asymmetries in the domestic chicks have been traced to prenatal sensory experience (Rogers, 1989). Most instances of avian lateralization have been demonstrated at the individual and population level. Additionally, behavioral asymmetries have been correlated with lateralized differences in structure and function, and neurochemical levels (see Hambley and Rogers, 1979; McCabe et al, 1988; Stewart, 1991). Experiments 2, 3, and 4 investigated the role of prenatal sensory and motor experience. Experiment 5 presents pilot data as to a possible underlying structural lateralization.

2.6 Experiment 2: Equipotentiality of Hemispheric Specialization: The Differential Effects of Prenatal Visual Stimulation on Left and Right Hemispheric Specialization and the Reversal of Function.

Experiment 1 demonstrated a turning bias in unmanipulated bobwhite quails' responsiveness to species-specific auditory and visual maternal cues. This experiment examined the possibility that either hemisphere has the potential to become specialized for control of spatial orientation abilities (as manifested in a turning bias).

When lateralization is present in an individual organism, it may be essential for efficient brain functioning to have one hemisphere given over to a collection of related behaviors (for example, communicative behaviors, or complex discrimination-learning performance) while the other hemisphere is involved with another set of functions (for example, spatial and emotional functions). However, whether each set of functions is specifically carried out by the left or by the right hemisphere may be irrelevant. Alternatively, a consistent direction of hemispheric specialization within a population may be conferred as a by-product of some other, seemingly unrelated, aspect of development or prenatal environmental influences (Corballis & Morgan, 1978; Hellige, 1993). For example, the invariant developmental position of the embryo in the egg during the last days of incubation results in differential visual experience to the left hemisphere. These differential experiences have been demonstrated to have a significant influence on the lateralization of a variety of affective and cognitive abilities (Rogers, 1990). As the last stages of incubation and hatching are characterized by the functional onset of visual abilities, it is during this period that the canalizing influence of sensory

experience may induce a population bias (Rogers & Workman, 1989). This experiment assessed whether the two hemispheres are essentially equal in their potential for becoming functionally specialized for a turning bias.

Specifically, this experiment tested whether prenatal visual stimulation to the RES (right eye-system) or LES (left eye-system) would facilitate the development of a left or right hemisphere dominance for spatial orientation/turning bias at the population level in bobwhite quail. Rogers and Sink (1988) demonstrated that lateralized visual experience plays a decisive role in determining the direction of brain lateralization at the population level for two behavioral functions in the domestic chick: copulation and visual discrimination. Rogers (1990) demonstrated that either hemisphere could be specialized for these behaviors, depending on the amount of visual stimulation each hemisphere received. Because the chick's left eye-system is typically occluded by the embryo's body and yolk sac, the right eye-system (and consequently the left hemisphere) receives a greater amount of visual experience during prenatal development. This "edge" in developmental timing apparently contributes to the population biases observed by Rogers (1990) in domestic chicks. This experiment examined this phenomenon with regard to the visuo-spatial abilities of bobwhite chicks.

Methods

One hundred bobwhite quail embryos, drawn from 3 separate hatches, served as subjects. During the second half of the 21st day of incubation (21 day, 1200-1600 hr), the shell and inner-shell membrane over the air space of the egg of each subject was removed and the embryo's head gently pulled out of the shell. The embryo's bill typically penetrates the air space early on day

21. The embryo begins to respire and vocalize following penetration into the air space (Vince, 1972). Consequently, exposing the embryo's head at this time (the embryo's body remains in the shell) does not interfere with the final stages of incubation (Heaton & Galleher, 1981; Lickliter, 1990). The procedure produces little or no bleeding and requires about 1 min per egg.

Right and left eye-systems were occluded with water-resistant white surgical tape. A piece of tape 1.5 cm by 1.5 cm was cut .75 cm down the middle. The tape was folded over to form a cone shaped patch. This patch was applied over the eye, thus preventing visual stimulation to the contralateral hemisphere. Following removal of part of the shell and eye occlusion, opened eggs were placed in a Hovi-bator portable incubator for the last 36 hr of incubation. This incubator was outfitted with a clear Plexiglass top, allowing both observation and stimulation of the embryos. Consistent temperature and humidity levels were maintained as during control incubation, therefore experimental embryos and control embryos should not have differed in their developmental age at hatch.

Group 1 consisted of 20 subjects that had both eye-systems (RES and LES) exposed to enhanced visual stimulation. Group 2 consisted of 20 subjects that had their right eye-system (RES) patched and their left eye-system (LES) given enhanced visual stimulation. Group 3 consisted of 20 subjects with their left eye-system (LES) patched and their right eye-system (RES) given enhanced visual stimulation. Group 4 consisted of 20 subjects with both eye-systems occluded. It has been suggested that light stimulation may affect hemispheric specialization by extra-retinal means. thus, chicks in group 4 served as a control group. Group 5 consisted of 20 subjects that had the top of

their eggs removed, their heads "uncorked" from the egg, but not given any enhanced sensory experience.

A light source was located immediately above (4 cm) the incubator's Plexiglass top (see Zappia & Rogers, 1983 and Lickliter, 1990 for similar procedures). Particular care was taken to insure that the presence of the light did not alter the ambient air temperature or relative humidity within the incubator. Embryos were exposed to the light of a 60-watt bulb for 10 min every hour for 36 hr prior to hatching. Thirty-six hours was chosen as the time period for prenatal stimulation because it is during this time that the embryo enters the air space of the egg and begins to breath (Freeman & Vince, 1974). Additionally, by 78 hr prior to hatching the embryo is oriented in the egg such that its left eye is occluded by its body and the right eye is exposed to receive light input entering the egg through the shell and membranes (Hendrickx & Hanzlik, 1965). Following hatching, chicks were placed in plastic rearing tubs with same aged conspecifics to mimic naturalistic brooding conditions.

Chicks were tested at 24, 30, 48, 54, 72, 78, 96, and 102 hr following hatch in a simultaneous choice test between two pairings of the bobwhite maternal call and a stuffed bobwhite hen one on the left and right sides of the T-maze (see General Methods sections for details).

Results

Group 1

Recall that unmanipulated bobwhite chicks were found to demonstrate individual and population level left-side biases (Experiment 1). Chicks in Group 1 of this experiment had their heads removed from the egg and both

eye-systems (RES and LES) exposed to enhanced visual stimulation. Thirty-five percent of subjects demonstrated a left-side turning bias, 45% a right-side bias, and 20% of subjects were found to be unbiased (see Table 4). The observed population bias was not significant, $t(19) = .64$, $p < .264$, (Mean left turns = 3.75, SD = 1.64; Mean right turns = 4.25, SD = 1.85). Therefore, while bobwhite quail chicks in this group demonstrated individual biases, no significant population bias was evident. Opening the top of the egg, removing the chicks head, and exposing both eye-systems to enhanced prenatal visual stimulation eliminated the left-side population bias.

Group 2

Chicks in Group 2 had their heads removed from the egg, their right eye-systems (RES) occluded, and their left eye-systems (LES) exposed to enhanced visual stimulation. Thirty percent of subjects demonstrated a left-side bias, 55% a right-side bias, and 15% were unbiased (see Table 4). The population bias was significant, $t(19) = 2.16$, $p < .05$, (Mean left turns = 3.05, SD = 1.84; Mean right turns = 4.85, SD = 1.42). Opening the top of the egg, removing the chick's head, and exposing only the left eye-system (right hemisphere) to enhanced prenatal visual stimulation eliminated the left-side population bias found in Experiment 1, while facilitating the development of a right-side population bias. It would seem that limiting prenatal visual stimulation to the right hemisphere, through the left eye-system, reverses the left-side population bias found in unmanipulated populations (see Experiment 1).

Furthermore, providing unilateral prenatal visual stimulation apparently facilitates a population bias that is not evident when providing both hemispheres with stimulation. This finding lends support to the

hypothesis that either hemisphere may become specialized for a turning bias. When prenatal visual experience is provided to the right hemisphere (which is typically not possible in unmanipulated chicks) a right-side turning bias is established. It also suggests that establishing a population bias requires unilateral visual experience. When both eye-systems were stimulated in Group 1, no population level bias was observed.

