

The Role of Binocular Vision in Mammalian Locomotion

by

Terence Reid Townsend Mitchell

Department of Evolutionary Anthropology  
Duke University

Date: \_\_\_\_\_

Approved:

\_\_\_\_\_  
Dr. Richard Kay, Supervisor

\_\_\_\_\_  
Dr. Matt Cartmill

\_\_\_\_\_  
Dr. Michael Platt

\_\_\_\_\_  
Dr. Daniel Schmitt

Dissertation submitted in partial fulfillment of  
the requirements for the degree of Doctor  
of Philosophy in the Department of  
Evolutionary Anthropology in the Graduate School  
of Duke University

2009

ABSTRACT

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## Abstract

One of the most striking characteristics shared by all primates is that when you look at them, they look right back at you. The reason for this is that all primates including humans have high optic convergence, eyes that point in more or less the same direction. The most well supported advantage of this unusual optic orientation is an increase in the width of the binocular visual field. Most vertebrates possess some overlap of the right and left visual fields. The region of overlap, the binocular field, contains unique visual cues that provide an accurate estimate of distance and three-dimensional shape. Current theories of primate origins such as the fine branch arboreal and nocturnal visual predation hypotheses incorporate convergent eyes as part of the crown primate adaptational suite. Adaptational hypotheses must provide a functional role for a given trait if we are to believe evolution had a role in shaping any form – function complex. To date there is no experimental evidence demonstrating a role for binocular vision in ecologically relevant animal behavior.

The praxic hypothesis states that the size of an animal's binocular field is correlated with the region over which it must make precise visually guided movements without reorienting, and provides a functional explanation as to why primates have such a wide binocular visual field. I tested this hypothesis by analyzing kinematic data of three *Lemur catta*, *Felis catus*, and *Rattus norvegicus* walking on continuous and

discontinuous substrates under binocular and monocular conditions. The results demonstrate that all three species show some alteration in behavior under monocular conditions.

These changes in behavior are interpreted as a shift to a more conservative kinematic strategy in response to the increasing uncertainty of distance estimations due to a loss of binocular information. A wide binocular visual field would be useful to animals that habitually interact with the environment over a wide region of space without reorienting. For early primates, an increase in the length and mobility of grasping forelimbs would benefit from an expansion in the binocular field.

The power of the praxic hypothesis is that it has the potential to explain why most mammals have some visual field overlap, and could predict differences in overlap from rats to lemurs. It provides a reasonable explanation as to why all extant primates have large binocular fields. Primates have developed a host of adaptations towards locomotion in arboreal environments at large body size relative to substrate diameter and relative to other organisms filling similar niches. Long mobile forelimbs are used to bridge gaps and distribute weight in a complex discontinuous environment. These long grasping forelimbs require a sensory system that can estimate distance and three dimensional shape for the next few hand placements. A wide binocular visual field is well suited to this task. Whether the earliest primates shared this intimate link between

long grasping forelimbs and a wide binocular field remains one of the most intriguing questions in primate origins.

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# 1. Introduction

All land mammals, and many other vertebrates, possess some overlap of the right and left visual fields (Walls 1942, Hughes 1977, Arrese et al. 2000). The region of overlap, called the binocular visual field, contains visual cues that provide an accurate estimate of distance and three-dimensional shape. These cues, not present in the monocular field, may enhance perception of a visual scene or guide precise movements. While it has long been assumed that binocular vision played an important role in primate origins, there is no experimental evidence to illustrate how binocular cues are advantageous during ecologically relevant behaviors. **Using kinematic experiments to measure performance, I propose to directly test for the first time how binocular cues are used to guide reaching, grasping, and locomotor movements.**

Visual scientists and ecologists have long sought to determine relationships between an animal's visual system and its ecology. The possession of forward facing eyes is a striking trait shared by all primates that does not currently have an agreed upon evolutionary explanation. While there have been many hypotheses proposed to explain why such a specialization might have evolved, there are currently two widely accepted evolutionary explanations. Based on observations of orbit orientation in a wide variety of arboreal mammals, the nocturnal visual predation hypothesis suggests that the ancestral primate was a nocturnal faunivore that captured prey manually

(Cartmill 1974). By contrast, the fine-branch arboreal hypothesis argues that forward facing eyes are required for navigating in terminal branches while foraging for fruits, insects, or flowers (Sussman 1991). These hypotheses are not mutually exclusive, and arguments based on comparative anatomy and paleontology alone, have not been able to falsify either. A third, lesser-known hypothesis, the praxic hypothesis, posits that forward facing eyes are advantageous to animals that must make precise visually guided movements over a wide area (Hughes 1977). The praxic hypothesis is attractive because it is a widely applicable idea with the potential to explain eye orientation and ecological behavior in a diverse array of species. The praxic hypothesis will not allow us to choose between the two competing hypotheses. Instead, because it focuses on a fundamental association between sensory input and motor output, it provides a proximate explanation for both.

While these three hypotheses have many similarities, each makes testable predictions about the types of niches occupied by animals with forward-facing eyes. If Cartmill's hypothesis is correct, then we would expect that all nocturnal predators have forward-facing eyes. The fine-branch arboreal hypothesis on the other hand predicts that animals that frequently forage in terminal branches will have forward-facing eyes regardless of diet. Praxis is a very broad concept that could provide an explanation for either of the other two hypotheses. Praxis predicts that optic orientation is correlated

with visually guided behavior rather than specific ecological variables. Animals with a large praxic field will have forward-facing eyes regardless of diet, substrate use, or activity cycle. Ideally, we would like to discover that one of these hypotheses is correct, and that the other two are not. It would then be possible to definitively resolve why primates have forward-facing eyes.

However, the answer might turn out to be a very complex one. If there are multiple uses for forward-facing eyes, then all three hypotheses could be correct, making it difficult to draw firm conclusions about the origins of convergent eyes in primates. Additionally, these hypotheses are not necessarily independent. For example, it is possible that praxis and not the other two hypotheses could explain forward-facing eyes. It is equally possible that praxis could provide an explanation as to why either of the other two hypotheses is correct.

I chose to examine the functional basis of the praxic hypothesis because it has the potential to explain the extreme convergence seen in primates as well as more moderate degrees observed in other animals. Additionally, the praxic hypothesis is well supported by the physiological and behavioral data, and lends itself to straightforward functional tests. Furthermore, it is imperative to examine binocular vision from a functional perspective, as a functional link is important in any study of adaptation, but most of the previous research has focused solely on morphology.

The praxic hypothesis states that **the size of an animal's binocular field is correlated with the region over which it must make precise visually guided movements without reorienting** (Hughes 1977). There are two assumptions built into this idea that have not been rigorously tested: 1) The visual system can extract cues from the binocular visual field that are useful for guiding precise movements and are not available in the monocular visual field, and 2) Increasing the binocular visual field is advantageous to animals that must make visually guided movements over a wide area. I propose to evaluate the praxic hypothesis by experimentally testing Assumption 1. **The overall aim of this study is to test the effect of removing binocular cues on reaching, grasping, and locomotion.** I am proposing four specific aims that by removing binocular cues elicit a gradient of hypothesized behavior deficits, from minor to severe.

Before testing such a specific hypothesis I will review previous attempts at answering why primates have forward facing eyes. To answer such a question from an evolutionary perspective it is necessary to demonstrate a link between form, function, and environment. I will first explore at a very general level how such a relationship might originate, and then review anatomical studies of the eye and orbit to determine if there are consistent associations between forward-facing eyes and specific niches. Finally, I will examine behavioral and physiological studies that provide a functional

explanation as to why forward-facing eyes are useful in different environments. I will demonstrate that the praxic hypothesis is consistent with the available anatomical and behavioral data, and based on this previous research devise a set of experiments that will test the underlying functional assumptions of the praxic hypothesis.

## **1.1 Adaptation**

Darwin's theory of descent with modification via natural selection (1859) is the only reasonable explanation of how forward-facing eyes could develop in primates as a means to cope with their environment. His theory, as applied to the evolution of optic orientation in primates, suggests that there must have been heritable variation in eye orientation among some ancestral population of primates. Variants with more forward-facing eyes were better suited to survive and reproduce in their environment, and thus contributed more offspring to future generations. To show that forward-facing eyes are an adaptation to a specific environment, we must first carefully consider the meaning of the term adaptation.

While many definitions of adaptation have been proposed, most fall into one of two broad categories – historical or non-historical (Ross 2002). The historical model states that adaptations are generated and maintained by natural selection for their current biological role (Gould and Vrba 1982, Sober 1984). To rigorously prove a historical adaptive hypothesis we would therefore need information on trait heritability,



trait polarity, allelic frequencies, and evidence of selection in a specific environment (Brandon 1990). Different authors choose to emphasize distinct subsets of these criteria to identify adaptations. Coddington, for example, requires phylogenetic information to show that an adaptation is apomorphic (1988). While the evolutionary history of a trait is interesting by itself, it should not be tied to a definition of adaptation.

A more appropriate and useful definition would permit us to show that forward-facing eyes are an adaptation because they make an animal better suited to survive and reproduce in a specific environment. Such non-historical definitions focus on the current utility of a trait (Bock and von Wahlert 1965). For example, Reeve and Sherman propose that an adaptation is a “phenotypic variant that results in the highest fitness among a specified set of variants in a given environment” (1993, p. 9). While this concept more closely approximates an intuitive understanding of adaptation, it is still very difficult to apply in most situations. Since a measure of fitness is required to identify adaptations, we cannot make adaptive hypotheses about fossil taxa.

Additionally, fitness for a given trait, whether defined as reproductive success or performance, is difficult to measure for most extant species. In an attempt to create a rigorous yet widely applicable definition, Kay and Cartmill proposed that a trait is likely to have a specific biological role in fossil taxa if it meets three criteria (1977). First, in all extant species possessing the trait, it must be used for the same biological role. Second,

there is no evidence that the trait evolved before the proposed biological role. Third, the trait has some functional relationship to the biological role. Such a definition allows us to recognize aspects of an animal's behavior and ecology from its morphology, but it does not necessarily imply that the given form-function complex is an adaptation. However, if the relationship holds for a large comparative sample, natural selection is the only process that can reasonably have created such convergences. Traits that have become fixed in a population probably had the highest fitness among all available variants, and can therefore be considered adaptations. While this assumption seems reasonable, we must consider potential pitfalls to this approach such as phylogenetic inertia, multiple functions, and phylogenetic distance (Ross 2002).

Phylogenetic inertia can maintain a trait that was initially selected for in a population even if the trait becomes neutral or even maladaptive at some future time. Epistasis, linkage disequilibrium, pleiotropy, and developmental constraints all have the potential to maintain maladaptive or neutral traits (Bell 1997, Cheverud 1988). For example, forward-facing eyes might have initially evolved as an adaptation for nocturnal predation. As neurological, osteological, and myological specializations occurred to accommodate this change it might become more difficult to evolve laterally placed eyes. Thus, even though most extant primates are not nocturnal predators they might maintain the forward-facing eyes of their ancestors. Moreover, if stabilizing

selection is acting to maintain a trait, considering multiple taxa that all gained the trait from a single evolutionary event could skew a comparative analysis. If either phylogenetic inertia or a phylogenetic bias is a potential problem, then a correction such as independent contrasts should be used as a control (Purvis and Webster 1999).

Another problem with using the comparative method to evaluate adaptive hypotheses is that a single trait can have many functions. Forward-facing eyes might be advantageous to nocturnal animals using vision in low-light conditions, to predators detecting cryptic prey, to saltators judging the length of a gap, and to prehensile animals estimating shape. By carefully defining the trait in question, it is possible to reduce the field of possibilities. For example, it is unlikely that forward-facing eyes are an adaptation for saltatory locomotion in primates, because binocular cues are reasonable estimates of distance only at close range (Cartmill 1970, Howard and Rogers 1995, Tresilian et al. 1999). It may be necessary to consider adding traits to an adaptive hypothesis. For instance, the combination of forward-facing eyes, high molar shearing crests, and small body size strongly suggest that a species is a visually guided predator.

Finally, while convergence of form and function in widely separated taxa can be strong evidence for an adaptive hypothesis, it also presents a potential problem. If we equate behaviors of phylogenetically distant species, we run the risk of making a spurious correlation. For instance, lions and tarsiers are both nocturnal predators, and

both have forward-facing eyes. However, tarsiers might be using binocular cues to estimate shape during grasping, while lions might simply be improving night vision. If the relevant behaviors and environments are very different, it might not make sense to use the same term to describe the foraging strategy of both taxa. In such cases, comparing homologies between sister taxa might provide more conclusive evidence (Larson 1998). Unfortunately, a comparative analysis based on homologies is extremely sensitive to the density and accuracy of the phylogenetic information. Furthermore, relative to convergence it is more likely that homologies could develop by non-selective mechanisms such as genetic correlation or genetic drift. Ideally, a comparative analysis should make use of both types of information.

A final problem associated with comparative tests is whether all animals with a given trait must have the same trait – function complex or vice versa should be the gold standard for a comparative definition of adaptation. Although the criteria delineated by Kay and Cartmill (1977) are often used as a definition for adaptation (Ross 2002), they are instead a formula for extrapolating form from function in fossil taxa. The importance of adaptation in creating this form-function complex is acknowledged, but the formula was not intended as a definition of adaptation itself. Cartmill (1990) argues that in a comparative definition of adaptation all animals that share some biological role must use the given trait for the same function.

Ideally, to be confident in our adaptational hypothesis we would like both to be true. The 1977 criteria reduce the chance of a false association in a common trait. If all animals had forward facing eyes, we would not be impressed that nocturnal visual predators also have forward facing eyes. The 1990 criteria increase our confidence in the functional link between morphology and biological role. However, we must acknowledge that convergence and multiple functions for a given trait will generally prevent either of these 1:1 rules holding true. We can relax these criteria and determine whether morphology and ecology evolve together more often than expected by chance or even use a more stringent cutoff without requiring a one-to-one association.

A careful application of the comparative method can suggest a form-function relationship that may reasonably be interpreted as an adaptation. Such an analysis should take phylogeny into account, precisely define the trait, function, and adaptive hypothesis, and use evidence derived from both convergences and homologies. While the origin of the trait and its relative fitness should be considered, the comparative method by itself can provide us with a wealth of information. Using the definition of Kay and Cartmill as a guide, I will examine the evidence for a link between estimates of forward-facing eyes, such as orbit orientation, visual field overlap, and optic axis orientation, and an animal's behavior and ecology. I will then review the support for a functional link between forward-facing eyes and their hypothesized biological role.

## **1.2 Form**

### **1.2.1 Orbit Orientation**

The earliest attempts to quantify eye orientation focused on the placement of the orbits within the skull (Mueller 1826). While orbital placement is not always an accurate estimate of eye orientation, it is strongly correlated (Heesy 2004). Orbital estimates are advantageous because they are easily measured on large comparative samples, and can be applied to fossils. While there are many possible measures of orbital direction, two features, frontation and convergence, capture most of the salient variation. Frontation measures the degree to which the eyes point forward and convergence measures the degree to which the eyes point in the same direction. Orbital convergence is the trait most easily linked to binocular visual cues, and I will therefore explore whether or not a high degree of orbital convergence is associated with certain types of substrate use, activity pattern, or foraging strategy.

An examination of orbit orientation within primates yields some support for the visual-predation hypothesis. Once body size is taken into account, it is clear that the most insectivorous nocturnal primates, tarsiers, lorises, and *Aotus*, have relatively high degrees of convergence (Cartmill 1970, Ross 1994). Lorises do not have particularly high values when compared to haplorhines, but they are much more convergent than other strepsirrhines. However, other nocturnal insectivores such as cheirogaelids and

galagids have relatively low values of convergence. Not much else can be inferred about the function of orbital convergence from comparative data on primates. This is in part because most haplorhines are diurnal and either herbivorous or omnivorous. While strepsirrhines show more niche diversity, it is still very difficult to tease apart the separate effects of substrate use, activity patterns, and foraging strategies. It is therefore necessary to expand our comparative sample.

A broad sample of arboreal mammals indicates that nocturnal predators have higher values of orbital convergence than more herbivorous mammals or diurnal predators (Cartmill 1970). Didelphid marsupials are all nocturnal omnivores. For the didelphids and for all species with orbital data, ecological information is taken from Cartmill (1970) and checked against Nowak (1999). Within didelphids orbital convergence is moderately high with little variation among species – even between the highly arboreal *Caluromys philander* and the largely terrestrial *Monodelphis brevicaudata*. Phalangerid marsupials are all nocturnal arborealists with moderate to high orbital convergence. Insectivorous species such as *Dactylopsila trivirgata*, *Dactylonax vulpecula*, and *Eudromicia caudata* have the highest values of orbital convergence, while the highly herbivorous species, *Pseudcheirus lemuroides* and *Trichosurus vulpecula* have relatively low values. Less folivorous species such as *Phalanger orientalis* and *P. maculatus* have intermediate values. The sciurine rodents are diurnal and mostly herbivorous. Overall

these animals have low convergence values, and there does not appear to be a consistent effect of arboreality on orbit orientation. The most insectivorous species *Rhinosciurus* and *Dremomys* have moderate values for convergence. Among tree shrews, all of which are at least partially faunivorous, the nocturnal *Ptilocercus* shows the greatest degree of orbital convergence. Additionally, it is important to note that while most tree shrews are largely terrestrial, the nocturnal arborealist *Ptilocercus* has high convergence values and the more diurnal arborealist *Tupaia minor* has moderate convergence. Procyonids are nocturnal carnivorans with diverse locomotor and dietary adaptations. Despite variation in behavior and ecology there does not appear to be much diversity in orbital convergence. The exception, *Nasua narica*, is a diurnal predator with relatively low values of convergence. Viverrids are nocturnal carnivorans with high values of orbital convergence. All of the species in which orbit orientation is available include a moderate to high degree of animal matter in their diets. However, most species fall within a narrow band of convergence values regardless of diet composition. The lowest values of convergence occur in the two most frugivorous species, *Arctictis binturong* and *Nandinia binotata*, and in *Herpestes edwardsi*, which often hunts by day. The species with the highest values of convergence, *Genetta rubriginosa*, is the most faunivorous taxon in the group.