Group 3

Chicks in Group 3 had their heads removed from the egg, their left eye-systems (LES) occluded, and were exposed to enhanced visual stimulation. Fifty-six percent of subjects demonstrated a left-side turning bias, 31% a right-side bias, and 13% were unbiased (see Table 4). The population bias was significant, $t(19) = -2.52, p < .01$, (Mean left turns = 5, SD = 1.78; Mean right turns = 3, SD = 1.05). Opening the top of the egg, removing the chick's head, and exposing the right eye-system (RES) to enhanced prenatal visual stimulation facilitated a significant level of left-side population bias. However, the overall left-side population bias was significantly reduced from those found in unmanipulated populations, $z = -3.63, p < .05$. When compared to other manipulations of this experiment, this configuration of stimuli presented to this group was closer to species-typical conditions, except that the embryo's head was removed from the top of the egg. As expected, a left-side population bias was established. However, as with the previous two groups the overall population bias was significantly reduced from unmanipulated populations. This suggests that some other factor besides prenatal sensory stimulation has a significant influence on the development of spatial turning bias.

Group 4

Chicks in Group 4 had their heads removed from the egg, both eye-systems (LES and RES) occluded, and were exposed to enhanced visual stimulation. Fifty-five percent of subjects demonstrated a left-side turning bias, 35% a right-side bias, and 10% were unbiased (see Table 4). The population bias was not significant, $t(19) = -1, p < .16$, (Mean left turns = 4.5, SD = 2.24; Mean right turns = 3.5, SD = 1.75). Opening the top of the egg, occluding both eye-systems, and exposing subjects to enhanced prenatal visual stimulation did not facilitate a significant level of left-side population bias. Clearly, some amount of visual experience is necessary for the development of a population level turning bias. However, it does not appear that any potential extra-retinal visual experience had a significant effect on the development of turning bias. In any case, overall left-side bias was significantly reduced from those found in unmanipulated populations, $z = -3.75, p < .05$.

Group 5

Chicks in Group 5 had their heads removed from the egg, but were not exposed to enhanced visual stimulation. Fifty-five percent of subjects demonstrated a left-side turning bias, 25% a right-side bias, and 20% were unbiased (see Table 4). The population bias was significant, $t(19) = -2.09, p < .05$, (Mean left turns = 4.8, SD = 1.70; Mean right turns = 3.2, SD = 1.75). Opening the top of the egg, and removing the chicks head, but not enhancing the amount of visual stimulation resulted in a small level of left-side population bias. However, the population bias was significantly reduced from those found in unmanipulated populations, $z = -3.75, p < .05$.

Individual degree of lateralization across experimental groups was analyzed with a one-way ANOVA procedure. No significant differences were found in degree of lateralization, $F(4, 99) = .976, p < .42$. This suggests that while the direction of individual and population level lateralization could be altered by differential exposure of eye-systems to visual stimulation prenatally, the degree of lateralization demonstrated by individuals was not significantly affected.

Individual latency scores across experimental conditions were analyzed with a one-way ANOVA procedure. No significant differences were found across groups in latency to complete the T-maze, $F(4, 95) = 1.13, p < .34$.

Discussion

Experiment 2 tested the hypothesis that there exists an equipotentiality for both hemispheres to become specialized for a turning bias (presumably demonstrated in Experiments 1 and 2). Further, it examines whether the invariant developmental position of the embryo and the consequent differential hemispheric sensory experience facilitate the direction of the population level turning bias.

The results from Groups 2 and 3 clearly support the idea of equipotentiality of the hemispheres, as well as the role of prenatal visual stimulation as an important inducer for lateralization. While removing the embryos' head from the egg apparently reduces the species-typical left-side bias, unilateral visual stimulation to either eye-system can facilitate right or left individual side biases. Bilateral exposure to visual stimulation appears to eliminate the population bias, as well as reducing individual bias.

Groups 3, 4, and 5 are interesting in that they suggest that in the absence of enhanced sensory experience, chicks are lateralized in about the same proportions regardless of specific manipulation. Left-side population biases were significantly reduced from unmanipulated populations, but in no instance was a right-side population bias seen. Only when enhanced unilateral visual experience was given to the right hemisphere (LES) was a right-side population bias established. Clearly, in the absence of enhanced prenatal stimulation, a left-side population bias is the species-typical norm.

Overall, these findings suggest factors other than prenatal visual stimulation can contribute to postnatal behavioral asymmetries. For example, removing the chick's head from the egg interrupts the hatching process. It is possible that some aspect of the hatching process itself may contribute to the development of turning bias. It is known that the hatching process is asymmetrical in nature, in that the chick cuts out of the egg in a counterclockwise rotational direction (Kuo, 1967). It is possible that eliminating the later motorical stages of the hatching process could serve to disrupt some of the lateralizing influences that may contribute to the emergence of a spatial turning bias.

2.7 Experiment 3: Differential Effects of Type of Prenatal Sensory Stimulation on the Development of Hemispheric Specialization for Turning Bias.

Experiment 1 demonstrated what could be characterized as a species-typical left-side turning bias in bobwhite quail. Experiment 2 demonstrated an apparent equipotentiality for hemispheric specialization, at least under conditions of unilateral, prenatal visual stimulation. The present experiment

investigated the potential role of prenatal auditory stimulation in the development of turning bias. Experiment 2 used enhanced visual stimulation to affect the reversal of hemispheric specialization. However, because the embryo is exposed to both auditory and visual stimulation prenatally, it is important to consider the possibility that auditory stimulation may also play a role in the development of hemispheric specialization (Gottlieb, 1968; Zappia & Rogers, 1983). Thus, this experiment tested whether the specific type (visual or auditory) of prenatal sensory experience could serve to impact the development of behavioral asymmetries in spatial orientation.

Method

Eighty bobwhite quail chicks, drawn from three separate hatches, were used as subjects. Group 1 consisted of 20 subjects with tops removed from the egg, but not given any enhanced sensory stimulation (control group). Group 2 consisted of 20 subjects given enhanced prenatal visual stimulation. Group 3 consisted of 20 subjects given enhanced prenatal auditory stimulation. Group 4 consisted of 20 subjects given concurrent enhanced auditory and visual stimulation.

All subjects underwent the same egg opening procedure. During the second half of the 21st day of incubation (21 day, 1200-1600 hr), the shell and inner-shell membrane over the air space of the egg of each subject was removed. The embryo's bill typically penetrates the air space early on day 21. The embryo begins to respire and vocalize following penetration into the air space (Vince, 1972). Consequently, exposing the embryo's head at this time (the embryo's body remains in the shell) does not interfere with the final stages of incubation (Heaton & Galleher, 1981; Lickliter, 1990). In this

experiment, eggs were only opened enough to allow exposure of the right eye and ear of the embryo. Unlike the egg opening procedures in Experiment 2, subjects in Experiment 3 did not have their heads extracted from the egg. This was done to maintain species-typical developmental conditions (as closely as possible) and to allow relatively normal hatching behavior on the part of the chick. In light of the findings in Experiment 2, it became doubly important that species-typical hatching behaviors be maintained. Thus, while the top of the shell was removed in this experiment, the embryos head was not "uncorked" from the egg. This allowed the species-typical embryonic right sided orientation to be maintained.

Following the egg opening procedure, the embryos in the enhanced visual stimulation condition (Group 2) were placed in a portable Hovi-bator incubator for the last 36 hr of incubation. Embryos were exposed to the light of a 60-watt General Electric Soft White bulb (120 volts, 870 lumens) for 10 min every hour until hatching. This light was positioned immediately above (4 cm) the incubator's Plexiglass top. Following hatching, chicks were numbered and placed in plastic rearing tubs containing 10-15 same aged chicks to mimic naturalistic brooding conditions.

The embryos in the enhanced auditory condition (Group 3) were exposed to previously recorded bobwhite quail embryonic vocalizations for 10 min every hour during the last 36 hr prior to hatching. As chicks typically vocalize in the egg following penetration into the air space, embryonic vocalizations were chosen to serve as the auditory stimulation (see Lickliter & Stoumbos, 1991) to more closely mimic naturally occurring developmental conditions. As in the previous experiments, chicks were numbered and housed in plastic rearing tubs with 10-15 same aged conspecifics.

Finally, in the combined auditory and visual condition (Group 4) the embryos were exposed to the same visual and auditory stimulation as subjects in Groups 1 and 2. However, in this condition embryos received concurrent visual and auditory stimulation for 10 min every hour until hatching. Following hatching, chicks were housed in plastic rearing tubs containing 10-15 same aged chicks.

Chicks in all three groups were tested at 24, 30, 48, 52, 72, 78, 96, and 102 hr following hatch in a simultaneous choice test between two pairings of the bobwhite maternal call and a stuffed bobwhite hen one on the left and right sides of the T-maze (see General Methods sections for details).

Results

Group 1

Chicks in Group 1 had the top portion of their eggs removed (their heads remained inside the egg), but were not exposed to any enhanced sensory stimulation. Fifty-five percent of subjects demonstrated a left-side turning bias, 30% a right-side bias, and 15% were unbiased (see Table 5). The population bias was not significant, $t(19) = -1.36$, $p < .09$, (Mean left turns = 4.65, $SD = 2.13$; Mean right turns = 3.35, $SD = 1.95$). Therefore, while bobwhite chicks in this group were individually biased, no population bias was evident. Merely opening the top of the egg significantly reduced the 85% left-side population bias found in unmanipulated populations, $z = -3.75$, $p < .01$. Once again, as in Experiment 2 interrupting the late stage hatching behaviors appears to significantly reduce the left-side population bias.

Group 2

Chicks in Group 2 had the top of the egg removed (their heads remained inside the egg) and were exposed to enhanced visual stimulation. Seventy-five percent of subjects demonstrated a left-side turning bias, 15% a right-side bias, and 10% were unbiased (see Table 5). The population bias was significant, $t(19) = -3.21, p < .002$, (Mean left turns = 5.2, SD = 1.67; Mean right turns = 2.8, SD = 1.55). Indeed, there was no significant difference between the level of population bias found in this group and that found in unmanipulated populations, $z = -1.25, p < .10$. Thus, opening the top of the egg (but not removing the chicks head) and exposing only the right eye-system to enhanced prenatal visual stimulation) restored the left-side population bias found in unmanipulated chicks. Once again, it would seem that limiting prenatal visual stimulation to the left hemisphere can remediate the effects of interrupting the hatching process (see Experiment 2).

Group 3

Chicks in Group 3 had the tops removed from their eggs (their heads remained inside the egg) and were exposed to enhanced auditory stimulation. Sixty percent of subjects demonstrated a left-side turning bias, 30% a right-side bias, and 10% were unbiased (see Table 5). The population bias was not significant, $t(19) = -0.76, p < .22$, (Mean left turns = 4.4, SD = 2.35; Mean right turns = 3.6, SD = 1.95). Exposing chicks to enhanced prenatal auditory stimulation did not facilitate either a left or a right side population bias. Indeed, distribution of subjects in this condition was not significantly different from that of Group 1. Prenatal auditory experience, therefore, does not appear to be an important influence on the development of turning bias in

bobwhite quail chicks. This has also been found to be the case with domestic chicks (Zappia & Rogers, 1987).

Group 4

Chicks in Group 4 had the top portion of the egg shell removed from their eggs (their heads remained inside the egg) and were exposed to the simultaneous presentation of enhanced auditory and visual stimulation. Fifty percent of subjects demonstrated a left-side turning bias, 45% a right-side bias, and 5% were unbiased (see Table 5). The population bias was not significant, $t(19) = -0.48, p < .31$, (Mean left turns = 4.1, SD = 1.89; Mean right turns = 3.7, SD = 1.13). Exposing the embryo to concurrent presentation of enhanced auditory and visual stimulation did not facilitate the 85% left-side population bias found in Experiment 1. Although visual experience can serve to facilitate a left-side population bias, when combined with prenatal auditory stimulation the bias is eliminated. This suggests that the overall amount of prenatal sensory stimulation may have a significant impact on the development of postnatal turning bias.

Individual degree of lateralization across groups was analyzed with a one-way ANOVA procedure. No significant differences were found in individual degree of lateralization across groups, $F(3, 79) = .35, p < .789$. Once again degree of lateralization was not significant. Variations in type of prenatal sensory stimulation did not appear to affect degree of lateralization in subjects.

Individual latency scores were analyzed across conditions with a one-way ANOVA procedure. No significant differences were found across groups in an subject's latency to complete the T-maze, $F(3, 76) = 1.67, p < .18$.

Discussion

Experiment 3 tested the hypothesis that specific type of sensory stimulation is a more important facilitator of hemispheric specialization than overall amount of sensory stimulation. This would seem to be the case. Binocularly tested chicks that were given enhanced prenatal auditory experience displayed a significant 61% left-side population level turning bias. Chicks given enhanced prenatal visual experience demonstrated a significant 75% left-side turning bias. Zappia and Rogers (1983) found that visual stimulation alone was more effective than auditory stimulation at facilitating lateralization of attack and copulation behavior in domestic chicks. Additionally, combined visual and auditory stimulation did not result in greater levels of laterality than visual stimulation alone. In addition, auditory stimulation alone has been shown to have little effect on the lateralization process in domestic chicks (Zappia & Rogers, 1983, 1987).

Taken together these findings suggest that visual stimulation may be the critical facilitator for hemispheric specialization in precocial avian chicks. However, chicks given enhanced prenatal auditory and visual experience displayed a non-significant 50% left-side population level turning bias, indicating amount of stimulation is likely an important factor as well (see Lickliter & Lewkowicz, 1995 for a related example).

2.8 Experiment 4: Effects of Enhanced vs. Attenuated Visual Stimulation on the Development of Hemispheric Specialization.

As expected, Experiment 3 demonstrated that visual stimulation is a more critical facilitator of turning biases in bobwhite quail chicks than is auditory

stimulation. This finding parallels similar results in the domestic chick (Bradshaw & Rogers, 1993). In the domestic chick, the direction of hemispheric specialization appears to be determined by differing amounts of light input received by the left and right eye of the embryo (Rogers, 1986). For example, Rogers (1982) demonstrated that chicks hatched from eggs exposed to light during incubation exhibit lateralization in the same direction for attack and copulation behaviors. This lateralization was present at both the individual and population levels. However, chicks hatched from eggs incubated in darkness were found to have hemispheric specialization for attack and copulation behaviors at the individual level, but not at the population level. That is, half of the chicks had lateralization in one direction and half in the other direction. Additionally, Rogers (1991) has shown that the direction of behavioral asymmetry for copulation in the male chick is determined by differential exposure of the embryo to light, and that lateralization is correlated with hemispheric specialization. Moreover, these effects occur at the stage of embryonic development when visual connections to the forebrain are becoming functional (Freeman & Vince, 1974). Therefore, this experiment assessed whether chicks incubated in darkness would develop individual turning biases, but not a significant population bias. Additionally, this experiment assessed whether greatly enhanced prenatal visual experience would result in unusually high degrees of lateralization.

Methods

Forty bobwhite quail chicks drawn from three separate hatches were divided in two experimental groups. Unlike chicks in previous experiments, chicks in this experiment did not have their eggs opened. Group 1 consisted of

20 chicks that were incubated in a Hovi-bator incubator in darkness from day 17 until 24 hr following hatching. After the first testing session, Group 1 subjects were reared under the same conditions as subjects in all other experiments (see General Methods section). Group 2 consisted of 20 bobwhite chicks that were incubated in a Hovi-bator portable incubator under constant illumination (using a 60-watt bulb) from day 17 of incubation until hatching. The Hovi-bator incubator was outfitted with a Plexiglass top, allowing both observation and stimulation of the embryos. The 60-watt bulb did not produce any significant increase in incubator temperature. Consistent temperature and humidity levels were maintained as during earlier incubation. Each subject in both conditions was tested in the same apparatus and with the same procedures as detailed in the General Methods section. Subjects were tested in the T-maze at 24, 30, 48, 52, 72, 78, 96 and 102 hr following hatching.