Additional support for the visual-predation hypothesis was provided by a study of orbital convergence in 31 felid species, 28 herpestid species, and 63 pteropodids (Noble et al. 2000). In general, the nocturnal predators, felids, show more convergence than herpestids, which are more active during the day. In turn, herpestids are more convergent than the nocturnal frugivores, pteropodids. However, within each of these groups there exists substantial variation in orbital convergence. Since values were not reported for individual species, we cannot make detailed ecological comparisons or determine if there is a phylogenetic bias.

A large database of orbital convergence values was recently introduced into the literature (Heesy 2008). In this exhaustive survey of mammalian orbits, faunivorous species demonstrate higher convergence values than non faunivorous or opportunistic feeders, nocturnal and cathemeral species have higher values than diurnal species, and arboreal mammals have higher values than terrestrial or aerial species. Activity pattern, food preference, and substrate use all remain significant even after removing anthropoids and marsupials from the analysis. Not until all strepsirrhines, marsupials, and anthropoids are removed does substrate preference drop out as a significant determinant of convergence. Food preference and activity pattern remain significant.

A further analysis was undertaken on ecological groups rather than individual ecological categories. For example convergence values were calculated for all nocturnal

arboreal predators and all diurnal terrestrial faunivores. When examining all mammals together eight of the top eleven most convergent categories are arboreal including all of the top five. Only one of the bottom eleven categories is arboreal. When only eutherian mammals excluding anthropoids are considered, six of the top ten categories are arboreal and two of the bottom eleven are arboreal. When only non primate eutherian mammals are examined four of the top ten are arboreal and three of the bottom half are arboreal.

There are no phylogenetic methods available for the MANOVA's used in this analysis. Broad phylogenetic comparisons were made by removing large taxonomic groups. Marsupials were removed because their circumorbital anatomy is highly constrained and anthropoids were removed because they are so highly divergent from both strepsirrhines and other eutherian mammals. Even after these changes it is not until strepsirrhines are removed from the analysis that substrate is lost as a significant determinant of convergence. Heesy argues this is strong evidence that substrate use does not contribute to evolution of convergence of the orbits.

While this is a reasonable assertion, it is difficult to dismiss the strong association between high convergence and arboreality seen in marsupials and primates. It is possible that this association is due to morphological constraints or phylogenetic inertia. Alternatively, a functional explanation cannot be rejected. Primates and some

marsupials might use a large binocular field to guide placement of long mobile grasping forelimbs on complex discontinuous substrates. Arboreal animals with shorter limbs and claws that primarily use large branches might not benefit from such a wide binocular field. Further analysis using more refined categories for arboreality and substrate use coupled with a phylogenetic approach are needed to make more definitive conclusions on theories of primate origins.

Do the visual predation, fine-branch arboreal, or praxic hypotheses receive strong support from the available data on orbit orientation? The visual predation hypothesis is supported by the fact that within taxonomic groups nocturnal predators usually have the highest degrees of convergence, and there are no nocturnal predators with low values of convergence. The fine-branch arboreal hypothesis is not supported because contrary to what it predicts, species that frequent fine branches, like *Caluromys* and *Microcebus*, do not appear to have particularly high values for orbital convergence relative to closely related species. On the other hand, the praxic hypothesis does receive some validation. Species that habitually use grasping for locomotion and foraging such as primates, didelphids, phalangerids, and some procyonids have the highest values of orbital convergence. While the nocturnal predators within these groups are extremely convergent, even the most herbivorous species show marked convergence.

While orbital convergence in mammals suggests some ecological explanations as to why primates have such a distinctive optic orientation, it would be beneficial to check these hypotheses against more direct anatomical measures of the visual system.

Information about the eye itself is more closely related to functional hypotheses involving vergence, stereopsis, optic flow fields, and summation, and might make it possible to refine ecological conclusions. There are at least two such measures, retinal visual-field overlap and optic axis orientation, available for a large comparative sample.

### **1.2.2 Ophthalmoscopically determined visual fields**

Two widely used methods, ophthalmoscopic and transcleral illumination have been used to measure visual fields in comparative samples. Ophthalmoscopic methods can be used to measure either the optic or retinal visual fields. The optic field is the region of space over which the pupil is visible. The retinal field is the region of space over which the retina is visible through the pupil. To determine the extent of each field the animal's head is placed in the center of an arc defined by a metal arm with a fixed radius. The arm is moved through a latitudinal plane, and an ophthalmoscope at its far end is used to record the angle at which the retina or pupil is no longer visible. After the limits are determined for one plane, the arm is incremented or decremented relative to the horizontal, and new limits are determined. The arc measurable by this apparatus

does not extend through a full 360°, and it is therefore necessary to determine anterior and posterior fields separately.

The second widely used method for estimating visual fields, transcleral illumination, was first developed by Tschermak-Sysenegg (1902). To determine the extent of the region of space imaged by the retina, most of the head is removed – leaving the posterior of the eye to the tip of the snout untouched. A light source is placed behind the eyes, and an observer determines the region of space over which the retina is visible through the pupil. I will discuss the importance of ophthalmoscopic and transcleral studies for primate optic orientation separately.

Ophthalmoscopic methods were first used as a comparative tool by Schneider (1954a, 1954b). However, since that time there has been little work done in this field. Two independent labs have examined visual fields in frogs and toads (Fite 1973, Grobstein 1980). Several Australian marsupials have been recently studied (Arrese et al. 2002). Finally, Graham Martin has examined a large number of avian species over the past 20 years (Martin 1999a). I will discuss the findings of each of these three groups separately, and then examine the comprehensive implications for the evolution of binocular vision in primates.

## Visual fields in frogs and toads

A study of the optic visual fields of North American frogs (*Rana clamitans*, *R. catesbeiana*, *R. pipiens*, and *R. palustris*) and toads (*Bufo americanus*, *B. terrestris*, and *B. marinus*), reveals two major points relevant to the evolution of primate optic orientation (Fite 1973). First, differences in visual fields are related to visually guided behavior, and not activity cycle. Second, the praxic field does not necessarily correspond to the width of the binocular field.

The frogs in this study are arrhythmic and aquatic, and the toads are nocturnal and terrestrial. Since aquatic species spend most of their time at the water level, prey will usually approach in the superior portion of the visual field. In terrestrial species, prey will usually be located in the inferior visual field. It is noteworthy that *Rana* has a wide superior binocular field, while *Bufo* has a wide inferior binocular field. Additionally, *Bufo* species have a smaller maximum binocular field width than the diurnal *Rana*.

It appears that variations in binocular field width are explained by behavioral differences between frogs and toads and not by activity cycles. Both frogs and toads capture prey by using tongue projection. Before attacking frogs will leap up to 45° from their starting position without reorienting, and miss 2-7% of the time (Fite 1973). On the other hand, toads will leap only up to 15° off of their starting position without

reorienting, and never miss. Therefore, frogs, which have a 45° praxic field, have a larger binocular field than toads, which have only a 15° praxic field. However, these differences are small and it is not clear whether or not they are statistically significant. Furthermore, in both groups the binocular field is much larger than the praxic field. Frogs and toads may use the additional overlap to guide orienting behavior or detect prey. Moreover, the simple environment and immobile prey may not be the best conditions for measuring praxis in these animals. Regardless, in the only study for which praxic and binocular field width are known the two do not correspond in any straightforward manner.

Despite these problems, it is clear that the nocturnal visual predator, *Bufo*, has a smaller binocular field than the diurnal visual predator, *Rana*. The greater binocular field in *Rana* might be related to its larger praxic field. With only two taxa available for comparison it is difficult to untangle these results from confounding ecological and phylogenetic factors. For example, *Rana's* large binocular field might also be related to the fact that it is more aquatic than *Bufo* (Martin 1999a). Without placing these species in a phylogenetic context we cannot deny the possibility that all frogs have large binocular fields relative to toads regardless of environmental conditions.

## Visual fields in Australian marsupials

The visual-field information available for Australian marsupials points to at least three broad ecological categories: nocturnal faunivores, nocturnal arborealists, and terrestrial herbivores. The northern native cat, *Dasyurus hallucatus*, and the fat-tailed dunnart, *Sminthopsis crassicaudata*, are nocturnal predators, forage in trees, but not in fine branches and have maximum binocular-field widths of 125° and 140° respectively (Rodger et al. 1998, Harman et al. 1986). The terrestrial herbivores, the tammar wallaby, *Macropus eugenii*, and the quokka, *Setonix brachyurus*, have maximum binocular-field widths of 60° and 80° respectively (Dunlop et al. 1997, Wye-Dvorak et al. 1987). The nocturnal arborealists, the brush-tailed opossum, *Trichosurus vulpecula*, and the honey possum, *Tarsipes rostratus*, eat very little animal matter and have maximum binocular field widths of 125° and 160° respectively (Sousa et al. 1978, Arrese et al. 2002). Finally, the numbat, *Myrmecobius fasciatus*, does not fit neatly into any broad ecological categories. It is the only diurnal marsupial for which visual-field information is known. It is almost completely terrestrial, feeds primarily on termites which it digs out of the ground or scratches out of decaying logs, and has a maximum binocular-field width of 80° (Arrese et al. 2000).

Four interesting conclusions can be drawn about the relationship between visual-field overlap and ecological variables in Australian marsupials. First, nocturnality by



itself is not sufficient to select for substantial overlap. In the nocturnal species, overlap ranges from 60° in the tammar wallaby to 160° in the honey possum. However, there are no diurnal-nocturnal comparisons that can be made for closely related species. Second, visual field overlap in predatory species ranges from 140° in the nocturnal fat-tailed dunnart to 80° in the diurnal numbat. However, given the specialized nature of prey detection and acquisition in the numbat, this may not be a particularly useful comparison. Third, nocturnal terrestrial herbivores have far less overlap than nocturnal faunivores. Finally, nocturnal animals with a large praxic space, such as the honey possum and brush-tailed possum, have at least as much overlap as nocturnal faunivores.

Unfortunately, these ecological conclusions do little to discriminate between our three initial hypotheses. While visually guided nocturnal predators have substantial overlap, there are not any visually guided diurnal predators for comparison. The fine-branch arborealist, *Tarsipes*, has a large binocular field, but so does *Trichosurus*, which exhibits visually guided grasping, but does not forage in fine branches. Thus, each hypothesis receives some support from at least one species, and there are no comparisons that would allow us to falsify any of the hypotheses.

These studies also show that unocular fields can vary greatly across taxa. Early comparative works hypothesized that the unocular field was about 170° in all vertebrates (Walls 1942, Duke-Elder 1958). Thus, animals had a fixed number of degrees

of visual field, which could be spent on either binocular overlap or panoramic vision. However, the honey possum and fat-tailed dunnart have a binocular field similar to primates, but also have almost complete panoramic vision. A large cornea, dorsal placement of the eyes, and an expanded retina account for the extensive binocular and panoramic fields. One disadvantage of this arrangement is that the dorsal placement of the eyes yields a narrow binocular overlap inferiorly – an area important for visual guidance of the forelimbs.

### **Visual fields in birds**

Over the last 20 years Graham Martin has generated a large body of literature on the visual fields of at least 23 species of birds. These studies have painted a broad picture of the relationship between visual fields and avian ecology. There are at least four groups of birds that share a similar visual-field topography: visually guided foragers; tactile foragers and filter feeders; owls; and diving birds.

Visually guided foragers such as the Cattle Egret, Night Heron, King Penguin, Humboldt Penguin, Ostrich, Stone-curlew, Rock Pigeon, Short-toed Eagle, White-chinned Petrel, and Widgeon have a binocular field that is long in the mid-sagittal plane, 80°-180°, and mediolaterally narrow, 20°-30°, throughout (Martin and Katzir 1994a, Katzir and Martin 1998, Martin 1999b, Martin and Young 1984, Martin and Katzir 1995, Martin and Katzir 1994b, Martin and Young 1983, Martin and Katzir 1999, Martin and

Prince 2001, Guillemain et al. 2002). The bill is located approximately in the center of the region of overlap, where the binocular field is at its widest. The species associated with this topography are diverse ecologically, behaviorally, and phylogenetically. The common trait linking these animals is that all take food with the bill or talons using visual cues.

The second ecological group is composed of species such as the Mallard, Shoveler, Eurasian Woodcock, and Antarctic Prion that are either filter feeders or probe in muddy environments (Martin 1986, Guillemain et al. 2002, Martin 1994, Martin and Prince 2001). Food is not usually inspected visually, and the binocular field is extremely narrow, generally less than  $10^\circ$ . Additionally, the total visual field covers a larger area posterodorsally. The bill is located within the ventral limit of the binocular field, where overlap is negligible.

The third group contains one species, the Tawny Owl, which exhibits a unique topography. The binocular field is wide horizontally,  $50^\circ$ , but narrow in the mid-sagittal,  $80^\circ$  (Martin 1984). Furthermore, the bill is located just inferior to the ventral limit of the binocular field. Owls could be using this additional region of overlap to improve acuity or contrast detection using binocular summation. Additionally, there is some evidence that owls could be using disparity as a cue to distance (Pettigrew and

Konishi 1976). It is not clear why owls, and not other nocturnal predatory birds, such as Stone-curlew and Night Herons, have such extensive overlap.

The final group spends significant time underwater and shows yet another interesting trend in visual-field topography. The King Penguin, Humboldt Penguin, Grey-headed Albatross, Black-browed Albatross, and White-chinned Petrel all have significantly more overlap, 30° -50°, than other birds – excluding the owl (Albatross from Martin 1998). Since the refractive index of avian corneas is similar to that of water, the monocular field in each eye will be significantly compacted upon submersion. However, the large binocular fields in these species preserve some overlap underwater, albeit considerably reduced.

The first three ecological categories have some relevance to the evolution of eye orientation in primates. The praxic hypothesis is supported by the fact that visual-field differences between groups one and two are related to whether or not foraging is visually guided rather than to differences in ecological variables. The visual-predation hypothesis is supported by the fact that owls have such a large overlap. However, other nocturnal predators such as Night Herons and Stone-curlews do not have substantial overlap. If the visual-predation hypothesis is correct, then an explanation must be proposed for this discrepancy.

### **1.2.3 Visual fields determined with transcleral methods**

Like ophthalmoscopic methods, transcleral illumination provides an estimate of an animal's visual field. There are several methodological problems with this technique that discourage a detailed analysis. Moreover, the original data come from old French and German manuscripts (Muller 1826, Tschermak-Sysenegg 1902, Rochon-Duvigneaud 1922, Thieulin 1927, Verrier 1927, Kahmann 1932, and Pisa 1939). I will make a few brief points based on several reviews (Walls 1942, Duke-Elder 1958, Polyak 1957, and Hughes 1977).

It has long been recognized that there is a general trend in increasing visual-field overlap from fishes, to amphibians, to reptiles and birds, to mammals. However, within these broad taxonomic classifications there is substantial variation, which seems to correlate with several ecological variables. Additionally, there is substantial overlap among these groups. In fishes, herbivorous species tend to have overlaps of 10°-20°, while predatory species have overlaps of 30°-40°. Many deep-sea fishes have forward-facing eyes, but also have a tubular eye design that prevents much overlap. Not much is known about overlap in amphibians, which appears to be generally small, although anurans and tongue-projecting salamanders have substantial overlap. The pattern of low overlap in herbivorous species and substantial overlap in predatory species is also seen in reptiles. Species that make rapid strikes from a distance, such as longneck turtles

and tree snakes have more overlap than other predators. Transcleral studies suggest that predatory birds ( $35^{\circ}$ - $70^{\circ}$ ) have larger overlap than herbivorous species ( $< 30^{\circ}$ ). In mammals, squirrels show a small overlap ( $25^{\circ}$ - $30^{\circ}$ ), followed by horses ( $60^{\circ}$ - $70^{\circ}$ ), sheep ( $60^{\circ}$ - $80^{\circ}$ ), and elephants ( $67^{\circ}$ ). Dogs have around  $100^{\circ}$  of overlap, while cats and primates have  $>120^{\circ}$ . The only consistent ecological relationship identified by these studies is the association between relatively high degrees of overlap and predation. There are not suitable data available to make the necessary comparisons to support or falsify the visual predation, fine-branch arboreal, or praxic hypothesis.

### **1.2.3 Optic axes**

Visual-field overlap is one consequence of forward-facing eyes, but it is not by itself a direct indicator of eye orientation. The optic and visual axes give a better indication of the position of the eye. Unfortunately, virtually nothing is known about the distribution of visual-axis orientation. However, the orientation of the optic axes has been reported for many mammals by Johnson (1901) and for birds by Martin. Rodents, marsupials, and ungulates have optic axes that diverge from the mid-sagittal plane by  $30^{\circ}$ - $80^{\circ}$ . Bats have divergences of about  $20^{\circ}$ , and prosimians have divergences of about  $10^{\circ}$ . Anthropoids have almost parallel optic axes. Interspecific differences in optic-axis divergence correspond well with visual-field overlap. Predatory species have more convergent optic axes than herbivorous species, and nocturnal predators and primates

have more convergence than all other species. Fruit bats and echidnas are interesting exceptions to this pattern. Both have convergences approaching that of nocturnal predators. In birds, the orientation of the optic axis does not appear to be correlated with any obvious ecological variables. The two species with the smallest overlap, the Eurasian Woodcock and Mallard, have the most divergent optic axes,  $\sim 170^\circ$ , and the species with the most overlap, the Tawny Owl, has the least divergent,  $55^\circ$ . Divergence in other species varies from  $112^\circ$  in the Short-toed Eagle to  $149^\circ$  in the Stone-curlew. In these species divergence does not seem to correlate with the width of the binocular or total visual field.