Results

Group 1

Sixty percent of chicks in Group 1 demonstrated a left-side turning bias, 35% a right-side bias, and 5% were unbiased (see Table 6). The population bias was significant, $t(19) = -1.75, p < .04$, (Mean left turns = 5, SD = 2.55; Mean right turns = 3, SD = 2.15). Incubating subjects in darkness did not eliminate the left-side population bias, but did significantly reduce the left-side bias from the 85% found in controls (Experiment 1), $z = -3.13, p < .01$. Thus, it appears that prenatal visual stimulation is an important component in establishing a left-side turning bias in bobwhite quail, even when the structural integrity of the egg is unaltered.

Group 2

Eighty-five percent of chicks in Group 2 demonstrated a left-side turning bias, 15% a right-side bias, no subjects were unbiased (see Table 6). The population bias was significant, $t(19) = -5.13, p < .0001$, (Mean left turns = 6.1, SD = 1.83; Mean right turns = 1.9, SD = 1.35). The overall percent of left-side biased subjects was not significantly altered from unmanipulated populations. Although it was hypothesized that Incubating subjects under constant illumination would increase overall degree of lateralization, this does not appear to be the case. Constant illumination during the last stages of incubation does not appear to affect the overall population percentages found in unmanipulated populations (see Experiment 1).

Individual degree of lateralization was analyzed across groups with a one-way ANOVA procedure. No significant differences were found in degree of individual lateralization across groups, $F(1, 39) = .078, p < .781$. This finding continues a trend found in previous experiments.

Individual latency scores were analyzed across conditions with a one-way ANOVA procedure. No significant differences were found in latency to complete the T-maze, $F(1, 38) = 2.48, p < .12$. This finding also continues a trend found in previous experiments.

Discussion

Experiment 4 tested the hypothesis that the presence or absence of prenatal visual stimulation is a critical factor in facilitating high levels of individual and population lateralization. Studies of attack and copulation behaviors in domestic chicks (Rogers & Sink, 1988; Rogers & Bolden, 1991) have found that chicks exposed to consistent levels of illumination prior to

hatching had stronger degrees of individual and population hemispheric specialization. This does not appear to be the case with bobwhite quail. While subjects that were incubated in darkness demonstrated a significantly reduced degree of population lateralization, subjects incubated in enhanced light exposure did not demonstrate any significant difference in individual degree of lateralization from unmanipulated controls. As this was the case in each of the experimental conditions in this study, the concept of "degree" of lateralization should perhaps be reexamined (see General Discussion)

What is significant about this experiment is that by attenuating light exposure, and thus prenatal visual experience, the overall population laterality was reduced by at least twenty percent. Clearly, prenatal visual experience is an important factor in facilitating the development of spatial turning bias. Additionally, the results of this experiment support the role of visual experience in the development of hemispheric specialization. Population level turning bias in bobwhite quail is dependent in part on prenatal visual experience. When chicks are incubated in darkness during the final stages of hatching the population level turning bias is eliminated. Chicks incubated under constant illumination demonstrated the same level of population bias as unmanipulated populations.

Behavioral and morphological visual asymmetries have been reported in adult pigeons (Gunturkun & Kesch, 1987). Gunturkun (1993) demonstrated that prenatal visual experience in homing pigeons facilitated the development of lateralized visual discrimination behaviors. Subjects incubated under constant illumination were visually lateralized with a behavioral superiority of the right-eye system. Additionally, neuronal cell bodies in the left tectum

were larger than in the right. No functional or anatomical asymmetries were found in subjects incubated in darkness.

2.9 Experiment 5: Unilateral Intercranial Injection of Cycloheximide to Test for Hemispheric Specialization in Turning Bias. (Pilot Study)

Experiment 1 demonstrated a left-side turning bias in bobwhite chicks when responding to species-specific maternal auditory and visual cues. It has long been recognized that asymmetrical behavioral responding is often accompanied by a contra-lateral hemispheric specialization for those behaviors (Bradshaw & Rogers, 1993). Following from this, Experiment 5 employed pharmacological techniques to examine hemispheric structural specialization for turning bias. Based on results from studies of spatially oriented behaviors in domestic chicks (Andrew, Mench, & Rainey, 1982) and mice (Denenberg, 1981), it was hypothesized that the right hemisphere would prove to be specialized for spatial orientation (as demonstrated by a turning bias) in bobwhite chicks. However, Experiment 2 suggested just the opposite, in that it appears that the left-side turning bias discovered in Experiment 1 is more likely to be controlled by the left hemisphere, not the right. Thus, this experiment is important to further clarify which hemisphere (if any) is structurally specialized for this behavior.

Rogers (1980b) detailed the procedures whereby pharmacological techniques can be used to unilaterally disrupt avian brain development. One of the drugs which has been most commonly used as a tool to reveal hemispheric specialization and behavioral asymmetries is cycloheximide. Cycloheximide is a ribosomal protein synthesis inhibitor. The possible

mechanism by which cycloheximide acts to disrupt hemispheric specialization has been discussed in greater detail elsewhere (Bullock & Rogers, 1986; Hambly & Rogers, 1979; Rogers & Drennen, 1978; Rogers, Drennen, & Mark, 1974). It is not known exactly which regions of the avian forebrain are affected by this agent, but its effects are thought to be confined to the telencephalon, and involve an interaction with neurons which process visual information (Rogers & Hambly, 1982). The action of cycloheximide is known to affect brain development by causing glutamate to accumulate in brain amino acid pools (Hambly & Rogers, 1979). It is known to disrupt the development of visual discrimination abilities in the domestic chick (Rogers & Drennen, 1978; Sdraulig, Rogers, & Boura, 1980). As such, it was expected that cycloheximide would prove effective in disrupting the development of spatial orientation abilities, as they are based primarily upon visual cues (Shone, 1984). Cycloheximide has been shown to effectively inactivate the neurons of the injected avian forebrain within 24 hr of injection (Rogers & Anson, 1979).

Method

Sixty bobwhite quail chicks drawn from three separate hatches were used as subjects. Subjects were incubated and hatched without experimental manipulation according to procedures specified in the General Methods section. The cycloheximide solution consisted of 30 μg of cycloheximide dissolved in 25 μl of saline. Subjects were randomly assigned to 3 groups of 20 subjects each. Group 1 consisted of 20 subjects that were injected with 5 μl of cycloheximide solution in the right hemisphere and 5 μl of saline into the left hemisphere at 24 hr following hatching. Group 2 consisted of 20 subjects that were injected with 5 μl of cycloheximide solution in the left hemisphere and 5

μ l of saline into the right hemisphere. Group 3 consisted of 20 subjects that were injected with 5 μ l of a sterile saline solution in both hemispheres as a control condition. The order of injection was randomized across subjects in all three conditions.

Although it was originally proposed that cycloheximide be administered to chicks prenatally, the findings of Experiments 2 and 3 made this impossible. Interrupting the hatching process by removing the chicks head prenatally appears to significantly reduce the population level turning bias. Therefore, chicks in Experiment 5 were injected with cycloheximide 24 hours following hatching. Injections were performed free-hand using sterile 10 μ l Hamilton syringes, which were fitted with plastic stops to ensure that the needles penetrated the cranium at a depth of no more than 3 mm. The injection sites were midway between the anterior and posterior extremities of either forebrain hemisphere approximately 1 mm from the midline and equidistant from the rostral and caudal poles of the hemispheres.

Chicks in all three groups were tested at 24, 30, 48, 54, 72, 78, 96, and 102 hr following hatching in a simultaneous choice test between pairings of the bobwhite maternal call and a stuffed bobwhite hen on the left and right sides of the T-maze arms (see General Methods section for details). Laterality indexes were computed for individual chicks.

Results

It was originally proposed that Experiment 5 test the hypothesis that the chicks' right hemisphere is specialized for turning bias. Based on what was found in Experiment 2 and 3, this original hypothesis seemed to be incorrect. The results of the foregoing experiments argue strongly that it is the left

hemisphere that is specialized for spatial turning bias not the right.

Therefore, Experiment 5 tested whether the spatial turning bias is associated with a morphological component of unilateral left hemispheric specialization.

Group 1

Chicks in Group 1 were injected with 5 μ l of cycloheximide in the right hemisphere and 5 ml of saline in the left hemisphere. Eighty percent of subjects demonstrated a left-side turning bias, 20% a right-side bias, and no subjects were unbiased (see Table 7). The population bias was significant, $t(19) = -2.69$, $p < .001$, (Mean left turns = 5.2, SD = 1.98; Mean right turns = 2.8, SD = 1.70). The overall percent of left-side biased subject was not significantly changed from those found in unmanipulated populations in Experiment 1, $z = -.626$, $p < .10$.

Group 2

Chicks in Group 2 were injected with 5 μ l of cycloheximide in the left hemisphere and 5 ml of saline into the right hemisphere. Fifty percent of subjects demonstrated a left-side turning bias, 35% a right-side bias, and 15% were unbiased (see Table 7). The population bias was not significant, $t(19) = -0.94$, $p < .17$, (Mean left turns = 4.4, SD = 1.90; Mean right turns = 3.6, SD = 2.15). The overall percent of left-side biased subject was significantly reduced from those found in unmanipulated populations, $z = -6.26$, $p < .01$.

Group 3

Chicks in Group 3 were injected with 5 μ l of a saline solution in both hemispheres as a control condition. Ninety percent of subjects demonstrated a

left-side turning bias, the remaining 10% were right-side biased (see Table 7). The population bias was significant, $t(19) = -7, p < .0001$, (Mean left turns = 6.05, $SD = 1.27$; Mean right turns = 1.95, $SD = 1.31$). The overall percent of left-side biased subject was not significantly changed from those found in unmanipulated populations, $z = .626, p < .10$.

Individual degree of lateralization was analyzed across groups with a one-way ANOVA procedure. As in previous experiments, no significant differences were found in degree of lateralization across groups, $F(2, 56) = 2.36, p < .104$.

Individual latency scores were analyzed with a one-way ANOVA procedure. As in previous experiments, no significant differences were found in latency to complete the T-maze, $F(2, 57) = .70, p < .49$.

Discussion

The data presented here are pilot data. Serious confounds may be present in the findings due to a high mortality rate in Group 1 and Group 2. Sixty-eight percent of subjects given left hemisphere injections of cycloheximide 24 hr following hatching died 24 hr later. Additionally, 33% of subjects died 24 hr following right hemisphere injection with cycloheximide. Controls given bilateral injections of saline did not demonstrate any abnormal patterns of mortality. Thus, the results of Experiment 5 are at best suggestive of an underlying morphological basis for spatial turning bias in bobwhite quail chicks. Further work is required to convincingly demonstrate that the left hemisphere has a structural specialization for the left-side bias demonstrated in unmanipulated controls. Specifically, the high mortality rates in Groups 1 and 2 must be explained and greatly reduced.

Nonetheless, based on what is known about the structure of the avian brain and the results of Experiments 2 and 3, the chicks' left hemisphere appears to be specialized for a left-side turning bias. The result of Experiment 5 also suggest such a trend. When cycloheximide was injected into the left hemisphere of the bobwhite chick, the 85% left-side population bias was eliminated. This did not occur when cycloheximide was injected into the right hemisphere. Control subjects that received a bilateral saline injection demonstrated a 90% population left-side population bias. While these findings must be considered pilot data, and potentially confounded by a high mortality rate, they nonetheless suggest that an underlying morphological basis for left hemispheric specialization for left-side turning bias in bobwhite quail.

3.0 General Discussion

Experiment 1 revealed that bobwhite quail have a left-side spatial turning bias at the individual and population level. Indeed, fully 85% of unmanipulated subjects were left-side biased. Experiment 2 showed that this population level left-side bias appeared to be based in a left hemispheric specialization. It was also revealed that unilateral prenatal visual experience to the right hemisphere could induced a right-side population turning bias. This suggested an equipotentiality of specialization between the hemispheres for the turning bias. The results of Experiment 2 also support the idea that unilateral visual experience is necessary for the development of a population level turning bias. Experiment 3 confirmed the hypothesis that visual experience was more effective than auditory experience in facilitating the development of a left-side turning bias. Experiment 4 further supported the role of prenatal visual experience as a necessary, but not entirely sufficient

facilitator in the development of left-side turning bias. Finally, the results of Experiments 2 through 4 revealed that late stages of the hatching process also appear to be a necessary facilitator of left-side turning bias.

These results lend support to the theory that behavioral asymmetries in avian species are the result of the asymmetrical positioning of the embryo, which provides the left hemisphere with differential sensory and motor experience in the final stages of incubation. During this period when the visual pathways are becoming functional, the body of the embryo is oriented in such a way that the right eye (left hemisphere) is given more visual stimulation than the contralateral left eye-system (right hemisphere). This period of asymmetrical orientation also coincides with the hatching process. The asymmetrical position of the embryo results in a counterclockwise rotation to successfully cut itself out of the egg. Both of these factors are present during the last 4 days of incubation. Both influences are affected by the position of the embryo.

Therefore, at least two principal prenatal influences on the development of turning bias in bobwhite quail have been identified in this study. The first is the invariant position of the embryo in the late stages of incubation and the resulting differential amounts of visual experience that the two eye-systems receive due to this asymmetrical embryonic posture. The second factor, also related to the invariant position of the embryo, is the asymmetrical motor behavior involved in the hatching process. Each of these influences appear to act inconcert to produce a population level left-side turning bias in bobwhite quail chicks. Taken together, results of the experiments of this study argue for a multiply determined prenatal induction of postnatal turning bias.

3.1 Embryonic position and prenatal visual experience.

Rogers and her colleagues have repeatedly demonstrated that the direction of lateralization in the chicken fore-brain is determined by the asymmetrical prenatal visual experience of the embryo (see Rogers, 1991 for review). At the onset of the several day long hatching process the embryo is oriented in the egg such that its left eye is occluded by the body and yolk sac, while the right eye is exposed to light filtering through the egg shell and membranes (Rogers, 1986). Furthermore, this particular orientation of the embryo occurs at a stage in which the forebrain's central visual connections are becoming electrochemically functional and when light stimulation begins to evoke motor responses (Freeman and Vince, 1974). The eye itself opens and closes during this period; yet, even when closed it is covered by transparent eye-lids which allows light to pass through.

Rogers (1982) has found that chicks hatched from eggs incubated in darkness during the last 3 days prior to hatching demonstrate no functional lateralization at the group (or population) level. Similarly, bobwhite quail chicks incubated in darkness show a reduced level of population bias. Both the bobwhite and domestic chicks retain individual lateralization. Thus, it appears that prenatal visual experience synchronizes the direction of lateralization of individuals in the same direction. Rogers (1991) argues that this differential prenatal visual experience also serves to facilitate the development of the left hemisphere in advance of the right. This initial left hemisphere bias provides the foundation for a wide range of behavioral asymmetries. The results obtained with bobwhite chicks in this study also support this hypothesis. However, as evidenced by the results present above some other factor is

indicated as a significant facilitator for postnatal spatial turning bias. The results of Experiments 2 and 3 suggest that by interrupting the later stages of the hatching process an important facilitating influence is removed.

3.2 The Effects of Hatching Behavior.

The experiments in this study demonstrated that prenatal visual experience serves to facilitate the development of left-side turning bias in bobwhite quail chicks. Additionally, the findings presented above strongly suggest that the population level left-side turning bias in bobwhite quail chicks is also the result of the asymmetrical hatching process working in combination with differential prenatal hemispheric visual experience. Subjects in experimental groups 2.5 and 3.1 had the hatching process interrupted by removal of the tops of their eggs. In both instances, the result was a significant decrease in left-side population bias from unmanipulated controls (Experiment 1).