The optic-axis information from mammals tends to support the nocturnal visual-predation hypothesis. Nocturnal predators, represented by a few felids, have highly convergent optic axes. The only animals with a large praxic space are primates, which of course have highly convergent orbits. Surprisingly, echidnas and fruit bats also have forward-facing eyes. It is not clear how these two animals relate to hypotheses of primate evolution.

#### **1.2.4 Methodological conclusions**

The methods used to determine orientation of the orbit and of the optic axis are reliable and relatively straightforward to interpret. On the other hand visual fields have been measured in a variety of ways, some of which were not presented here, that are not

always consistent. While a large body of comparative data exists for transcleral illumination, there are several problems with this method. First, a standard position of the eye was never determined. Thus, it is impossible to tell whether overlap is due to natural orientation or an artifact of eye realignment during transection of the head. Additionally, it is not known how effective this method is at actually determining the extent of the retina. Postmortem tissue degeneration may make this task particularly difficult. Despite these drawbacks, studies based on transcleral illumination comprise the bulk of our knowledge on visual-field overlap. Until better data are available, they should be used as an initial guide.

When using ophthalmoscopic methods, retinal and not optic criteria should be used to determine visual fields. In *Rana*, optic measurements overestimate the true retinal field by up to 70° (Grobstein 1980). It is not clear why this should be the case. Hughes (1977) suggests that animals with forward-facing eyes might avoid using peripheral optics for objects directly in front of them. Thus, the retina does not capture all available light, because rays falling on the periphery may be badly distorted by spherical aberration. However, this optic-retinal discrepancy does not apply only to frontal-eyed animals (Martin 1999a). In any case, optic fields should not be used as a proxy for visual fields.



Ophthalmoscopic determinations of the retinal visual field give a good estimate of the visual information available to an organism. This method is relatively non-invasive and can be used to gather data on a large number of species in a short period of time. Unfortunately, eye movements and variation in sensitivity across the retina are difficult to accurately take into account with this method alone. The effects of eye movements can be incorporated into the total visual field by estimating the total dynamic visual field. Novel sounds or lights are used to attract a subject's attention peripherally, thereby determining the lateral extent of the dynamic visual field. Watching the position of retinal landmarks should give an indication of whether or not the animal attempts to fixate on the new stimulus. Variation in sensitivity is more difficult to quantify. To do so, it would be necessary to train animals to fixate on a given point, and make them respond to stimulus detection. Eye movements would also have to be tracked throughout the course of such an experiment. Visual fields in humans are tested using an automated perimeter, which creates a topographical map of sensitivity. It might be possible to train a small number of animals to use a similar device to ensure that retinal estimates of overlap correspond to what subjects can actually see.

If ophthalmoscopic measures of retinal visual fields are biologically meaningful, they should correspond to behaviorally and physiologically determined measures. In *Rana pipiens*, behaviorally determined estimates coincide within  $\pm 10^\circ$  with the

ophthalmoscopically determined results (Grobstein 1980). However, there is substantial variability around the means, and statistical significance was not determined. Visual fields have also been determined behaviorally for cats and dogs. In cats the binocular visual field is about 90°, which is 30° less than the ophthalmoscopically determined visual field (Sherman 1973). In dogs the behaviorally determined 60° field is also 30° less than the ophthalmoscopically determined field of 90° (Sherman and Wilson 1975). These three comparisons suggest that in some cases there may be a discrepancy between the area of space over which light reaches the retina and the area over which animals can respond to visual stimuli. However, the behavioral methods used are very crude, and should be viewed skeptically.

Another method developed for use in human infants is more accurate, and has safeguards against experimental bias (Cummings et al. 1987). In these studies, an infant's attention is drawn to a central blinking light. One observer follows the subject's gaze while looking through a pinhole, and estimates when the infant is fixating the central light. On a signal from the observer another researcher begins lighting up LED's, arranged along 24 meridia at 7° intervals, moving from the periphery toward the center along a pre-determined meridian. The observer determines the point at which the infant switches fixation from the central to peripheral LED. This technique would transfer well to animal studies and should be considered in the future.

### 1.2.5 Ecological conclusions

Studies of visual fields, eye orientation, and orbit orientation reveal many correlations between forward-facing eyes and ecology. Several of these associations have important implications for the study of primate origins. The visual predation and praxic hypothesis each receive some support, while the fine-branch arboreal hypothesis is seriously challenged.

The visual predation hypothesis receives the strongest – though not unconditional – support from comparative anatomy. For any given taxon, nocturnal visual predators always have the highest orbital convergence. Studies of visual-field overlap in Australian marsupials show that two nocturnal predators do in fact have a large binocular field, but there are no diurnal predators for comparison. Some evidence based on visual fields provides a challenge to the visual-predation hypothesis.

First, species of *Rana*, which are diurnal predators, have larger binocular fields than *Bufo* species, which are nocturnal predators. Furthermore, while some species of owl do have large binocular fields, other predatory birds that hunt at night have a small degree of overlap. The sample of frogs and toads is not broad enough to determine if correlated ecological variables or phylogenetic constraints might be responsible for the observed differences. In birds, the patterns of visual-field topography appear to be very

different from anything seen in mammals. Though they demand further investigation, these counterexamples are not strong enough to falsify the visual-predation hypothesis.

Conclusions about the veracity of the fine-branch arboreal hypothesis and praxic hypothesis are closely linked. It is true that all fine-branch arborealists show moderate to high degrees of convergence. However, based on orbital and visual-field evidence they do not appear to be different from closely related species that exhibit visually guided grasping but are not active in terminal branches. Therefore, the earliest primates might have foraged in fine branches, but evidence from eye orientation alone suggests that they used vision to guide grasping. There are no examples of species that could potentially falsify the praxic hypothesis. However, a praxic field has only been quantified for a few species of frogs and toads. Animals that clearly have large praxic fields, such as all primates and some phalangerids, didelphids, and procyonids, also have large binocular fields. Without a repeatable quantitative method for measuring praxic fields, it is impossible to make definitive conclusions about the praxic hypothesis.

After sifting through all of the anatomical data fruit bats, some deep-sea fishes, and echidnas appear as strong outliers. All three have highly convergent eyes, and do not appear to fit with the fine-branch, praxic, or visual-predation hypotheses. It might be that operating in extreme low-light conditions provides selection for forward-facing

eyes. If this is the case, it is unclear why other nocturnal species do not appear to have substantial overlap.

If the earliest primates were visually guided nocturnal, insectivores, with grasping hands, they would certainly have been subjected to strong selection for forward-facing eyes. It is also possible that nocturnality or a large praxic field alone could have first selected for forward-facing eyes in primates. The existing data is not sufficient to satisfactorily prove or disprove any of these hypotheses, and further anatomical studies are required. Since praxis and the visual-predation hypothesis receive some support, I will review behavioral and physiological studies to determine if there is a functional link between these hypotheses and forward-facing eyes. For the purposes of this study it is important to note that while the praxic hypothesis is not the only viable explanation, it does fit the available anatomical data.

### **1.3 Function**

To show convincingly that forward-facing eyes are related to a specific adaptive hypothesis, we must provide some ecologically relevant function for the trait. For example, if a reduction in an organism's binocular visual field inhibits its ability to capture prey, then we could conclude that forward-facing eyes are functionally related to prey detection and acquisition. Unfortunately, there are very few experiments that actually link the benefits of forward-facing eyes to a specific ecologically relevant

behavior. However, there is a substantial body of physiological and behavioral evidence to suggest that many animals have the biological potential to make use of forward-facing eyes. The myriad benefits of this distinctive optic orientation can be directly linked to the anatomic variables described above.

### **1.3.1 Convergent optic axes**

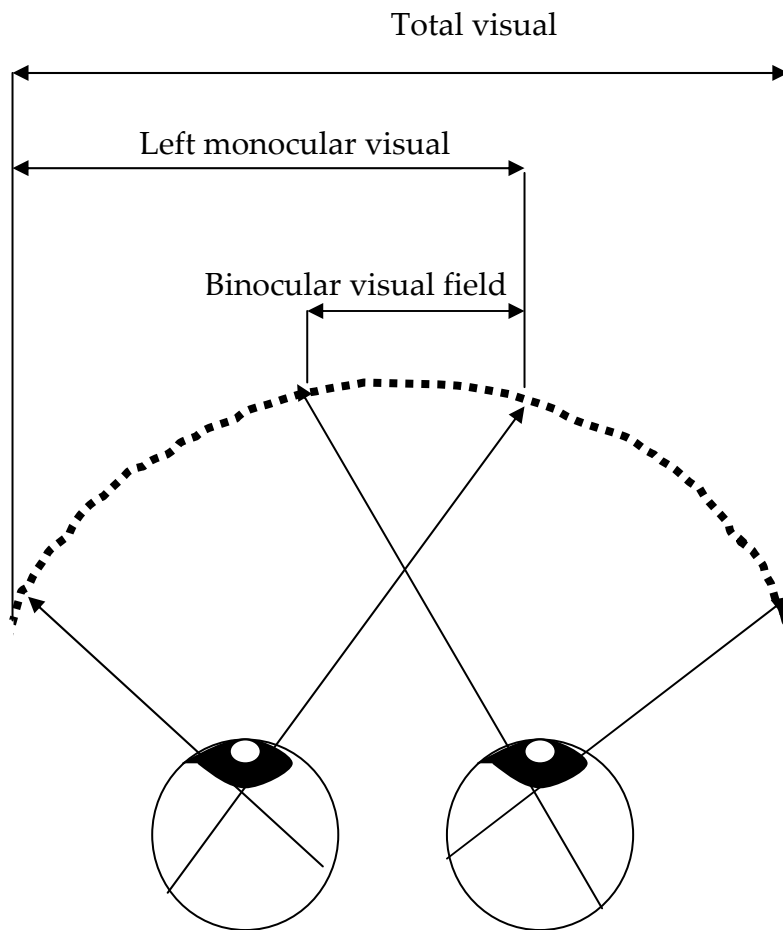
As the optic axes are swung forward, two major benefits accrue. First, the visual axis and optic axis can be closely aligned. The visual axis is a line passing through the area of highest acuity, the fovea, and the center of the points in visual space imaged on the fovea. The fovea is usually positioned on the retina so that it images objects directly in front of the animal. The optic axis is a line passing through the axis of symmetry of the lens and cornea. Light following this path is of the highest optical quality, because it has undergone the least distortion from spherical aberration. Thus, aligning these axes will provide the area of highest acuity with the light of the highest quality. Diurnal animals may accomplish this to some degree by narrowing the pupil width so that only light passing through the center of the lens and cornea reaches the fovea. However, in a nocturnal animal the pupil must be wide open to admit as much light as possible (Allman 1977). Thus, only by swinging the eyes forward can nocturnal animals align these two axes. While this phenomenon could explain frontal vision in such animals as deep-sea fishes, owls, some primates, echidnas, and fruit bats, there is no experimental

work to support it. Lenses found in organismal systems can change shape and vary optic properties with eccentricity avoiding some of the problems seen in manufactured lens systems. In fact some animals, such as rabbits and owls, do not have the predicted decrease in image quality at peripheral locations (Hughes and Vaney 1978, Murphy and Howland 1983). Neither animal shows the predicted peripheral astigmatism.

A second advantage of convergent optic axes is that the region over which both eyes can fixate simultaneously is increased. This is particularly important for primates, who usually image objects of interest on the foveae of both eyes. One advantage of bifoveation is that if the angle through which each eye must rotate to fixate the same object, the vergence angle, is known, then the distance to the object can be estimated. Vergence has a particularly strong effect on distance estimations for close objects and when few other cues are available such as during low light conditions (Tresilian et al. 1999). Moreover, vergence is more accurate than other cues when judging distance to small objects (Rogers and Bradshaw 1995). There is experimental evidence to suggest that the nervous system estimates vergence using either proprioceptive information from the extraocular muscles or an efferent copy of motor commands (Lal and Friedlander 1990, Toyama et al. 1984). Neurophysiological studies indicate that the amplitude of a neuronal response to horizontal disparities is changed in response to variations in vergence (Maunsell and Van Essen 1983, Roy et al. 1992). Thus vergence

may also be used to calibrate retinal disparities. While qualitative observations of vergence eye movements have been reported in a wide variety of vertebrates (Walls 1942), these observations have been quantified for rabbits, cats, macaques, and humans (Zuidam and Collewijn 1979, Hughes 1972, Howard and Rogers 1995). Among fishes, some species like *Haplochromis burtoni* show coordinated vergence movements to stimuli presented within their binocular visual field (Schwassmann 1968, Fernald 1985).





**Figure 1:** Diagrammatic representation of the total, monocular, and binocular visual fields

### **1.3.2 Increasing the contra lateral monocular visual field**

There are three potential advantages to increasing the contra lateral region of the monocular visual field, summation, symmetric optic-flow fields, and retinal disparity. A schematic of retinal fields is presented in Figure 1. First, binocular summation gives animals a better chance of detecting a stimulus with two eyes as opposed to one. Such an advantage could occur because two detectors have an improved probability of detecting any stimulus or because the signal-to-noise ratio is reduced (Pirenne 1943, Campbell and Green 1965). Empirical studies have shown that human subjects have improved contrast detection when using two eyes, but only near threshold capabilities (Legge 1984, Bearnse and Freeman 1994).

Second, radially symmetric optic-flow fields, generated by the movement of a scene across the retina during self-motion, can be used to estimate direction of travel and time to contact with approaching objects (Davies and Green 1994). There is some physiological evidence in birds, bees, and macaques of neurons that respond to symmetrically expanding images (Frost et al. 1994, Krapp and Hengstenberg 1996, Merchant et al. 2003). To obtain a radially symmetric image an animal must obtain symmetric points from the left and right portions of the visual field. Even an animal with no visual field overlap can do this if the images are combined at some point in visual processing. Therefore, the only advantage of having a large contralateral portion

of the monocular visual field would be if it were more efficient to acquire the symmetric points from a single eye rather than a combined image.

Third, retinal disparities can be used to estimate the distance and shape of targets (Howard and Rogers 1995). Horizontal disparities, caused by a slight mediolateral displacement of an image in the two eyes, provide the visual system with information about the three-dimensional shape of an object. A large number of physiological and behavioral studies demonstrate the ability of some animals to detect and act upon horizontal disparity cues.

### **1.3.3 Evidence for use of retinal disparity**

A neurophysiological basis for stereopsis was first demonstrated in the cat when neurons in the primary visual cortex were found to respond maximally to a narrow range of horizontal disparities (Barlow et al. 1967). A population of such neurons could code a wide range of positions in depth. Several other mammals such as sheep, rabbits, goats, and macaques were found to have similar cells in their primary visual cortex (Clarke et al. 1976, Hughes and Vaney 1982, Hubel and Wiesel 1970). Cells responsive to binocular disparity have also been found in the optic tecta of goldfish, trout, and *Rana pipiens* (Guthrie 1990, Galand and Liege 1974, Finch and Collett 1983). Among birds, barn owls, *Tyto alba*, great horned owls, *Bubo virginianus*, and burrowing owls, *Speotyto*

*cunicularia* show evidence of cells in the Wulst that are sensitive to a narrow range of disparity (Pettigrew 1979).

While there is an abundance of data showing that a diverse group of animals possess the ability to process binocular information, it is not clear how this information is used for either perception or motor control. Disparity-sensitive cells could potentially be useful for linking features, guiding vergence eye movements, depth perception, and motor control (DeAngelis 2000). Relatively few experiments have attempted to link disparity tuning in binocular neurons with complex behaviors, or have assessed the behavioral effect of altering disparity information in a population of binocular neurons.

The posterior parietal cortex (PPC) of macaques is one region where we are beginning to understand the link between binocular neurons and behavior. The PPC integrates sensory information during movement planning, and associates the physical properties of an object with the potential actions required to interact with that object (Andersen and Buneo 2002). Subregions of the PPC are responsible for planning specific types of actions such as reaches, grasps, and eye movements. For example, neurons located in the anterior region of the posterolateral intraparietal sulcus (AIP) are active during visually guided grasping (Mountcastle et al. 1975). A subset of these neurons is active when subjects grasp an object with a specific shape and orientation (Sakata et al. 1997). Additionally, these same neurons fire when the animal is presented with the

object even when grasping movements are not initiated. It is possible that these neurons are responsible for visuomotor transformations during grasping. The response properties of these neurons show subsets that are selective for axis orientation, shape orientation, and three-dimensional shape. All of these neurons respond vigorously to binocular stimuli, and poorly or not at all to monocular stimuli. The AIP provides an example of a neurological system associated with a known set of behaviors that requires information from both eyes to function optimally. Yet even in such a well-documented case it is not known which binocular cues are important nor how they are being used.

DeAngelis et al. (1998) discovered an even more precise role for binocular information during certain behaviors. In this study, macaques were first trained to recognize visual patterns in random-dot stereograms containing noise. Electrodes were used to find populations of neurons with similar disparity tuning in area MT. Microstimulation was then used to excite these neurons while the macaque performed a depth discrimination task. In almost all cases, stimulation caused subjects to misjudge depth in the direction of the disparity tuning previously recorded. Thus disparity cues are used in MT during a task that resembles the detection of cryptic moving objects in nature. While our understanding of the physiological basis of binocular vision has increased greatly over the last few decades, in most cases it remains difficult to link disparity tuning to complex motor or perceptual tasks.

Experiments that alter the visual system or visual cues have made some headway in determining the role of binocular vision in animal behavior. There are a number of experimental studies that demonstrate the use of binocular vision in several species by either changing disparity using prisms or removing binocular cues altogether with surgery. For example *Tenodera aridifolia sinensis*, a praying mantis, adjusts the distance at which it strikes prey when prisms are used to alter binocular disparity (Corrette 1989). Furthermore, the altered strike occurs at precisely the distance predicted by the change in disparity. A similar set of experiments was used to demonstrate stereopsis in toads. Placing a negative lens in front of an animal with one eye open caused it to undershoot its prey – suggesting accommodative depth estimation. However, if a negative lens is placed in front of an animal with both eyes open, prey acquisition is not affected (Collett 1977, Collett et al. 1987). Therefore, it is likely that disparity is being used to correct faulty accommodative information.