Kuo (1967) identified the stages of the hatching process in the avian embryo. In the domestic chick prehatching behaviors begin at 16 to 17 days of incubation. Prehatching is marked by the appearance of behavior patterns that are remarkably different from behaviors seen at earlier stages. Early embryonic behaviors typically consist of jerky, convulsive movements of the entire organism. Prehatching stages produce new behavior patterns that are characterized by smooth, tonic-like coordinated movements (Oppenheim, 1972). These later motor patterns are more highly organized and stereotyped than that of earlier behavior patterns. These behavioral patterns represent the first phase in a sequence of events which are preparatory to, the actual hatching process.

Oppenheim (1972) identified a specific, invariant pattern of successful hatching behavior. For example, there are four major behavioral events in the hatching process which occur between 17 and 20-21 days of incubation (for the domestic chick): (a) tucking, the process of getting the head under the right wing and the subsequent shift in position that brings the beak and right shoulder region into the air space; (b) membrane penetration and effective lung respiration (Kuo & Shen, 1937); (c) pipping, the first crack made in the egg shell; and (d) climax and emergence. This final stage of hatching has a sudden onset, in which the embryo makes a series of counter-clockwise (left to right) rotations around the shell circumference. The embryo rotates its entire body within the egg by means of periodically occurring coordinated movements of the head, neck, and legs. The shell cap is then pushed off through muscular flexion of the so-called "hatching muscle" (Fisher, 1958, 1962).

Oppenheim (1974) found a rather sudden onset to hatching climax in embryos of 11 species, followed by more or less sustained stereotyped hatching movements. These consisted of deep rapid exhalation (depressing the beak towards the chest), a strong extension of the tarsal joints deeper into the narrow (non-airspace) end of the egg, and a vigorous up thrust of head and beak towards the shell. Such sequences usually lasted 1-3 seconds and were repeated every 11-30 seconds. All but the earliest sequences included a rotation of the embryo's entire body. This turning was always counter-clockwise from the site of the original pipping and resulted in steady chipping of the shell circumference (O'Connor, 1984). Each of the preceding hatching events is accomplished by a stereotypical motor pattern that differs little from

bird to bird, or species to species, and which almost invariably leads to the successful emergence of the bird from the shell.

The results of Experiments 2 and 3 suggest that hatching behaviors are a significant influence on the development of postnatal spatial turning bias. In every instance where the top was removed from the egg and the embryos were not given any enhanced sensory stimulation, a significant decrease of left-side population bias was observed. This was true when the embryo's head was "uncorked" from the egg (as in Experiment 2) and also when the head was undisturbed (as in Experiment 3). This suggests that it is not merely the asymmetrical position of the embryo's head within the egg that exerts a canalizing influence, but it is the hatching behaviors themselves that are important. The physical act of cutting out of the egg, the first coordinated physical exertion of the chick, appears to be a powerful facilitating influence on the development of postnatal left-side turning bias.

Clearly, the hatching process is very complex and coincides with many other important physiological, morphological, and experiential influences on behavioral development. It should not be surprising that an asymmetrical hatching process that consists of multiple left-right rotations contributes to the development of a spatial turning bias postnatally. However, the hatching process is not the only important factor involved, as the results of Experiment 4 make clear. Unilateral visual experience prenatally is also an important canalizing influence. The coaction of both prenatal visual experience and hatching behaviors appear to produce the 85% population level left-side bias observed in unmanipulated bobwhite quail chicks.

3.3 Degree of lateralization

The initial proposal for this study was based on the assumption that a direct relationship exists between the degree of behavioral asymmetry and the degree of cerebral lateralization. The results of the foregoing experiments calls this assumption into question. In Experiments 2, 3, 4, and 5 no significant differences in degree of lateralization as measured by the laterality index were demonstrated across groups. While significant differences in direction of population lateralization were readily apparent and individual subjects were clearly lateralized, in general there appeared to be no significant difference between subjects' degree of lateralization. This finding calls into question the assumption of degree of lateralization on the grounds that: (1) the degree of lateralization may be solely a product of the measurement procedures, and (2) the concept of "degree" may be inappropriately applied to discussion of lateralization and behavioral asymmetries.

In human lateralization studies, differences in degree of lateralization are often inferred from differences between left and right auditory or visual hemi-field responding. Typically, these differences are computed in terms of a "laterality coefficient" or "laterality index." However, questions about the validity of such measures arise from the fact that the relative level of performance in the left and right eyes or ears is found to vary with such factors as the signal-to-noise ratio, the exposure to stimuli, and duration of testing (Colbourn, 1978). Thus, the value of the laterality coefficient may also vary with these factors. This may also be the case with bobwhite quail responsiveness in the T-maze. Factors such as overall behavioral reactivity of chicks might impact an individual subject's turning bias. For example, while a

clear bias may be identified (left or right), the "degree" of the bias might be obscured by a highly reactive subject.

If a laterality index is supposed to be a measure of some fixed property of the brain (i.e., hemispheric specialization) then this variability should not be the case (Berlin, 1977). Even if the laterality coefficient were less susceptible to changes in experimental conditions, there remains the interpretive problem of what is meant by differences in the size of any coefficient between groups or individuals. Differences in the size of a particular laterality coefficient or index are generally regarded as reflecting different degrees of cerebral lateralization. But if, for example, cerebral asymmetry for turning bias is a matter of degree (Zangwill, 1960; Shankweiler and Studdert-Kennedy, 1975), what is it that specifically varies? Would this mean that when the chick makes a left turn the right hemisphere is controlling the behavior, but when that same chick makes a right turn, the left hemisphere is in charge? Such an instance would undermine the entire concept of cerebral lateralization and behavioral asymmetry. Laterality indexes and coefficients may therefore provide a false sense of quantification of underlying brain processes.

Because of these difficulties, Colbourn (1978) has argued that laterality should not be measured on a ratio scale. Colbourn suggests that we should not compare different individuals or groups in terms of their degree of laterality. Instead, he argues that investigators should note the direction of laterality since this, at least in theory, bears a specific relation to underlying hemispheric specialization. Thus, different groups of subjects can be compared in terms of the number of individuals showing a lateral bias for one side or the other. In any case, there is no denying that interpretation of

behavioral asymmetry and the related issues of "degree" requires more careful thought than it has received in the past.

3.4 Models of lateralization

A cooperative interactional model was postulated to underlie bobwhite quail species-typical perception. Indeed, pilot data suggested that species-typical recognition of maternal auditory and visual cues in bobwhite quail chicks is likely based on a cooperative interactional process, in that both hemispheres appear to be involved in behavioral responding (see Table 1). With specific regard to the development of spatial turning bias, it would appear that the left hemisphere is specialized for the left-side bias demonstrated by unmanipulated bobwhite chicks. The results from the previous experiments support the idea that only one hemisphere is typically specialized for spatial turning bias, but that under certain conditions either hemisphere may become specialized. However, specialization of the right hemisphere results in a right side bias, not a left-side bias.

What this suggests is that while species-typical responding to maternal auditory and visual cues may be the result of a cooperative model of lateralization, the specific left-side turning bias may be the result of a "functional unilateralization." That is, only the left hemisphere appears to produce a left-side bias, while only the right hemisphere specialization results in a right-side bias. Direction of turning bias is dependent upon which hemisphere becomes specialized. A side bias can be produced by either hemisphere becoming specialized, but each hemispheric specialization results in different turning biases.

It may be that this left-side turning bias is based more on a motor response system than specifically related to the right hemisphere processing of spatial information. In other words, bobwhite quail have a left side bias because they acquire this bias during the asymmetrical, counterclockwise hatching process and the differential amounts of prenatal visual experience. Future experiments should investigate whether the turning bias is present in the absence of species-typical maternal cues. If the bias occurs independent of the bobwhite maternal assembly call, than we might be more confident in ascribing the turning bias to motor response. Species-typical perception of maternal cues may still be best understood in terms of a cooperative interactional model of lateralization, but with regard to the specific turning bias a functional unilateral model appears more likely.

3.5 An epigenetic theory of hemispheric specialization.

Kuo (1967) divided the principle determining factors that underlie behavioral development into five main categories: (1) morphological, (2) biophysical and biochemical physiology, (3) developmental history, (4) immediate stimulus array, and (5) environmental context. These five groups of determining factors are seen as interwoven, interrelated, and acting in unison. Therefore, every behavior is a functional product of the dynamic interrelationship of these five groups of determining factors. This system of transacting constraints and fluctuating degrees of freedom can be seen in the developmental relationship between prenatal sensori-motor experience, hemispheric specialization, and behavioral asymmetries. This epigenetic perspective on the developmental process is supported by the findings of this study.