Other experiments remove all binocular cues by eliminating vision in one eye. For example, predatory insects such as tiger beetles, water scorpions, and dragonfly larvae experience difficulty capturing prey after one eye is removed (Cloarec 1978). In the jumping spider, *Trite planiceps*, the monocular visual fields of the pair of anterior-lateral eyes overlap substantially (Forster 1979). Removal of one of these eyes results in a substantial decrease in jumping accuracy. It is possible that these deficits are related

to the reduction of the total visual field, and not just the loss of binocular information. It is also possible that if given more time subjects could recover and capture prey normally. Studies of *Rana pipiens* indicate that after a brief recovery period subjects capture prey normally even though the optic tract of one eye has been severed (Ingle 1972). This is especially odd considering that toads are known to use binocular cues to estimate distance.

In addition to these experimental studies, observational data suggests that several species have the ability to use binocular information. In random-dot stereograms, patterns can be picked out of a noisy background only through the use of horizontal disparities. Psychophysical studies using stereograms have shown that humans, macaques, falcons (*Falco sparverius*), cats, meerkats (*Suricata suricatta*), and horses can perceive three-dimensional shape in a stimulus when horizontal disparity is the only depth cue present (Juelsz 1964, Bough 1970, Fox and Leguire 1978, Pitto et al. 1991, Timney et al. 1983, Timney and Keil 1994).

### **1.3.4 Kinematics of grasping in humans**

The most detailed account of the relationship between binocular visual input and motor output can be derived from kinematic studies of human grasping. To successfully grab an object a person must be able to discern extrinsic properties about an object such as its distance, direction, and orientation relative to their own position. In addition,

intrinsic object properties such as size and shape must be taken into account (Jeannerod 1988). These properties are thought to be used by the brain to guide two separate but coupled phases of movement, a reach and grasp. During the reach phase, distance and direction properties are used to guide movement of the arm so that the hand is placed in close proximity to the target. In the grasp phase, size and shape are used to guide the fingers in seizing the target.

There are many visual cues that could potentially distinguish object properties. Monocular cues such as linear perspective, texture gradients, motion parallax, and accommodation all provide some depth information. However, binocular cues such as convergence and retinal and horizontal disparities provide more accurate information (Tresilian et al. 1999). The contribution of specific visual cues to prehension can be studied by selectively perturbing sensory information. The response of the visuomotor system can be recorded by comparing the accuracy and variability of successful reaches before and after visual perturbation (Servos et al 1992). Additionally, it is possible to discriminate finer differences in performance by comparing kinematic measures of grasping.

In most grasping kinematic studies optic or infra-red markers are placed on the lateral side of the thumb nail, the medial side of the index finger nail, and the skin above the styloid process of the radius. These markers yield position data throughout a grasp,



which are used to calculate total movement time, peak velocity of the wrist, time to peak velocity of the wrist, maximum grip aperture (distance between thumb and index finger), and time to maximum grip aperture. These kinematic variables can then be used to discriminate fine differences between reaches under various environmental conditions.

In 1992 pioneering studies by Philip Servos, Melvyn Goodale, and Lorna Jakobson showed that there is a characteristic pattern to kinematic variables during reaches made under normal environmental conditions. During reaching, the velocity at the wrist follows a bell-shaped curve with respect to time. At the end of the movement there is a period of low velocity where final adjustments are made. Furthermore, peak velocity is consistently higher for reaches to further objects. The grasp component is characterized by a maximum grip aperture that scales with the size of the object. Additionally, the maximum aperture shows size constancy. Even though an object's angular extent increases at closer distances, the maximum grip aperture remains the same across distance. These results are very different from grasping movements made when vision was occluded in one eye. Accuracy measurements were unaffected by monocular vs. binocular vision – subjects were successful in grasping the targets 100% of the time. Similarly, trial to trial variability did not increase under the monocular conditions. However, kinematic variables were significantly different under monocular

reaches. These monocularly guided movements were characterized by lower peak velocities of the wrist, longer onset times, longer movement times, smaller grip apertures, and more time spent decelerating at the end of the movement.

Subsequent studies sought to determine whether or not binocular cues are useful for on-line control. Preliminary experiments showed that binocular information was of little use for guiding the hand during movement (Servos and Goodale 1994). Subjects were given an initial view of the target that was either monocular or binocular, and an on-line view that was either monocular or binocular. Results showed that when the initial view was monocular, subjects had difficulty grabbing objects whether or not they had a binocular view during the grasp. Later studies showed that when the view was changed at a start signal rather than at movement onset, initial view had no effect on the kinematic variables (Jackson et al. 1997). However, monocular feedback after a binocular view caused increased movement times, decreased peak velocity, an increased deceleration phase, and increased grip aperture. Thus under these conditions binocular information seems superior to monocular for on-line control, but not for the initial view. The apparent discrepancy between these two experiments can be resolved by an understanding of the neural control of grasping. Current theories suggest that the dorsal visual stream, responsible for guiding motor commands, retains object information for only a few hundred milliseconds (Goodale and Milner 1992). Thus,

when occlusion occurs at a start cue and movement is not initiated until seconds later, the dorsal stream no longer has access to accurate information about the target. It is forced to rely more heavily on on-line mechanisms of control. On the other hand, when vision is occluded at the onset of movement, the dorsal stream has access to accurate target information. Under normal conditions binocular information is extremely important during the planning stages of movement, but if the initial viewing conditions have been degraded the dorsal stream can make use of on-line binocular cues.

Motion could potentially provide additional monocular and binocular cues for the guidance of grasping. Time to contact can be estimated from the inverse rate of dilation of an object on the retina, which can be computed from either binocular or monocular cues (Servos and Goodale 1998). Two additional cues, stereomotion and opposite-edge velocities, can be used to calculate the direction a target is moving. While stereomotion, a binocular cue, yields information about depth in the horizontal plane, opposite-edge velocities, which can be computed binocularly or monocularly, can be used to estimate depth in both the vertical and horizontal planes. In fact, perceptual tests show that thresholds for detecting motion in depth are similar for monocular and binocular viewing (Regan and Kaushal 1994). However, binocular information on optical expansion is potentially twenty times more accurate than monocular

information. There is thus theoretical support for an advantage of either binocular or monocular vision.

To test the effects of motion on grasping, Servos and Goodale designed an experiment in which subjects grabbed a ball swinging on a pendulum under both monocular and binocular conditions. The pendulum's base was centered at the subjects' midline, and released at 0°, 30°, and 60° – where 0° was along the midline sagittal plane. Three trajectories were used to discriminate the effects of cues like stereomotion that provide more information in one only one plane. Grasping under monocular conditions was virtually indistinguishable from grasping under binocular conditions for all trajectories. However, when subjects grabbed the ball moving along the 0° line under monocular viewing, maximum grip aperture was significantly larger. This is puzzling because stereomotion is most effective in the horizontal plane. Thus, if subjects were using stereomotion as a cue for grasping, monocular viewing should have a negative effect on the 30° and 60° trajectories. While monocular cues are sufficient for grasping under these experimental conditions, binocular vision may be more useful when reaching for rapid or erratically moving objects that do not possess constant velocity and direction (Regan 1993).

### **Implications of human studies for theories of primate origins**

There is currently little evidence to show that non-human primates use binocular cues to guide grasping movements. However, the studies above point out several important facts relevant to primate evolution. For example, since many insectivorous primates close their eyes before attacking prey, there is a premium placed on the quality of information available in the initial view. Open versus closed-loop experiments in humans suggest that binocular cues might be particularly important when on-line control is not possible (Connolly and Goodale 1999). Insects also move rapidly and erratically relative to other targets a primate might grab such as fruits, leaves, and branches. Research in humans suggests that objects moving with a predictable direction and velocity provide additional monocular cues, which decrease the importance of binocularity (Servos and Goodale 1998). However, binocular information might be useful to primates attempting to acquire elusive prey.

Other studies suggest that binocular cues may be useful to primates under a wider range of circumstances. For example, binocularity may be of general importance when grasping an object, but not when reaching towards it (Watt and Bradshaw 2000). Retinal disparities might provide shape information useful for calibrating grasp. However, reaching only requires distance information, which is available from monocular cues. Thus, animals with claws that primarily need distance and not shape

information might have less use for retinal disparities. Furthermore, binocular cues have been shown to be particularly useful when selectively grasping objects in a cluttered space – a distinct advantage for primates living in a complex three-dimensional environment (Jackson et al. 1997).

Extrapolating from humans to other primates leads to the conclusion that binocular cues can be particularly useful for guiding movements towards objects with insect-like properties, but may also be useful under a wider variety of circumstances. While initial work on rhesus macaques has shown that the grasping kinematics of at least one other species is similar to humans, there is currently no information regarding how sensory information is used to guide these movements (Christel and Billard 2002).

### **1.3.5 Difficulties in drawing evolutionary conclusions from physiological data**

Before drawing any conclusions from these behavioral and physiological experiments, it is necessary to first consider three factors, which have the potential to drastically influence the implications of these studies on primate evolution. First, the additional distance estimates gained from binocular vision appear to be redundant. Second, many of the functional advantages rely on overlap in the peripheral regions. However, sensitivity to many stimuli such as, color, spatial frequency, and contrast, decrease rapidly with increasing eccentricity. Third, it is also possible that forward-

facing eyes do not offer any functional advantages, but are instead constrained from evolving into a more lateral-eyed orientation.

### **Redundancy**

An adaptive hypothesis that suggests a specific trait evolved for a biological role that is already accomplished by a preexisting trait does not have much power. Some explanation must be offered as to why several traits are needed to do the same job. Distance estimation receives the strongest support as a potential advantage for binocular vision. However, most vertebrates estimate distance through a variety of monocular cues. Simple pictorial cues such as interposition, familiar size, perspective, and elevation can be used as a guide to distance. For example, since objects that are further away are usually higher in the visual field, elevation is an environmental cue providing relative information about depth (Sedgwick 1986).

Kinematic studies show that humans can in fact use elevation as a cue to depth (Marotta and Goodale 1998). Motion parallax, which occurs when the eye undergoes translation during head or body movements, provides an even more accurate estimate of depth. In this case, disparity cues are generated even when information is available from only one source. Perceptual studies in humans show that object discrimination is better when the head is free to move (Biguer et al. 1984). Additionally, there is anecdotal evidence that arboreal animals sometimes make large head movements before jumping

between supports. Experimental studies indicate that the Mongolian Gerbil increases the size and frequency of head movements as the distance between supports increases (Ellard et al. 1984). Grasping research on humans shows that when a subject's head is restrained, movements are less efficient under monocular conditions. In such cases, there are several additional velocity peaks towards the end of the movement signifying increased on-line corrections (Marotta et al. 1998). Another extremely accurate monocular cue, accommodation, is used by ballistic predators such as the chameleon and sandlance (Ott et al. 1998, Pettigrew et al. 2000). Distance estimation in these species depends on rapid high amplitude accommodation. Although mammalian lenses have low refractive power, accommodation has the potential to provide some distance information.

The redundancy of binocular depth cues is also supported by the fact that the removal of binocular information does not appear to have a dramatic effect on behavior. As mentioned above, frogs have the ability to estimate depth based on disparity, but their ability to capture prey is not diminished when information is available from only one eye (Ingle 1972, Grobstein 1980). Kinematic studies show that humans are just as accurate at grasping objects with one eye or two (Servos et al. 1992). Interestingly, humans who have had one eye enucleated are not only as accurate at grasping as their two-eyed counterparts, but also have a similar kinematic profile (Marotta et al. 1995).



Thus, there is strong evidence that the distance information provided by binocular cues is redundant. Why, then, did primates undergo such dramatic evolution to fill a biological role that already appears to be full?

The simplest answer is that vergence and retinal disparities provide primates with a more accurate estimate of distance. While less accurate estimates might be sufficient for most animals, primates might need a more fine-grained measure of shape and distance. As mentioned above, at least two other cues, accommodation and motion parallax, have the potential to provide highly reliable distance information. While accommodation is not likely to be a good source of distance information in mammals, motion parallax could provide primates with as much information as binocular disparities. Moreover, there would be no need to undergo major morphological changes to make use of motion parallax. If binocular cues are providing such accurate information, it is troubling that their removal does not drastically alter performance. So is a slight gain in accuracy the only reason to add one more cue to an already redundant system?

The fact that redundancy is seen in a wide variety of sensory systems suggests that something else is going on. In migrating birds for example, directional information can be gleaned from the sun, the stars, and the earth's magnetic field (Wiltschko and Wiltschko 1994). In most cases the sun appears to be the best cue to direction; however

it is necessary to calibrate this internal compass with another measure, such as a magnetic compass. Additionally, environmental factors such as cloud cover or magnetic storms can reduce the reliability of one cue; forcing individuals to rely on an alternate source of information. The need for calibration and the ability to estimate distance under a wide variety of circumstances might also explain redundancy in primates.

The role of horizontal disparities in distance estimation highlights both of these possibilities. While disparity provides high-quality depth information, it can also be very ambiguous. An object with the same horizontal disparity can be interpreted as deeper if it is relatively far or shallower if it is near. However, the visual system can make use of vergence information to correctly scale horizontal disparity (Rogers and Bradshaw 1995). In fact, as more cues are added, humans can better estimate distance (Mon-Williams and Tresilian 1999). Thus, the cues are not truly redundant – each tells the visual system something slightly different about an object's position in space. Additionally, as other cues are artificially degraded, the visual system automatically places emphasis on the remaining reliable cues (Tresilian et al. 1999). Furthermore, horizontal disparities are only useful under certain conditions. For example, binocular disparity is not accurate for tasks that involve estimating distances much greater than an arm's length away. Other cues such as familiar size and motion parallax can instead be used to estimate larger distances. On the other hand, disparity cues are useful in

situations where other cues are not. If, for example, an organism needs to estimate distance while remaining still, motion parallax will be useless, but disparity cues will still be accurate. Thus, binocular vision augments the accuracy and reliability of a redundant system, which needs to operate under a variety of conditions.

Horizontal disparity might also provide primates with a unique and powerful advantage. Horizontal disparity provides information about the relative, not absolute, distances between multiple points. Therefore it must be scaled by some other cue such as vertical disparity or vergence. Once scaled, horizontal disparities can provide detailed information about the relationship of points across a continuous textured surface, thereby giving a vivid sense of three-dimensional shape (Rogers and Bradshaw 1993). Such information is crucial for calibrating the hand during any grasping movement, and as a result would be an invaluable guide for a behavior common to all primates.

### **Peripheral sensitivity**

As mentioned above, there is a problem with using horizontal disparity as a functional advantage for forward-facing eyes. The difficulty arises because even the most lateral-eyed mammals have a moderate region of visual-field overlap, and thus could extract disparity cues from a wide range of space. For primates then, it must be argued that peripheral regions of the retina provide additional disparity cues that are a

useful guide in grasping. Unfortunately, little is known about the sensitivity of peripheral regions of the retina to disparity. However, for primates visual acuity falls off rapidly as a scene is imaged away from the fovea, and at least for small eccentricities in humans visual acuity is proportional to stereoacuity (Ogle 1950). Even with diminishing acuity humans can still make reasonably accurate distance estimates at eccentricities as high as 50°. For the present it must remain an open question as to whether or not peripheral regions of the retina provide primates with useful binocular information.

I would like to propose another means through which forward-facing eyes might facilitate the use of disparity cues without relying on information from the peripheral retina. Aligning the eyes to point in the same direction increases the region of space over which bifixation is possible. As a result, an animal with a region of high stereoacuity and mobile eyes can acquire fine-grained stereopsis over a larger expanse of visual space. While binocular overlap in the peripheral retina could still provide limited stereopsis, it might primarily be a byproduct of the need for bifoveation.

### **Phylogenetic inertia**

A final problem with functional arguments for forward-facing eyes in primates is that there might no longer be a functional explanation. If the initial selective pressures, which gave rise to this condition disappeared, the now selectively neutral trait could be

lost through genetic drift. However, “drifting” to a more lateral-eyed position would require a change in a highly integrated system of osteological, myological, and neurological factors. Such a change might be plausible if in addition to the neutrality of convergent eyes, there was positive selection for laterally directed eyes. The benefit of a lateral orientation is that it can greatly increase the extent of the total visual field, thereby facilitating the detection of objects of interest such as predators or food.

However, primates have largely obviated the need for a large static visual field by evolving highly mobile eyes and a flexible neck. Coupled with scanning behaviors these traits create a huge dynamic visual field. For example, observational studies of captive tamarins indicate a high base scanning rate, in which the head and eyes are rotated during a stereotypical sweeping motion (Caine 1984). During scans subjects are more likely to detect hidden objects. Additionally, the introduction of novel or threatening objects increases the rate of scanning. Sociality can also increase an individual’s visual field – assuming group members reciprocally identify predators and food sources. It is therefore plausible that primates might retain forward-facing eyes without stabilizing selection for any functional advantage. This will make it difficult to interpret negative results for experimental studies involving primates. Accordingly, it is advisable to look at the function of forward-facing eyes in a wide variety of animals.