Lickliter (1993) points out that "one of the most compelling examples of the uniform and invariant nature of specific aspects of developmental contexts is the timing of sensory experience normally available during ontogeny (p. 106)." The coincident influences of lateralized prenatal visual experience and asymmetrical hatching behaviors that produce a spatial turning bias in bobwhite quail populations are further examples of such uniform, potentially invariant influences on the developmental system. These two influences, one endogenous (hatching) and one exogenous (visual experience), provide an important source of structure and order which help to determine postnatal motor behaviors. The 85% left-side population turning bias revealed in unmanipulated subjects (Experiment 1) appears to be dependent at least in part, on these two canalizing influences.

In many ways, postnatal life can be seen as continuation of prehatching or prenatal life, except that the organism's environment has changed more or less radically, and this change requires a reorganization of behavioral patterns from those acquired prior to hatch. The importance of the hatching period for later postnatal development illustrates this point. The bobwhite organismic systems begin to function in typical adult fashion several days before hatching. The functional activities of the respiratory, digestive, excretory, and sensory systems, both mechanical and chemical, have begun long before hatching (Kuo, 1967). The hatching process involves an increasing coordination of motor, respiratory, and sensory systems in the embryo/chick. In this study, interfering with the hatching process disrupted the development of the bobwhite's left-side turning bias. However at the same time as the hatching process is ongoing, the orientation of the embryo facilitates differential exposure of the eye-systems to visual experience. It is

also at this time that the embryos forebrain central visual connections are becoming electrochemically functional and when light stimulation begins to evoke motor responses (Freeman and Vince, 1974). Thus, the coincident timing of these important developmental events appears to underlie the population level left-side bias observed in bobwhite quail chicks.

Developmental timing, as Turkewitz and Devenny (1993) argue, consists of the temporal relationships between the elements of a complex, integrated system. The concept of "timing" is important with regard to the developmental relationship that exists between the various subsystems that come to characterize the entire developmental process. In the case of the bobwhite quail turning bias, two significant subsystems are prenatal visual experience and the asymmetrical hatching process. Turkewitz and Devenny (1993) point out that environmental influences on development include not only external stimulation (such as intensity of light), but also the organism's endogenous sources of stimulation that control the impact of that environment on the organism's postnatal behaviors (such as muscular exertions during hatching). The timing of such temporal relationships has a formative role in facilitating emergent properties in development (such as the left-side turning bias). Therefore, it is not merely the appearance of a particular subprocess that promotes developmental change, but the temporal relationships of these multiple sources of development.

3.6 Summary and Conclusions.

An understanding of the nature and origins of brain lateralization in vertebrate organisms has become a prominent goal of current comparative psychobiology. With this study, I have attempted to demonstrate that bobwhite

quail nervous system lateralization and corresponding behavioral asymmetries derive, at least in part, from the asymmetric nature of embryonic development.

The studies presented above address only a small part of this much larger question. The discovery of a left-side turning bias is interesting in that it parallels turning biases found in mammalian species. It is also interesting that the turning bias is dependent on differential visual experience prenatally, as well as being influenced by the chicks counterclockwise hatching behaviors. However, there is more work to be done. What other aspects of behavioral responsiveness to the bobwhite maternal auditory and visual cues are lateralized? What are the prenatal influences that underlie their development? Is the turning bias present only in response to a combination of visual and auditory maternal cues? Or would the bias be present even in the absence of approach eliciting stimuli? These questions remain to be addressed.

The theory presented here posits that hemispheric specialization is the result of probabilistic events in the developing organism's prenatal environment; in particular, the final stages of prenatal development appear critical. The environmental constraints of the prenatal environment exert a canalizing influence on the development of hemispheric specialization that results in reliable postnatal perceptual and behavioral asymmetries. One future direction this work might take is to examine other avian species for spatial turning bias. Domestic chicks have very similar developmental patterns to bobwhite quail chicks. It would seem logical that if the left-side turning bias in bobwhite quail is the result of prenatal visual experience and the asymmetrical hatching process, than this should also be the case with the

domestic chick. Indeed, the effects of prenatal visual experience on assorted postnatal behaviors in the domestic chick have been systematically studied (see Bradshaw & Rogers, 1993 for review). What has not been studied in the domestic chick is a spatial-motor bias such as the turning bias in bobwhite quail identified in this study.

Future research should also focus on explicating the role of the hatching process in the development of species-typical behaviors. While the hatching process has been extensively described, it has not received much attention with regard to its influence on postnatal behaviors. What is the role of the so-called "hatching muscle" in the development of left-side turning bias? Also, while this study examined the development of a left-side turning bias at the individual and population level, it was beyond the scope of this study to examine the developmental processes that underlie the minority right-side bias (10% of subjects in unmanipulated populations). One possible avenue to pursue would be to examine if right biased subjects had a reverse orientation in the egg resulting in the left eye receiving unilateral visual experience and the hatching process proceeding in a clockwise pattern.

Songbirds, chicks, rats, and nonhuman primates have been found to have brain laterality associated with behavioral asymmetry. Asymmetrical behavior in many species appears to be dependent on differential, lateralized prenatal experiences. The prenatal environment provides a highly structured, reliably consistent, system of constraints that canalize the developmental trajectory of brain lateralization. As seen in the development of the bobwhite quail embryo, extra-embryonic and endogenous stimulation (i.e., light and hatching) appear to determine the direction of hemispheric

specialization. The findings presented here support an epigenetic theory for hemispheric specialization.

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Table 1.

Bobwhite quail chick preferences in simultaneous auditory & visual choice test with either the right eye-system or the left eye-system occluded.

<u>ES occluded</u>	<u>N</u>	<u>Preference</u>		
		<u>BW call/BW hen</u>	<u>BW call/Scaled hen</u>	<u>No preference</u>
LES	55	17	19	19
RES	50	15	17	18

Table 2.

Laterality scores for pilot control subjects in simultaneous presentation of BW call/BW hen model (right arm of T-maze) vs. BW call/BW hen model (left arm of T-maze).

Subject No.*	% Left turns	% Right turns	Laterality index
1	100	0	-2.84
2	50	50	0
3	90	10	-2.13
4	25	75	1.42
5	90	10	-2.13
6	100	0	-2.84
7	62	38	-.71
8	90	10	-2.13
9	75	25	-1.42
10	90	10	-2.13

*Subjects were tested in 8 individual trials that were separated by at least 6 hours.

Table 3.

Experiment 1: Assessment of turning bias in naive bobwhite quail chicks.

	<u>Turning Bias</u>		
<u>N</u>	<u>Right Bias</u>	<u>Left Bias</u>	<u>No Bias</u>
20	2	17	1

Table 4.

Experiment 2: Equipotentiality of hemispheric specialization: The differential effects of prenatal visual stimulation on left and right hemispheric specialization and the reversal of function.

<u>Group</u>	<u>N</u>	<u>Turning Bias</u>		
		<u>Right Bias</u>	<u>Left Bias</u>	<u>No Bias</u>
2.1	20	9	7	4
2.2	20	11	6	3
2.3	20	5	12	3
2.4	20	7	11	2
2.5	20	5	11	4

Table 5.

Experiment 3: Differential effects of type of prenatal sensory stimulation on the development of hemispheric specialization for turning bias.

<u>Group</u>	<u>N</u>	<u>Turning Bias</u>		
		<u>Right Bias</u>	<u>Left Bias</u>	<u>No Bias</u>
3.1	20	6	11	3
3.2	20	3	15	2
3.3	20	6	12	2
3.4	20	9	10	1

Table 6.

Experiment 4: Effects of enhanced vs. attenuated visual stimulation on the development of hemispheric specialization for turning bias.