### **1.3.6 Implications of functional studies on theories of primate origins**

Although there is a rich body of physiological and behavioral literature demonstrating binocular vision in a wide variety of animals, little is known about how binocular cues are used to guide animals in naturalistic conditions. However, each of the binocular cues reviewed above provides functional support for at least one of the ecological categories derived from comparative anatomy. Symmetric optic-flow fields, retinal disparities, and vergence help predators to estimate distance, speed, and direction while attempting to catch prey. Retinal disparities and convergence add to a redundant system that provides highly accurate and reliable distance estimates, which are essential for estimating placement of the hands. Additionally, disparities provide the only accurate information about three-dimensional shape, a property of supreme importance during grip calibration. Binocular summation increases contrast detection and sensitivity in nocturnal animals allowing them to see better at night. Furthermore, summation, disparity, vergence, and optic flow fields would be beneficial to nocturnal predators in a fine-branch niche. Finally, alignment of the visual and optic axes would be beneficial to nocturnal predators, which have high visual acuity and are active in scotopic environments.

The anatomical and functional data support the praxic and nocturnal predation hypotheses, but not the fine-branch arboreal hypothesis. Fine-branch arborealists do

have convergent orbits and eyes and a high degree of visual-field overlap, but not relative to closely related species that are largely terrestrial. Rather, the praxic hypothesis explains why all animals that exhibit visually guided interaction over a wide area have forward-facing eyes. The main problem with accepting the praxic hypothesis is that praxis has only been quantified for a handful of species. Until data are available from more rigorous experiments, these conclusions should be viewed as tentative.

Before positing tests of the praxic hypothesis it is also important to consider whether there is any functional data that might question the link between binocular vision and reaching and grasping. While there is a wealth of functional data supporting this link, several recent papers have called the association into question. These criticisms have been incorporated into a new theory of primate origins involving snakes (Isbell 2006). This theory suggests that primate brain expansion is related to a predator prey co-evolution with snakes. It is suggested that the brain expansion is due in part to increases in the size of the binocular visual field that evolved to detect snakes at close distance before they strike.

The supposition that increasing the width of the binocular visual field is an adaptation to detecting predators does not in and of itself challenge the idea that binocular vision is an adaptation for guiding reaching and grasping movements. It certainly may turn out that binocular vision is an adaptation to many niches, and

deciding which is relevant for primates becomes more difficult. There are however several pieces of evidence cited that question the nocturnal visual predation hypothesis.

In actuality the nocturnal visual predation hypothesis does not rest on a functional explanation involving binocular vision at all. Rather the current functional explanation as mentioned above is that aligning the optic and visual axes is particularly useful to nocturnal predators. The praxic hypothesis is however susceptible to arguments against the association between binocular vision and grasping movements. These arguments include the mosaic nature of evolution in early primates, lack of a correlation between convergence and brain structures associated with grasping, and lack of kinematic evidence of a binocular advantage for grasping in humans.

The recent discovery of *Carpolestes simpsoni*, has generated vigorous debate as to what the earliest primates might have looked like (Bloch and Boyer 2002). The assertion has been made that this creature is closely related to euprimates. The presence of a divergent hallux with a flattened nail and lack of marked orbital convergence is argued as evidence that primate like grasping occurred before expansion of the binocular visual field. While it is not universally assumed that this species is in fact a close relative of Euprimates (Kirk et al. 2002), granting this supposition still does not rule out a link between reaching and grasping and convergence in primate evolution.



*Carpolestes simpsoni* has a divergent hallux with a nail, short metacarpals, and long phalanges, traits which have been associated with primate like grasping. While reaching and grasping is frequently mentioned in theories of primate origins, skilled reaching and grasping movements are quite common in a number of mammalian clades including rodents and marsupials and probably predates the last common ancestor of primates and rodents (Iwaniuk and Whishaw 2000). Finding an arboreal mammal that demonstrates tendencies towards powerful grasping is therefore not particularly surprising. The increased binocular field would only become needed with the lengthening of the forelimbs, increased mobility of the shoulder joint, and a behavior that used these traits to manipulate or grasp small objects.

Even if *Carpolestes simpsoni* does typify an early step in the evolution of primate grasping, it does not rule out the association between binocular vision and grasping posited for extant primates. The nocturnal visual predation and fine branch arboreal hypotheses are primarily concerned with the evolution of crown primates. Presumably the last common ancestor of all extant primates had long mobile grasping forelimbs and convergent eyes. It is certainly possible that one evolved before the other in a stem primate, but the combination of the two would have served a different biological role and allowed crown primates to invade a new niche.

Additionally, it is highly dubious as to whether orbital convergence should be used to predict eye orientation in single extinct species. Orbit orientation is best suited to studies of correlation between ecology and morphology in large extant datasets. To date we know virtually nothing about how orbit orientation correlates with eye orientation or visual field overlap. A single study has demonstrated a correlation between orbit orientation and visual field overlap in a handful of species (Heesy 2004). However, this study also showed that the correlation shifts drastically in different taxonomic groups. Therefore it is not clear what kind of a correlation we should expect in extinct species.

The bulk of the comparative data on eye orientation was collected before 1901 (Johnson 1901) and the bulk of the data on visual field overlap was collected between 1902 and 1939 using questionable methodologies (Tschermak-Sysenegg 1902, Rochon-Duvigneaud 1922, Thieulin 1927, Verrier 1927, Kahmann 1932, Pisa 1939). Recent work on a small number of marsupials, birds, and anurans has added some rigorous data on optic variables (Arrese et al. 2002, Martin 1999b, Fite 1973). From the few species in which we do have reasonable data we know animals like *Tarsipes rostratus* with eyes that are not particularly convergent can have large binocular fields (Arrese et al. 2002), and behavioral estimates of binocular fields do not even correspond to anatomical estimates of binocular fields (Sherman 1973, Sherman and Wilson 1975). Much additional data on

the relationship between orbit orientation, eye orientation, anatomically determined visual fields, and behaviorally determined visual fields is required before we can make predictions about the eye orientation of extinct species.

Lack of correlation between the number of neurons in the magnocellular pathway has been posited as a criticism of the association between reaching and grasping and binocular vision (Barton 2004). The correlation between number of neurons in and volume of the parvocellular pathway and size of other visual regions of the brain with increasing convergence is taken as evidence that the need for fine grained stereopsis is driven by perceptual rather than motor demands. The assumption stems from the fact that the magnocellular pathway contributes primarily to the dorsal stream which is associated with action and the parvocellular pathway contributes to the ventral stream associated with perception.

There are several problems with this line of reasoning. First, these pathways are not nearly as discrete as sometimes assumed. There is substantial communication between elements within the dorsal and ventral pathway (Milner and Goodale 1995, 2008). A region in the posterior parietal cortex associated with planning the motor commands used in grasping such as posterolateral intraparietal sulcus receives information from both the magnocellular and parvocellular pathways and is in fact highly dependent on binocular information (Sakta et al. 1997). Second, the ventral

pathway is not responsible for directing action, but it is intimately involved in the planning of which actions to take (van Doorn et al. 2007). Therefore, even if primates do not use a wide binocular field to direct motor output such as precise placement of the hand or size of the grip aperture, binocular vision might be used to choose a path and type of action based on detailed information about the substrate.

Third and most importantly, we would not necessarily expect an increase in the magnocellular pathway due to increasing binocularity. In the lateral geniculate nucleus where these pathways form very little visual processing has occurred. Assuming no changes in the total visual field or changes in acuity, increasing the binocular visual field would not necessarily augment the quantity of information being carried from the retina. Not until V1 or even further downstream would large increases in neuron populations be required to handle the demands of stereopsis. The correlation between convergence and the number of neurons in the parvocellular pathway might be related to a correlation between visual acuity and convergence. An increase in visual acuity would add visual information necessitating an increase of neuronal populations in the lateral geniculate nucleus.

Finally, lack of kinematic evidence for the utility of binocular vision for humans reaching blocks on a table, was put forth as a potential criticism of the link between grasping and binocular vision. The one cited paper found that removing binocular cues

did not alter kinematics associated with the transport component of the wrist, but did alter kinematics of the index finger and thumb associated with the grasping phase (Watt and Bradshaw 2000). Rather than weakening the argument for an association between binocular vision and primate like grasping, this paper strengthens the support. It implies that binocular vision is not needed for simply touching an object, such as when an animal with claws and poor grasping ability reaches for a substrate. When grasping the objects is a requirement, such as primates gripping a branch, binocular cues are useful. Additionally this paper is only one of dozens starting with Servos et al. 1992 and reviewed extensively in Loftus et al. 2004 that demonstrate changes to the kinematics of both reaching and grasping between monocular and binocular conditions.

While we cannot falsify the praxic or fine-branch hypotheses, the visual predation hypothesis receives the strongest positive support. The most compelling evidence relevant to the evolution of forward-facing eyes, orbital information, suggests that nocturnal visual predation is the most likely explanation of primate-like eye orientation. To date, these are the only reliable observations for which we have a reasonable sample of individuals and species. Some of the visual-field and optic-axis data tend to support the praxic over the visual-predation hypothesis. However, these data were collected on an arbitrary assortment of animals, and do not yield many useful comparisons. While visual predation is currently the most powerful explanation

available, alternatives cannot yet be disregarded. Additional studies are needed to resolve this issue definitively.

### **1.4 A test of the praxic hypothesis**

While not yielding a definitive answer, the comparative and functional data support nocturnal predation as the most likely explanation as to why primates first evolved forward-facing eyes. Nocturnal predators share with primates an extreme convergence of the orbits and eyes. Additionally, there are an abundance of functional studies to suggest why forward-facing eyes would be a benefit to nocturnal predators. However, there are many other ecological and behavioral conditions that appear to give rise to moderate to high degrees of optic convergence. Praxis in particular might help to explain why all extant primates have forward-facing eyes, and could be a proximate explanation as to why most nocturnal visual predators have forward-facing eyes.

#### **1.4.1 Learning from previous experiments**

Prior to designing a functional test of the praxic hypothesis it would be beneficial to consider whether previous studies of binocular vision are suited to the question at hand, and whether these methods can be adapted to awake unrestrained animals. While there is an abundance of data showing that a diverse group of animals possess the ability to process binocular information and that binocular cues provide an additional set of unique visual input, there are three reasons why we cannot infer that binocular

cues are used to guide a particular behavior. First, disparity information is useful for much more than just depth perception. It can be used to link common features independently imaged on each retina, guide eye movements, focus an image, and detect movement (DeAngelis 2000). Second, most studies are concerned with visual perception, and not visuomotor behavior. It is currently believed that perception and action are handled by two distinct yet interconnected systems, which access and process visual cues differently (Milner and Goodale 2008). A final problem with interpreting much of the work to date is that visuomotor behaviors themselves are handled by the brain in a modular fashion. For example in rhesus macaques, neurons located in the anterior region of the posterolateral intraparietal sulcus (AIP) are active during visually guided grasping, but not during reaching without grasping (Sakta et al. 1997). The posterior parietal cortex contains some areas that are associated with reaching only, area 7a, and other regions associated with reaching and grasping, area V6A (Fattori et al. 2004). We cannot safely assume that a visual cue relevant to one task will automatically be used in all tasks. To test the praxic hypothesis, we need to assess whether or not there are any motor deficits associated with the loss or alteration of binocular visual cues during specific behaviors.

Kinematic studies of reaching and grasping in humans, on the other hand, provide a good model for experimental tests of the praxic hypothesis (Servos et al. 1992,

Loftus et al. 2004). While these studies have found that monocular guided movements were characterized by lower peak velocities of the wrist, longer onset times, longer movement times, larger grip apertures, and more time spent decelerating at the end of the movement, there are many reasons why these experiments must be replicated in other animals if we are to truly test hypotheses about primate origins. To begin with, not all studies have supported the role of binocular vision in motor control. Watt and Bradshaw report that depriving subjects of binocular information has no effect on the kinematics of reaching and little affect on grasping (2000). In addition, humans and other primates could process the same visual cues differently. For example, the negative repercussions associated with a misstep high in a tree place a premium on any cue that can accurately guide limb placement. Thus, the visuomotor system of arboreal primates might require a greater reliance on information from binocular cues, and removing these cues might influence performance more drastically than it would in a human. Alternatively, non-human primates could have evolved a more redundant system than humans by making use of additional visual cues or processing existing cues more efficiently. Under these circumstances removing binocular cues might have little effect. A final reason to expand kinematic studies is to evaluate performance under a wider array of behavioral and environmental conditions.



A kinematic study of animal behavior under monocular and binocular conditions is the best place to start in determining the functional role of forward facing eyes. An ideal experiment would test whether altering the width of the binocular field has an effect on the region of space over which subjects are able to interact with the environment. Unfortunately, our current lack of understanding of the interrelationship of optic variables, practical restrictions on experimental design, and a limited ability to alter the width of the visual field confine the scope of possible experiments. I will briefly discuss the nature of these limitations and propose a set of experiments that obviate these problems while still answering fundamental questions about the evolution of forward-facing eyes.

#### **1.4.2 Methodological difficulties associated with tests of praxis**

Our ability to design testable hypotheses is currently limited by a lack of understanding of the interrelationship of optic variables and a dearth of data on praxic fields. The most direct measure of eye orientation is the optic axis, the line passing through the center of the lens and cornea. There are unfortunately few systematic studies of the optic axes with the only extensive work in mammals coming from Johnson (1901) and more recent studies in birds (Martin 1999a). There is however extensive work on the orientation of the orbits in mammals (Cartmill 1970, Ross 1994, Ravosa and Savakova 2004, Heesy 2004, Heesy 2008). Although it is generally assumed that orbit

orientation is correlated with optic orientation, no study to date has examined the relationship quantitatively.

Early researchers assumed that changes in eye orientation were related to changes in visual fields, where the visual field for a given eye is defined as the region of space from which light can reach the retina, and the binocular visual field is the area of overlap between the right and left monocular fields (Walls 1942). However, the relationship between eye orientation and binocular vision is not a simple one. For example, some birds with highly convergent optic axes have very little visual field overlap (Martin 1999a), and the Honey-creeper possum, *Tarsipes*, has divergent optic axes but a high degree of overlap (Arrese et al. 2002). By changing the relative sizes of the cornea and retina it is possible to drastically alter the extent of the visual fields without altering eye orientation. Thus, it is dangerous to assume that an animal with convergent eyes necessarily has a large binocular field or that an animal with divergent eyes has a small binocular field.

There are two other salient topics that have an effect on the relationship between eye orientation and binocular vision-- stereoacuity and eye movements. Stereoacuity, defined as sensitivity to retinal disparities, is unknown for most animals. However, in humans visual acuity is proportional to stereoacuity at eccentricities less than 50° (Ogle 1950), and visual acuity drops off dramatically at increasingly peripheral locations. If

different regions of the binocular field have different sensitivities to shape and distance in a single species, then it is difficult to attach meaning to interspecific comparisons of binocular field width. A macaque and a honey-creeper have similarly sized binocular fields, but the function of the fields is likely very different in these two animals (Arrese 2002).

Eye movements are another factor complicating the relationship between eye orientation and visual fields. In species like primates that make large coordinated eye movements, the orientation of the optic axis and size of the binocular field are not fixed. Therefore, it is necessary to collect data on a range of orientations and field widths and not simply estimate a single value. One intriguing possibility that can only be tested with information on eye movements is that convergence of the optic axes increases the region of space over which bifixation, the ability to direct the fovea of each eye to the same point in space, is possible. As a result, an animal with a region of high stereoacuity and mobile eyes can acquire fine-grained stereopsis, depth perceived on the basis of retinal disparities, over a larger expanse of visual space. While binocular overlap in the peripheral retina could still provide limited stereopsis, it might primarily be a byproduct of the need for bifixation.

Eye orientation has been estimated by measuring the optic axis, orbit orientation, and width of the binocular visual field. It is assumed there is a general correlation

among these variables, but we do not currently know the strength of this relationship. In fact, we do not know the value of all three variables for a single individual or a single species of any vertebrate. The majority of the reliable comparative data comes from studies of the orbits, which have identified large differences in orbit orientation between nocturnal visual predators and other mammals (Cartmill 1970, Heesy 2004). However, it is impossible to choose any two closely related species that vary ecologically or behaviorally, and discern whether or not small differences in orbit orientation correspond to differences in eye position or binocular field width.

While information on optic variables is plentiful but incomplete, there has not been a single study that quantifies the range over which animals interact with the environment during specific behaviors, the praxic field. Given that animals can interact with the environment in a vast number of ways it is difficult to supply more than a very general definition of the praxic field. For a given animal it is easier to attain an understanding of this concept. For example, one way in which frogs interact with their environment is capturing insects with a long sticky tongue. We might get a rough idea of a frog's praxic field by measuring the length and mobility of its tongue or by filming its behavior during prey capture to measure tongue excursion. For most mammals, the praxic field will be determined by the region over which an animal can interact with other objects using its limbs and muzzle. In general animals with longer, more mobile

limbs should have a larger praxic field. Since we are interested in the visual guidance of movement it is necessary to establish boundary conditions to focus our attention on only a portion of the praxic field.

To begin with it is necessary to consider only behaviors for which visual information is available and useful. Many rodents for example have nimble digits, which they use to manipulate food items. However, most of the praxic field is beneath the head and trunk and foraging behaviors are probably guided primarily by olfactory and tactile cues. Primates, however, use visual information to guide placement of the forelimb during locomotion in complex environments, but most likely use proprioceptive and memory cues to guide placement of the hindlimb. Additionally, animals might use visual information to guide a movement in one situation, a raccoon placing its forelimb on a branch, and another cue to guide movement in a different situation, a raccoon using tactile information to forage for invertebrates in a streambed. If we are searching for a relationship between behavior and eye orientation, it is crucial that we are certain the behavior in question is guided by visual cues. Unfortunately, this may at times be difficult to determine without extensive experimentation.

The second boundary condition requires that movements must be made with minimal reorientation of the head, eyes, and body. Given sufficient time an animal can reposition its body to bring any portion of the visual field to bear on a given point in

space. If an animal has a relatively long time to make a movement and the reorientation does not pose a significant disadvantage, such as increasing the visibility to predators or disrupting balance, then a small binocular field would suffice to cover a large praxic field. In this case there would not necessarily be a relationship between the size of the praxic and binocular field.