<u>Group</u>	<u>N</u>	<u>Turning Bias</u>		
		<u>Right Bias</u>	<u>Left Bias</u>	<u>No Bias</u>
4.1	20	7	12	1
4.2	20	3	17	0

Table 7.

Experiment 5: Effects of unilateral intercranial injection of cycloheximide on structural hemispheric specialization underlying turning bias.

<u>Group</u>	<u>N</u>	<u>Turning Bias</u>		
		<u>Right Bias</u>	<u>Left Bias</u>	<u>No Bias</u>
5.1	20	4	16	0
5.2	20	7	10	3
5.3	20	2	18	0

1. Early experiences can induce and/or enhance laterality.
2. Affective processes are lateralized (Right hemisphere).
3. Spatial processes are lateralized (Right hemisphere).
4. Postural asymmetry in infancy is lateralized.
5. The manipulation of testosterone prenatally can cause a shift in laterality.
6. There is evidence for transcortical inhibition of a lateralized affective response.
7. Interhemispheric coupling correlations vary as a function of sex and prior handling infancy.

Figure 1. The Major Findings Concerning Behavioral Lateralization in the Rat.
(Adapted from Denenberg, 1981)

1. Functions present in one hemisphere and independent of the other hemisphere:

a) Left Hemisphere specialized:

song (chaffinch, white-throated sparrow, white-crowned sparrow, canary)

Visual discrimination learning (chicks)

Auditory habituation (chicks)

Attention switching (chicks)

Peck-no peck decisions (chicks)

b) Right Hemisphere specialized:

Hypothalamic-pituitary-gonadal axis (chicks)

2. Functions dependent on interaction between hemisphere:

Activated by Right hemisphere and normally inhibited by Left hemisphere:

Attack (chicks)

Copulation (chicks)

Detection and response to novelty (chicks)

Figure 2. Summary of Functional Laterality in the Avian Fore-Brain.
(adapted from Rogers, 1980)

<u>Species</u>	<u>Behavior studied</u>	<u>Major findings</u>
Mice	Paw preference	50:50 distributions
Parrots	Foot preference	80% of species have a dominant left foot
Songbirds	Neural parts of song production	Dominant left hemisphere
Domestic chicks	Visual discrimination	Dominant left hemisphere
Domestic chicks	Auditory habituation	Dominant left hemisphere
Domestic chicks	Attack	Dominant right hemisphere
Domestic chicks	Copulation	Dominant right hemisphere
Rats	Infantile handling	Reduced emotionality
Rats	Enriched environment	Enhanced cognitive abilities.

Figure 3. Summary of Lateralization Research Findings in Multiple Species.

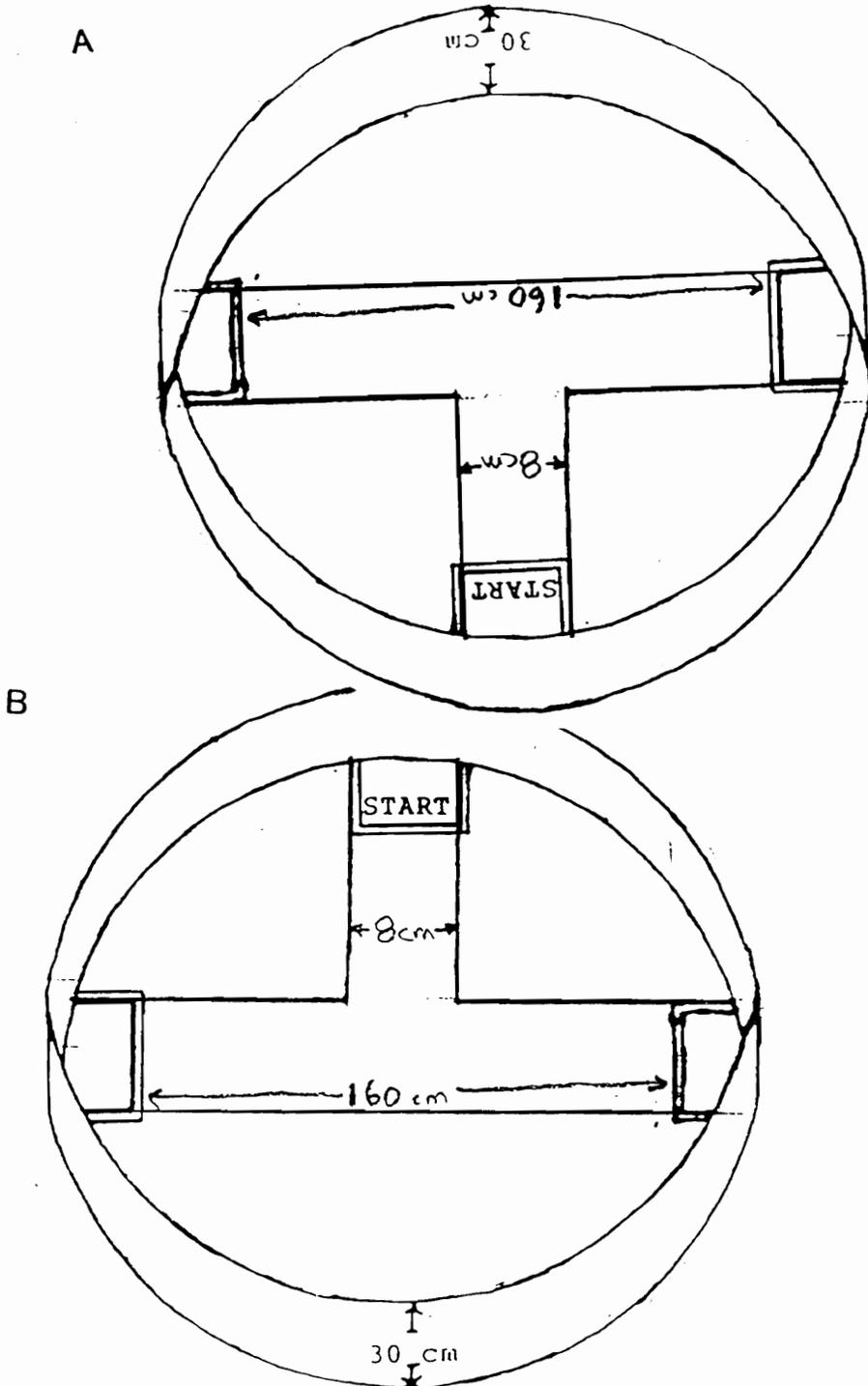


Figure 4. The T-maze testing apparatus: (A) The T-maze stem (starting position) facing away from the observer (facing the top of the testing arena). (B) The T-maze stem will face towards the observer (facing the bottom of the testing arena).

Appendix A
Turning bias data sheet

Group: _____ **Week:** _____ **Subject:** _____
Day 23: _____ **Hatched:** _____ **Tester:** _____

Experiment: _____

Date: _____ **Time:** _____ **Age:** 24 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 30 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 48 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 54 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 72 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 78 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 96 **Turn:** _____
Latency: _____
Comments:

Date: _____ **Time:** _____ **Age:** 102 **Turn:** _____
Latency: _____
Comments:

Laterality Index: _____ **Sex:** _____

Curriculum Vitae

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Education

Ph.D. in Developmental Psychology

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Casey, M. B., & Sgro, J. A. (1992). Readings in Psychology. Boston: Ginn Press.

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Casey, M. B. and R. Lickliter. April, 1992. Alarm call responsivity of bobwhite quail chicks: Developmental and contextual effects. Presented at the Virginia Psychological Association, Roanoke, VA.

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Supervisor: Dr. C. Hahn

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Research project: Maternal induction of emotion in preschoolers.
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Grants

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Awards

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Professional Service

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Professional Memberships

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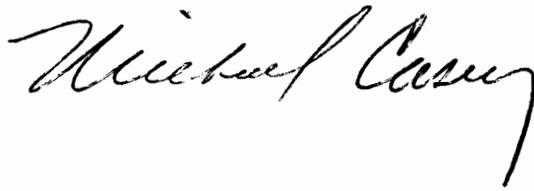
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A handwritten signature in black ink that reads "Michael Casey". The signature is written in a cursive style with a long, sweeping tail on the letter 'y'.