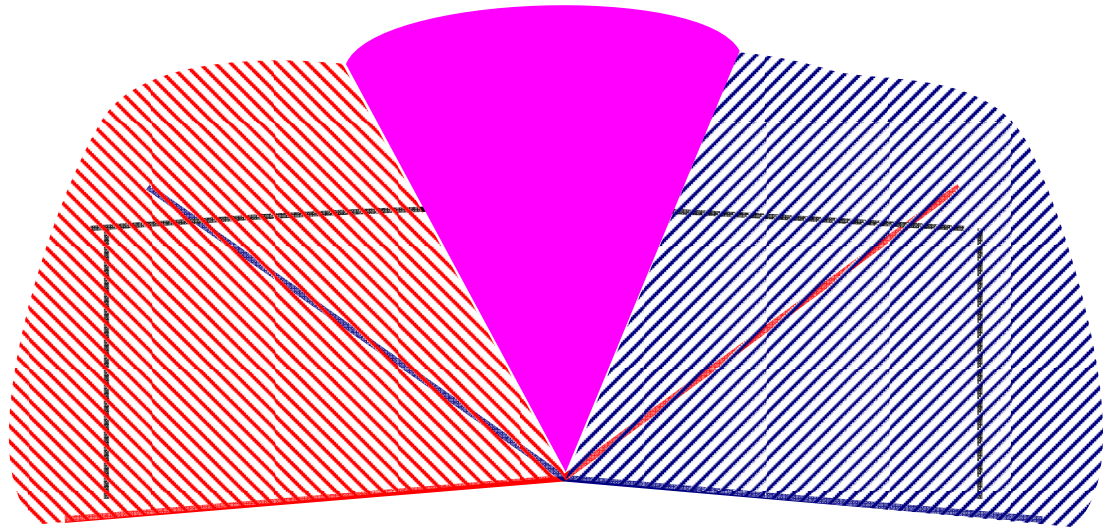


Figure 2: In an ideal experiment the region of space covered by the binocular field is reduced by small increments while the total visual field remains unchanged. Here the red and blue lines represent the initial visual fields. The peripheral regions of the binocular field have been removed leaving only the purple region in the center. The black lines represent a hypothetical praxic space.

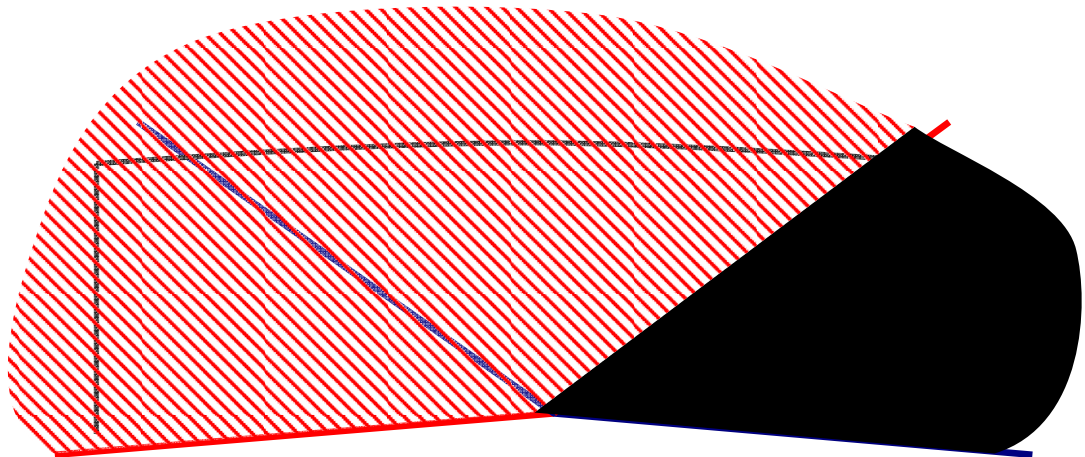


Figure 3: When a patch is used to completely occlude vision to the right eye, the width of the binocular field can only be set to 0% or 100%. Additionally, the right monocular field is removed thereby reducing the total visual field.

In addition to our inability to form specific testable hypotheses, there are practical problems related to our ability to alter the width of visual fields. The functional underpinning of the praxic hypothesis is that binocular depth cues are useful for guiding precise movements, and that a larger binocular field is useful for guiding movements over a wider region of space. To test this idea directly we could design an experiment that evaluated performance on a series of tasks that require an animal to interact with increasingly larger portions of its praxic field (Figure 2). We could then remove portions of the binocular field starting at the periphery and moving centrally, while leaving the total visual field unaltered. The praxic hypothesis predicts that removal of even the most peripheral regions of the binocular field will be associated with a decrease in performance on the wide tasks but not the narrower tasks. As we remove successively larger portions of the binocular field we will begin to see performance deficits in narrower tasks.

Unfortunately, there is currently no method available to remove a small portion of the visual field in each eye. Though it might be possible using partially occluded contact lenses, verifying that the desired portion, and only the desired portion, has been removed would be next to impossible. After experimenting with several methods myself and after exhaustive discussions with other researchers, I have decided that the



only feasible method of removing binocular cues involves occluding the entire visual field of a single eye, Figure 3. There are two major problems associated with this technique.

First, removing the entire visual field from one eye eliminates a portion of the monocular field. Thus, some of the performance deficit might have nothing to do with the loss of binocular vision. We can minimize this effect by using a narrow task that does not involve the monocular portion of the visual field. The second problem is that it does not allow for a portion of the binocular visual field to be removed – it is all or nothing. While this restricts our ability to test the praxic hypothesis directly, because we can no longer examine the importance of the width of the field, it is still possible to ask whether binocular cues are used at all during certain tasks. Will examining this question provide us any additional insights into evolution of the mammalian visual system?

### **Summarizing design concerns for tests of praxis**

In summary, while there are several practical problems that make it difficult to study the functional importance of binocular vision, there is sufficient data to posit hypotheses and methods available to test these ideas. A lack of information about the optics of mammalian eyes makes it difficult to predict which animals rely most heavily on binocular vision and impossible to interpret any potential differences between species. Additionally, the only methods available for altering binocular vision,

occluding vision to an entire eye, do not allow us to adjust the width of the binocular field in increments and also remove a portion of the total visual field. Thus, we cannot determine for a given species whether a wide binocular field is better than a small binocular field. What we can resolve is whether a particular species uses binocular cues to guide a specific task. Since binocular cues are only one stream of information feeding a highly redundant visual system, the differences between tasks guided under binocular and monocular conditions are likely to be very small. Kinematic studies will allow us to detect even the most subtle differences between behaviors.

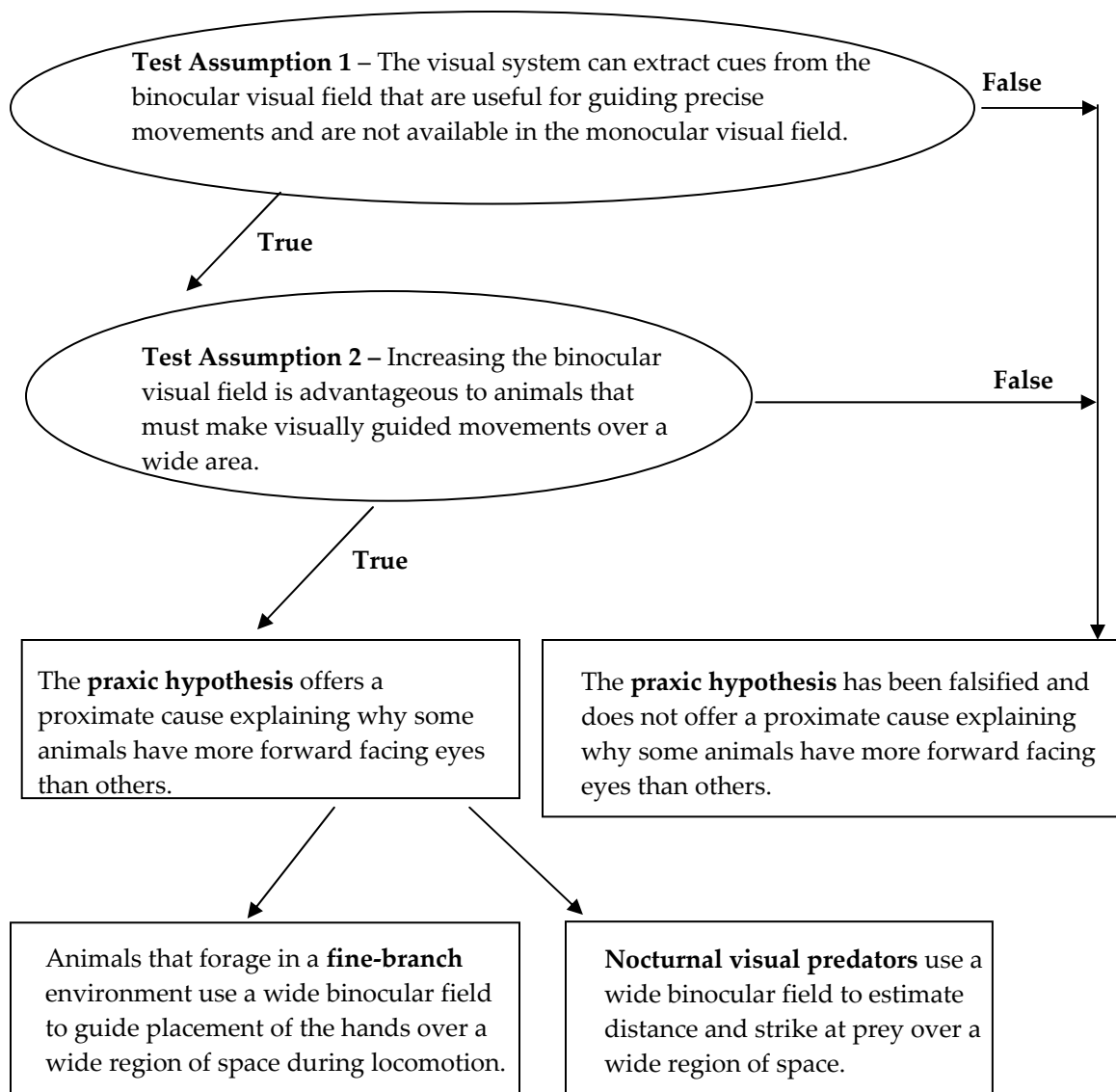
### ***1.5 Assumptions of the Praxic Hypothesis***

The praxic hypothesis posits that the degree to which an animal's eyes are forward facing is correlated with the region over which it must make precise visually guided movements without reorienting (Hughes 1977). There are two assumptions built into this idea that have not been rigorously tested:

**Assumption 1** – The visual system can extract cues from the binocular visual field that are useful for guiding precise movements and are not available in the monocular visual field;

**Assumption 2** – Increasing the binocular visual field is advantageous to animals that must make visually guided movements over a wide area.

Primates use reaching and grasping to accomplish a wide variety of tasks, such as manipulating food items, moving on top of branches, gripping supports after a leap, grooming, and guiding the hands during suspensory locomotion. I propose to evaluate performance under monocular and binocular conditions on a series of locomotor tasks. The tasks are similar to natural behaviors, and are general enough that they can be performed by a diverse array of species.



**Figure 4: A flow chart depicting the relationship between the praxic, nocturnal visual predation, and fine-branch arboreal hypotheses.**

In Figure 4, tests of Assumption 1 are related to hypotheses regarding primate origins. I propose to test Assumption 1 using kinematic data to evaluate performance. If locomotor tasks are not disrupted by the loss of binocular information, then Assumption 1 is false and the praxic hypothesis cannot claim that binocular cues guide precision movements. In this case, it is not necessary to test Assumption 2. If the loss of binocular cues disrupts locomotor tasks, then Assumption 1 is true and is a possible explanation as to why all mammals have at least some binocular vision. Further testing will be necessary to evaluate Assumption 2.

While my data will not directly address Assumption 2, it is necessary to consider its validity to understand how my project relates to primate origins. If Assumption 2 is false and an increase in the binocular visual field does not help animals complete tasks involving a wide region of space, then the praxic hypothesis cannot explain why some animals have forward facing eyes and large binocular fields. A falsification of either Assumption 1 or Assumption 2 does not falsify the nocturnal visual predation or fine-branch arboreal hypothesis. Instead, it suggests that another proximate cause, such as alignment of the optic and visual axes, must be sought to explain these hypotheses. If further testing reveals that Assumption 2 is true, then praxis provides a proximate explanation as to why some animals have forward facing eyes. For example, animals navigating in fine branches need to make reaches over a wide area, and use binocular

cues to help choose supports and guide their hands to branches. Similarly, a nocturnal predator attempting to catch moving prey with its paws must be able to strike over a wide area, and uses binocular cues to estimate distance to its target.

## **1.6 Specific Aims and Hypotheses**

The specific aim of this study is to test the effect of removing binocular cues on reaching, grasping, and locomotor behaviors.

### **Aim 1: To test the effect of binocular cues on performing locomotion in a simple environment**

The simple locomotion tasks are comparable to situations in which arboreal animals walk along a wide branch or terrestrial animals walk on a flat surface. For this project, the substrate will be composed of a flat surface wide enough to accommodate each animal. The direction, distance, shape, and size of the support remain relatively constant with each step, and monocular visual cues coupled with tactile information should be enough to guide behavior.

Hypothesis 1: The loss of binocular information does not reduce performance in simple locomotion tasks.

### **Aim 2: To test the effect of binocular cues on performing precision reaching**

The precision locomotion tasks are comparable to situations in which arboreal mammals bridge gaps or are required to use multiple smaller supports. Terrestrial

animals might encounter a similar situation when walking on uneven or rocky terrain. For this project, the substrate will resemble a horizontal ladder with slats instead of rungs. During precision reaching animals must make an accurate estimate of distance with each step. Although there are many monocular cues to distance, vergence and vertical disparity, two binocular cues, provide the best measure of absolute distance.

Hypothesis 2: The loss of binocular information significantly reduces performance in precision reaching tasks.

**Aim 3: To test the effect of binocular cues on locomotion requiring grasping on a simple substrate**

For this project, the simple grasping substrate will be a horizontal pole. Like the simple reaching task direction, distance, shape, and size of the support remain relatively constant with each step, and monocular visual cues coupled with tactile information should be enough to guide behavior.

Hypothesis 3: The loss of binocular information does not reduce performance in simple grasping tasks.

**Aim 4: To test the effect of binocular cues on performing precision grasping**

For this project, the substrate will resemble a horizontal ladder with cylindrical rungs. During precision grasping animals must also estimate a target's shape to correctly calibrate grip. While there are many monocular and binocular cues the visual

system can use to estimate distance, horizontal disparities are one of the only cues that can be used to calculate three-dimensional shape.

Hypothesis 4: The loss of binocular information significantly reduces performance in precision grasping tasks.

### **1.7 Possible outcomes**

My research will provide important new information about the role of binocular vision in primate origins. The interpretation of the data will depend on a complex interaction of the results in the four tasks. There are sixteen possible combinations of effect vs. no effect for the three Aims. In addition, the magnitude of the effect will also have an influence on the interpretation. A simplified summary of the possible results is provided in Table 1. I predict that results for **Aim1 – simple reaching** and **Aim3 – simple grasping** will be similar and will just consider the role of Aim1, Aim2, and Aim4.



**Table 1: Summary of the possible outcomes of removing binocular cues in Aim1, Aim2, and Aim4**

Possible outcome	Task			Assumption 1 of praxic hypothesis
	Aim 1	Aim 2	Aim 4	
A	No effect	No effect	No effect	Reject
B	No effect	Moderate	Large	Accept
C	Moderate	Moderate	Moderate	Accept
D	Large	No effect	No effect	Reject

**Outcomes A-D** are a representative sample of all possible outcomes, and are sufficient to demonstrate the range of interpretations available for this project. The **effect** refers to the motor deficit associated with a loss in binocular vision for a given task. The right hand column shows whether **Assumption 1** of the praxic hypothesis would be rejected or accepted for a given outcome.

If the removal of binocular cues does not alter performance in any of the Aims (Outcome A, Table 1), then Assumption 1 and therefore the praxic hypothesis can be rejected. Another proximate explanation must be posited for the origin of forward facing eyes. Additionally, depth perception is usually the explanation given as to why all land mammals have binocular vision, but this has never adequately been tested. There are other advantages of forward facing eyes that do not involve binocular vision such as the alignment of the optic and visual axes and redundant optic flow, which should be tested as alternative hypotheses (Allman 1977, Martin 1999a).

If the removal of binocular cues alters performance in only **Aim4- precision grasping** or Aim4 and **Aim2 – precision reaching** (Outcome B, Table 1), then Assumption 1 cannot be rejected. It would be the first experimental evidence of an

advantage for binocular vision in non-human animals. The strongest support would be provided by an outcome in which no effect was detected in **Aim1-simple locomotion**, a moderate effect was detected in Aim2, and the largest effect was detected in Aim4. The hypotheses were designed so that when comparing Aim1 to Aim2 to Aim4 an increasing amount of depth and shape information is required to complete each task. This relationship should be reflected in the magnitude of motor deficits experienced upon losing binocular cues. Precision guidance of reaching movements provides a reasonable explanation as to why so many animals have binocular vision. At some point most animals will need to make a precise distance judgment to guide motor action, such as when running through rocky or uneven terrain. Additionally, a severe disruption of Aim4 would suggest that primates might be under increased selection to improve binocular vision.

If the removal of binocular cues alters performance in all three Aims to roughly the same degree (Outcome C, Table 1), then Assumption 1 cannot be rejected. However, the magnitude of the effect does not vary as predicted by the amount of depth and shape information required by each task. While Aim1 and Aim2 might require as much information as Aim4, it is also possible that losing vision in one eye might affect locomotion at a more fundamental level. For example, binocular cues might be used to help ascertain heading or maintain balance.

Finally, if the removal of binocular cues has a strong affect on Aim1 and little or no affect on Aim2 and Aim4, then Assumption 1 and therefore the praxic hypothesis can be rejected (Outcome D, Table 1). There is not any obvious way to reconcile such unusual findings. This result is unlikely because if binocular cues are useful for walking across even ground, they should be at least as beneficial in walking across a more complex substrate.

If Assumption 1 of the praxic hypothesis is correct, then all mammals with binocular fields should use binocular cues to guide precise movements. The species studied in these experiments are composed of a phylogenetically diverse sample of mammalian taxa. The comparative aspect of this project is not primarily a test of interspecific differences, but rather a test of the pervasiveness of the praxic hypothesis. The inclusion of carnivorans, primates, and rodents will allow me to test whether the trait was present in early eutherians.

If binocular guidance of precision movements were a primitive trait, then early primates would have inherited a system that could be easily augmented to meet increased visuomotor demands. If only primates are affected by a loss of binocular cues, then the praxic hypothesis can still be upheld albeit in a much weakened form. It would be necessary to add boundary conditions that would restrict the hypothesis to a subset of animals making it potentially more difficult to apply to theories of primate origins.

My research will demonstrate that binocular cues are advantageous for guiding precision tasks, Assumption 1. It is reasonable to assume that if binocular cues are useful to guide tasks directly in front of an animal, then a wide binocular field would be useful to animals that must make precise movements over a broad area, Assumption 2. If true this could explain why primates have forward facing eyes. However, to truly answer this question, it is necessary to compare performance in tasks requiring primates to interact with the environment over narrow vs. wide regions of space.

## 2. Materials and methods

### 2.1 Subjects

The primary goal of my dissertation is to establish whether binocular cues are useful for guiding precise movements. If this hypothesis cannot be refuted, then it would provide a partial explanation of variation in eye orientation across mammals and would suggest a functional underpinning for theories of primate origins. I studied the importance of binocular vision during locomotion for three individuals of *Lemur catta*, *Felis catus*, and *Rattus norvegicus*. *Lemur catta* participated in all four aims while *Felis catus* and *Rattus norvegicus* did not attempt the precision grasping or reaching tasks. Although the high degree of visual field overlap and fine grained stereopsis seen in primates are rare traits, most land mammals have a moderate amount of visual field overlap and at least the basic neurological connections necessary to interpret binocular cues. I predict that the use of binocular cues to guide precise movements is a primitive trait. Primates, *Lemur catta*, and non-primates, *Felis catus*, with good binocular vision, and non-primates with poor binocular vision, *Rattus norvegicus*, will show some motor deficits in tasks performed under monocular conditions.

Three Long Evans strain, six-week-old, male rats were obtained from Charles River Laboratories. The Long Evans strain was created by Dr. Long and Dr. Evans in

1915 by crossing Wistar female rats with a wild grey male, and obtained by Charles River in 1978 from the Canadian Breeding Farm and Laboratories. Long Evans individuals have white bodies with a black hood, and are an outbred strain frequently used in behavioral studies. Three *Lemur catta* males, Licinius, Aracus, and Teres, were obtained from the Duke Lemur Center. Three *Felis catus*, two females and one male, were obtained from Liberty Research, Inc. All research was approved by the Duke University Institutional Animal Care & Use Committee, protocol A032-05-01.

## **2.2 Substrate design**

Performance was evaluated under binocular and monocular conditions on a separate task for each of the four aims, Aim 1 - simple locomotion, Aim 2 - precision reaching, Aim 3 - simple grasping, and Aim 4 – precision grasping. The simple locomotion task required subjects to walk across a flat board or straight pole, and in the precision tasks subjects walked along a structure resembling a ladder placed parallel to the ground. Each rung is a flat plank in the reaching task and a cylindrical rod in the grasping task. Individual rungs vary in their size, distance to the next plank or rod, and height above the floor. If these variables remain constant, subjects would be able to guide much of the movement from memory. In natural settings an animal would need to calculate these parameters for each step.

The substrates are a total of 12 feet for cats and lemurs and 3 feet for rats. For the precision reaching and grasping tasks the gap between each rung varies within 5% of each individual's average stride length as determined from the simple locomotion task. For most species there is not previous quantitative data on substrate use, so I determined the smallest rung size on which each individual can safely move. The substrates were covered in varnish and sand for traction, and fixed in a heavy wooden frame. The substrates were housed in a small plexiglass enclosure for cats and rats and a wood framed structure covered with mettalic mesh for the lemurs. Substrates are presented as frames from video data in Figures 5 and 6 for rats, Figures 7 and 8 for cats, and Figures 9 through 12 for lemurs.



Figure 5: Single frame from a cat walking on a board substrate



Figure 6: Single frame from a cat walking on a slat substrate





Figure 7: Single frame from a rat walking on a board substrate



Figure 8: Single frame from a rat walking on a slat substrate

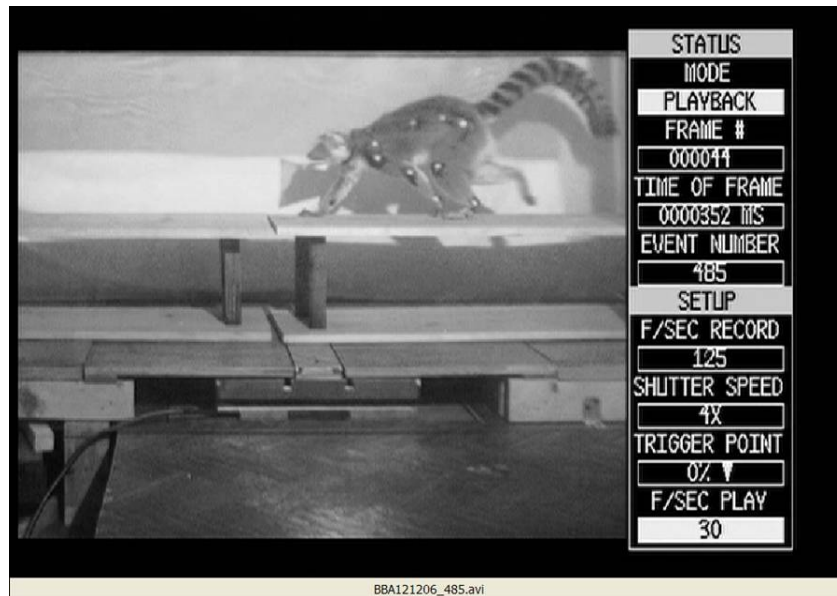


Figure 9: Single frame from a lemur walking on a board substrate

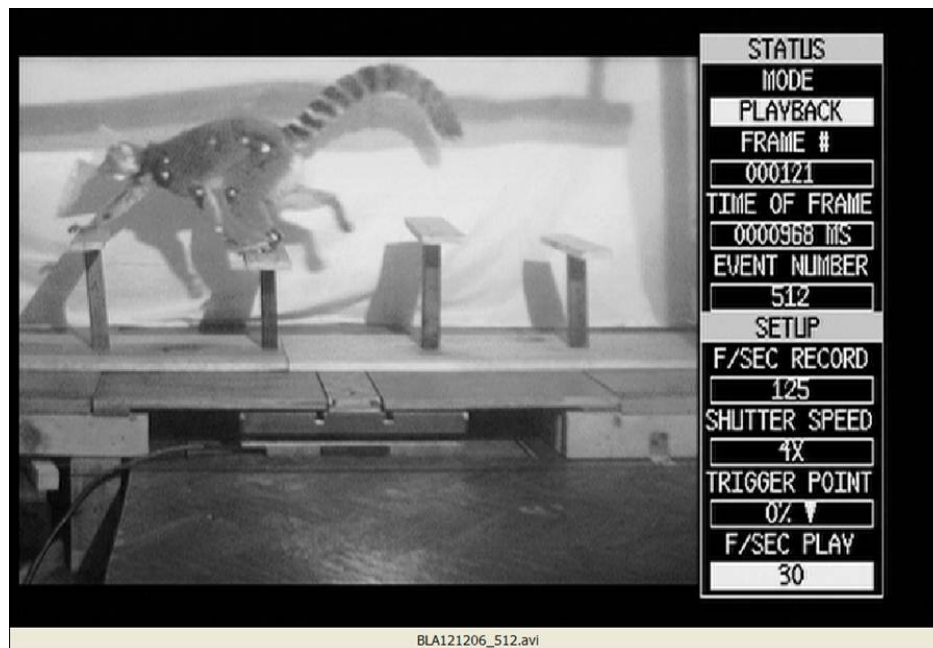


Figure 10: Single frame from a lemur walking on a slat substrate

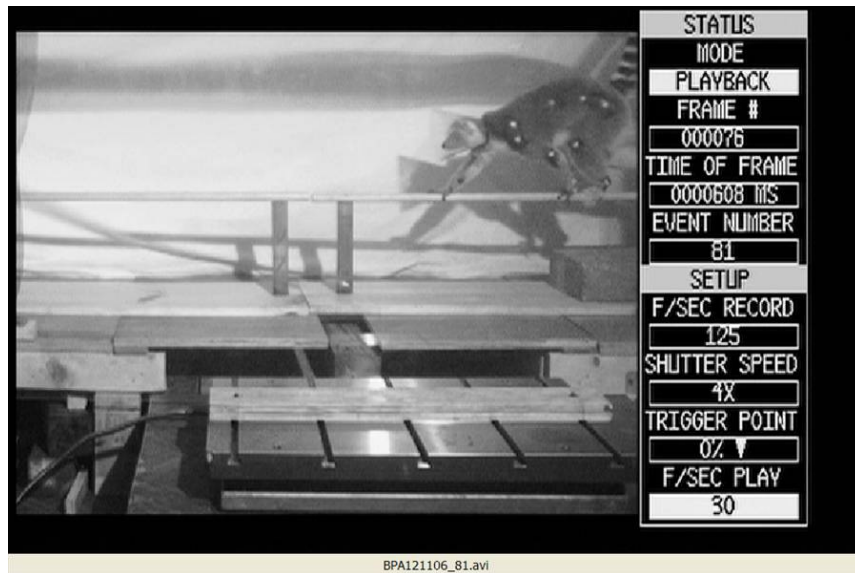


Figure 11: Single frame from a lemur walking on a pole substrate

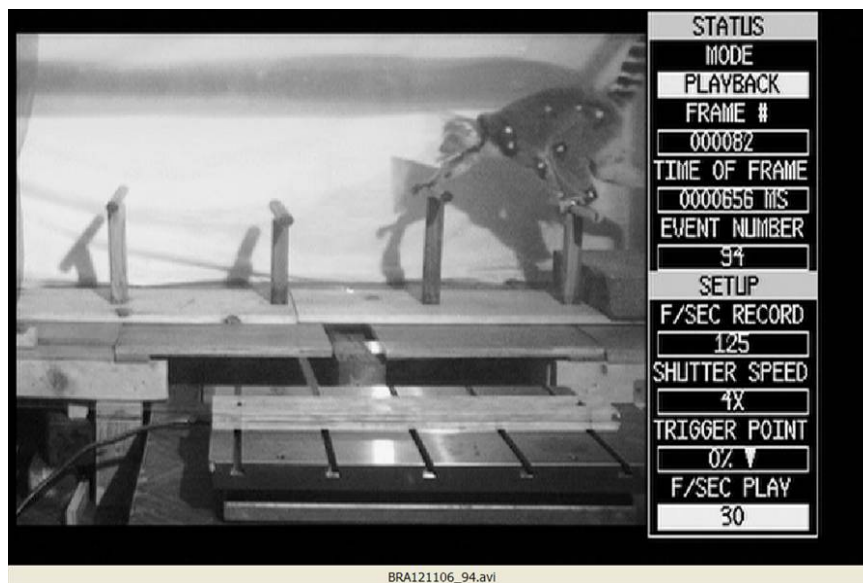


Figure 12: Single frame from a lemur walking on a rung substrate



Figure 13: Eye wrap and collar on *Lemur catta*

### **2.3 Monocular vision**

I produced monocular vision, thereby temporarily eliminating all binocular cues including vergence, binocular summation, and disparity, by wrapping veterinary tape across the face to cover one eye. A strip of elasticon was placed over the tape to keep the patch from shifting during experiments (Figure 13). For rats a small piece of a strong adhesive tape was used to secure vet wrap over the eye. A complete wrap around the head tended to slip, and interfered with both micro and macrovibrissae. In all experiments the right eye was occluded, and a transparent collar was also used to prevent the animal from removing the patch. This is similar to techniques used by veterinarians after eye surgery, and is safe and effective. During placement of the collar and wrap subjects were hand restrained by a Duke Lemur Center technician for lemurs and by the investigator for cats and rats.

There are several potential problems with using a collar and wrap to remove binocular vision. First, the collar itself might interfere with the mechanics of locomotion, thereby altering kinematic variables. Therefore, all binocular conditions were conducted with a control hood that did not occlude vision in either eye. Any deficits in the monocular condition were due to the restriction of light, and not an artifact of wearing the wrap. Second, occluding vision to one eye removes the monocular portion of the visual field as well as the binocular portion, and any differences between conditions

might be due to the change in the total visual field. In this project, subjects were required to guide movement along a narrow substrate, and the monocular portion of the field did not contain information essential to the completion of the task. Third, subjects could suffer temporary motor deficits because either the visuomotor system is calibrated to receive input from two receptors and needs time to adjust to one receptor, or because they are distracted by the occluder. In humans, the motor deficits are associated with a decrease in uncertainty about object location, and not simply a disruption to normal visuomotor transformations (Loftus et al. 2004). All subjects were given as much time as needed to habituate to the wrap and substrates.

## ***2.4 Habituation and training***

Subjects were first placed in an empty enclosure while wearing the wrap and collar, and were considered habituated when they no longer exhibited signs of distress and did not attempt to remove the collar. Lemurs and cats habituated to the equipment in two to three forty minute sessions. The rats were trained to accept handling and food rewards for two to three weeks. After the rats were willing to accept ten minutes of continuous handling, the collar and wrap were applied. It took an additional two to three weeks before the rats were comfortable wearing the patch.

All subjects were trained on the precision and simple substrates under binocular conditions. Cats, lemurs, and rats were first trained to walk across boards for food

rewards. Since all three species were fed *ad libitum* with standard laboratory chow pellets, rewards consisted of novel items such as, raisins for the lemurs, tuna for the cats, and yogurt covered seeds for the rats. After traversing the substrate lemurs returned to the starting position on their own, cats were moved by hand, and rats were moved in a small box to limit handling time. Subjects were considered habituated to the board when they could successfully cross the substrate thirty times in a one hour session – one to two sessions for lemurs and cats and one week for rats.

At this time subjects were introduced to the discontinuous substrates. Initially the planks and rungs were evenly spaced, at the same height, and equal in size. Subjects were considered habituated to the planks or rungs when they could successfully cross the substrate thirty times in a one hour session – one to two sessions for all three species. The habituation process was repeated using planks with uneven spacing, differing heights, and unequal size – one to two sessions for all three species. The uneven plank and rung substrates were then rearranged before the start of data collection, and kept in this configuration throughout the data collection process.

## **2.5 Data collection**

Data was collected no more than once in a 24 hour period in 45 to 90 minute sessions. A session consisted of ten steps on a given substrate under monocular conditions and ten steps under binocular conditions. The goal was to collect five usable

steps per day over a four day period for a total of twenty steps for each substrate under binocular and monocular conditions. For some conditions it was necessary to use as few as two days worth of data with 8 – 10 steps per day.

Two cameras were used to record video data of all locomotor behaviors. A single high speed camera, Motion Scope (Red Lake Imaging Co., Morgan Hill, CA), was placed in a lateral position perpendicular to the direction of motion. Lateral images were recorded at 125 frames per second (fps) for cats and lemurs and at 250 fps for rats. The video was shuttered at 1/1000 – 1/4000 s to reduce motion blur with faster shutter speeds used as permitted by lighting. The aperture was opened only as wide as needed to clearly see the animal and substrate, thereby preserving as much depth of field as possible. A manual trigger was used to save video when subjects crossed the substrate. If the subject crossed the entire substrate while moving in a straight path at a constant velocity, the video was played back at 30 fps and recorded on a DVD.

A second camera, a Panasonic VCD-5100, was used to record a frontal view at 60 fps and shuttered at 1/1000 s. The frontal camera ran continuously and recorded all trials in a given session on a Panasonic DMR ES15 DVD recorder for most trials and a Panasonic AG - 7350 VHS recorder for a few of the early lemur trials. For cats and rats, the frontal and lateral camera were synchronized by an event & video control unit (Peak Performance Englewood, CO) which placed a flashing white bar in the upper left hand



corner of the frontal video when the high speed trigger was depressed. In lemurs, the cameras were synchronized using a red LED which was connected to the high speed trigger and visible in the upper right hand corner of the frontal camera.

Before data collection a water based whiteout solution was used to create a 1 – 2 cm marker on the shoulder, elbow, wrist, hip, knee, and ankle for cats and lemurs. Previous research has demonstrated that skin markers are not good indicators of anatomical landmarks for the shoulder, elbow, hip, and knee in rats due to movement of the skin during locomotion (Bauman and Chang 2007). Therefore, a water soluble face paint was used to create a 0.5 cm marker on the wrist and ankle to follow the placement of the limbs, and a single 1 cm marker was placed just ventral to the articulation of the caudal most palpable rib and its associated vertebrae. The axial marker was used as an indicator of overall body height during locomotion. The skin over each joint was shaved to better identify landmarks and to facilitate the application of the markers. Lemurs were hand restrained by Duke Lemur Center staff during shaving and marking, while cats and rats were hand restrained by the investigator.

Data recorded from the lateral high speed camera on DVD was converted to uncompressed Audio Video Interleave (avi) files using the shareware program VirtualDubMod 1.4.13.1. Trials were clipped to a single stride per crossing from liftoff to touchdown of the left forelimb. For cats and rats the video clip was extended to include the

additional frames necessary to capture the entire swing phase of the left hindlimb. The transition to digital data caused video recorded from the redlake high speed camera to improperly display interlaced lines as distinct images leading to severe blurring during motion capture. The second field was discarded leading to a slight decrease in image quality, but a drastic reduction of motion blur.

The cropped video files were imported into Matlab version 7.2.0.232 (The Mathworks, Inc.,) and digitized in DLTdataviewer, Figure 14, a program written by Ty Hedrick for the analysis of kinematic data (Hedrick 2008). Using DLTdataviewer, the x and y coordinates of the nose, shoulder, elbow, wrist, hip, knee, and ankle were recorded for each frame with a minimum of 51 frames per stride and a maximum of 204 frames. For rats the location of the nose, wrist, ankle, and caudal most rib were digitized. Points marked with whiteout or paint were automatically tracked using DLTdataviewer's built in tracking capabilities. The program uses a double exponential algorithm to predict the location of a marker based on previous frames, and then finds the centroid of the white or black pixels within the search area, 7 – 9 pixels for this study, within a certain color threshold, set to a value of 1 for this study. The program places a visual marker on the selected location for each frame, which the researcher followed for each joint. It was almost always necessary to manually digitize the nose. Other points required manual digitizing for a variety of reasons. At times a subject's fur might obscure the view of a marker.

Frequently black markers could not be distinguished from shadows on the background, and white markers could not be distinguished from the background or surrounding fur.



Figure 14: A single digitized frame in DLTdviewer. In the right window digitized points are displayed after direct placement from user input or automated tracking. In the left window, parameters for autotracking, point creation, and video navigation are available.

In addition to the frame, x, and y coordinates of the seven anatomical landmarks on cats and lemurs and four landmarks on rats, the position and time at which touchdown and liftoff occurred were recorded for each limb throughout the stride duration – nine total events. To define the complete swing phase of the hindlimb for cats and rats, it was necessary to record a tenth event, left hindlimb touchdown, as this occurred outside of the stride duration marked by the left forelimb. In the absence of force data, liftoff was defined as the frame preceding definitive visual evidence that a limb had lost contact with the substrate. During touchdown it was often difficult to tell when the phalanges first contacted the substrate. Therefore, touchdown was defined as the point at which the metacarpals first contacted the substrate, usually within one frame of presumed phalangeal contact. In the first frame two points were used to mark the location of boards and poles, and three points were used to mark the location of planks and rungs on the discontinuous substrates.

After digitizing the anatomical landmarks, gait sequence, and substrate, the x and y coordinates for every frame were saved in pixels at 720 X 480 resolution for each point. The pixels were converted to meters using a calibration board of known dimensions videotaped at the end of each session. The zero point for the y axis was set as the average y value of the two substrate markers for boards and poles, and as the average of the y values of the

first and third rung or plank for discontinuous substrates. The zero point for the x axis was set to the right side of the video.

## **2.6 Derived variables**

Following calibration, the Microsoft Excel file for each stride was loaded into a Matlab script. The following derived variables were calculated from the basic x, y, and frame data.

**Instantaneous horizontal and vertical velocities** were calculated as the change in position between two successive frames divided by the frame rate (1/125 for cats and lemurs, 1/250 for rats).

**Speed** is defined as the average instantaneous horizontal velocity of the shoulder during a stride.

**Stride duration** is defined as the time elapsed from liftoff of the left forelimb to touchdown of the left forelimb [ (# frames – 1) / fps ].

**Stride length** is defined as the horizontal distance between the point of liftoff and point of touchdown.

**Swing time** is defined as the time a limb is not in contact with the substrate during a given stride.

**Contact time** is defined as the time a limb is in contact with the substrate during a given stride.

**Angles** are calculated as the arccosine of the dotproduct of two limb segments divided by the product of their length [ elbow angle =  $\text{acos}((X_{\text{elbow}} - X_{\text{shoulder}}) * (X_{\text{elbow}} - X_{\text{wrist}}) + (Y_{\text{elbow}} - Y_{\text{shoulder}}) * (Y_{\text{elbow}} - Y_{\text{wrist}})) / (\text{humeral length} * \text{radial length})$  ]. The shoulder angle was calculated from the hip-shoulder and shoulder-elbow vectors. The hip angle was calculated from the hip-shoulder and hip-knee vectors. The knee angle was calculated from the hip-knee and knee-ankle vectors.

**Protraction** is defined as the shoulder or hip angle at touchdown.

**Retraction** is defined as the shoulder or hip angle at liftoff.

**Excursion** is defined as the protraction angle minus the retraction angle.

## ***2.7 Examination of the wrist trajectory***

Previous research has indicated that binocular vision is of particular importance during placement of the forelimb during grasping and reaching movements (Servos et al. 1992). To examine whether this finding holds for mammalian locomotion, I decomposed the trajectory of the wrist during swing phase into four subphases. The subphases were designed to capture important changes in slope, horizontal velocity, and vertical velocity, and were defined differently for simple and complex substrates. The phases for simple substrates are described below.

The **separation phase** ends at the second frame with vertical velocity  $> 0$  m/s, and is characterized by low horizontal and vertical velocity and high horizontal acceleration

(Figure 15). The **ascent phase** begins at the third frame with vertical velocity  $> 0$  m/s, and is characterized by high horizontal and vertical velocities. The **plateau phase** begins with at least 2 successive frames with a vertical velocity  $< 0.1$  m/s, ends at the first of 2 successive frames with vertical velocity  $< -0.1$  m/s, and is characterized by high horizontal velocity with some deceleration and low vertical velocity. The final, **descent**, phase is characterized by low horizontal velocity with high deceleration, and a high negative vertical velocity with rapid negative acceleration.

The phases for complex substrates are similar to those defined above. With the exception that there is no **separation** phase as the wrist begins to ascend immediately after liftoff, and there is an additional **placement** phase at the end of the movement, Figure 16. During the **descent** phase on complex substrates rather than starting with an immediate horizontal deceleration, the wrist continues to move at a high horizontal velocity as it begins to fall. The **placement phase** is marked by a dramatic horizontal deceleration yielding a low horizontal velocity and a steep drop off in the trajectory curve. Additionally this phase is generally characterized by high negative vertical velocities. Though in lemurs it can begin with a short period of vertical velocity near 0 m/s causing a plateau in the trajectory curve.



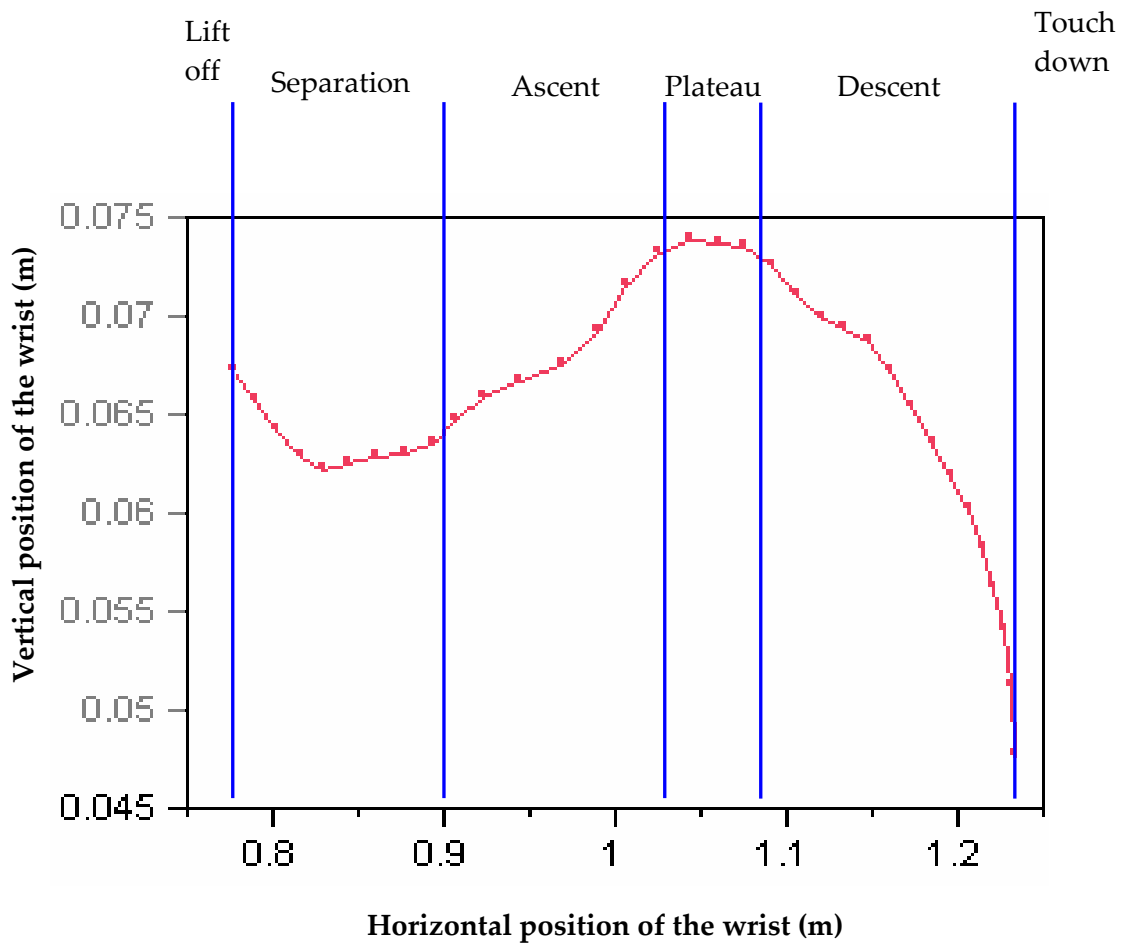


Figure 15: Example of phases for a lemur walking on a board under binocular conditions

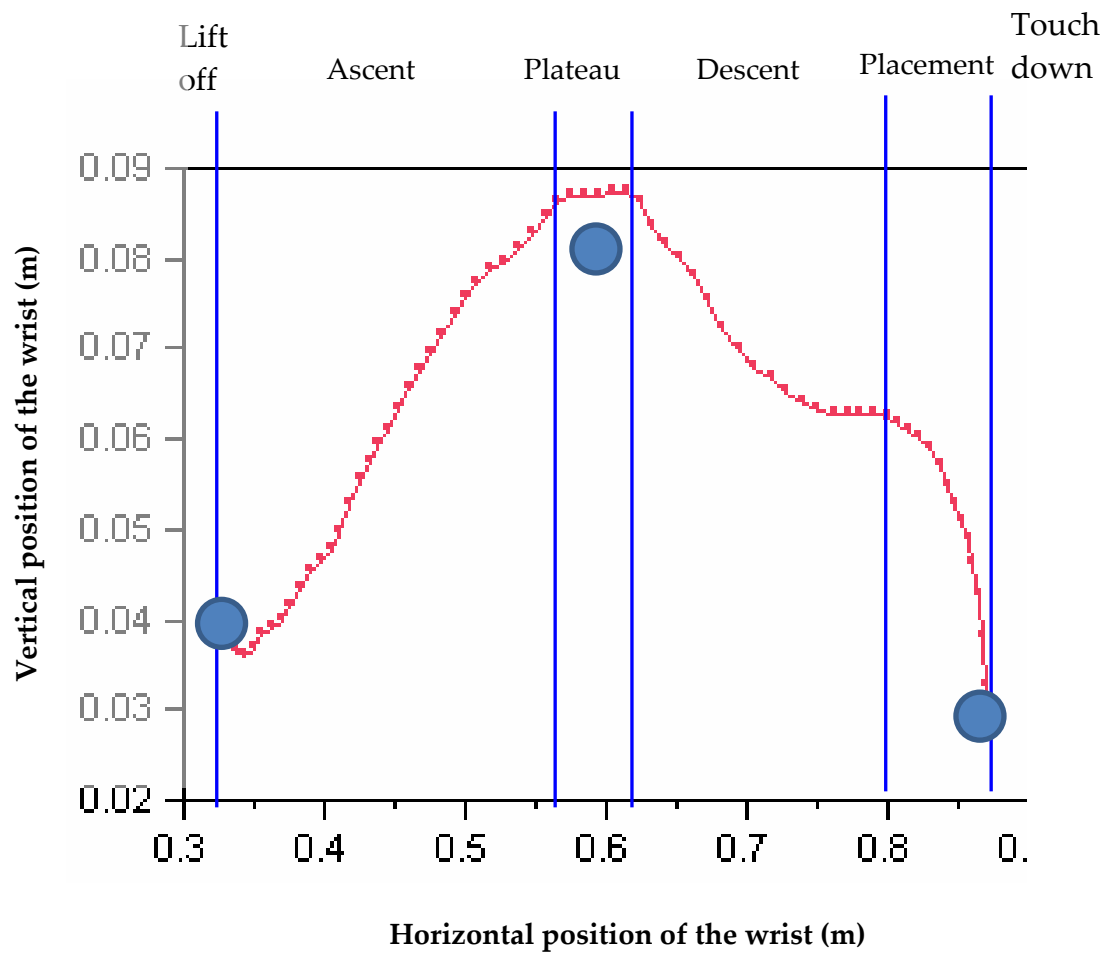


Figure 16: Example of phases for a lemur walking on rungs under binocular conditions.

## **2.8 Analysis**

The primary question posed in my dissertation is do animals guiding locomotor behaviors with one eye walk different than animals guiding behavior with two eyes. Given a sample size of approximately sixty strides per species for each substrate under both binocular and monocular conditions a parametric test such as a Student's t-test could be used to test for a difference in means. For example, does mean speed differ in animals walking under binocular vs. monocular conditions? While assumptions such as normality can be relaxed at large sample sizes, my data contain distributions with differences in skew and outliers for which there is no plausible biological rationale for exclusion. As such, I have chosen to use the nonparametric, two – tailed, Kruskal – Wallis test to analyze my data. The Kruskal – Wallis, and all other statistical tests for this study, were performed in Jmp 7.0 (SAS Institute, Inc.) with a significance level of 0.05. The null hypothesis for the Kruskal – Wallis is that the data are sampled from populations with similar locations or that the mean ranks are the same. In general the Student's t and Kruskal – Wallis yield similar results. The exceptions appear for variables with several outliers, which violate the assumptions of the parametric test.

While the primary goal of this dissertation is to examine the role of binocular vision in locomotion, it is necessary to consider the effect of speed on other kinematic variables. For example, a Kruskal – Wallis test demonstrates that monocular cats walking on planks

move more slowly and spend more time during placement of the wrist. Each result can be interpreted as having biological significance. Subjects might slow down as a general response to an increase in uncertainty, and subjects might be spending additional time placing the wrist due to an increase in on-line corrections at the end of swing phase. From these experiments, it is not possible to determine whether changes in one of these variables is causally related to changes in the other. However, speed is a well known correlate of many kinematic variables. In the data presented here, almost all variables are correlated with speed in at least one condition, and many variables are highly correlated with speed in all conditions.

To better understand the effects of speed in my data set a least-squares multiple regression was calculated with the variable of interest, shoulder height, protraction, time spent in deceleration, etc., as the dependent variable, and speed, eye condition, and a speed \* eye condition interaction term as independent covariates. Multiple regression is a statistical technique used to regress the dependent variable on several independent variables simultaneously, and can be used to determine whether there is a significant effect of each of the covariates on the dependent variable after removing variation due to all other covariates (Sokal and Rohlf 1995). The interaction term accounts for variation explained when the effect of one covariate depends on the level of another. When the covariates are a nominal and a continuous variable, the interaction term is a test for homogeneity of slopes.

For this analysis a significant interaction term signifies that the independent variable changes with speed differently depending on whether the animal is walking under binocular or monocular conditions. Such a result confounds an attempt at a simple analysis of the main effects, speed and eye condition, and requires a more thorough discussion of how the independent variable changes with speed under binocular and monocular conditions. If on the other hand the interaction term is not significant, it should be removed from the model (Engqvist 2005). In the case of two covariates the multiple regression is now equivalent to an analysis of covariance. For this analysis, the interaction term could be removed for all independent variables.

Before conducting a multiple regression it is necessary to test whether the data meets the assumptions of the model. A multiple regression assumes that residuals maintain linearity, equal variance, and a normal distribution. Plots of residuals vs. predicted values and studentized residuals vs. predicted values can be used to graphically assess linearity and equal variance. The normality of residuals can be tested graphically with a stem and leaf plot and statistically with a Shapiro-Wilk test. While the data presented here largely meet the requirements of linearity, equal variance, and normality of residuals, there are a few variables for which the appropriateness of a multiple regression could be questioned due to the presence of outliers. I therefore ran a separate analysis without outliers, defined as a point with a studentized t-value  $> 2$ . Removing the outliers usually reduced the total

sample size,  $N \sim 120$ , by 3 – 5 points. The outlier – free analyses yielded few differences in tests of significance.

### **3. Results**

The results are broken up into three sections. The first section deals with kinematic variables commonly used to describe locomotion including speed, stride length, and stride duration. Several other variables were included to capture the degree to which subjects were crouching including minimum shoulder height, protraction, retraction, and excursion. The second section deals with variables associated with the path followed by the wrist during swing phase. These variables, including maximum wrist height, wrist speed, and swing time, summarize a subject's performance during placement of the forelimb. Additionally the path taken by the wrist was broken up into four distinct phases for a more thorough analysis. Finally, the third section focuses on the effect that speed has on the previously discussed variables. Results that remain significant after using a multiple regression to remove the effects of speed will be discussed.

#### ***3.1 Whole body and forelimb kinematics***

In Figure 17 the horizontal shoulder velocity of cats on slats under binocular conditions is compared to horizontal shoulder velocity under monocular conditions. The data has been analyzed using a two sided Kruskal – Wallis Rank Sums test. The p-

value is reported under the **Prob>|Z|** column. The null hypothesis for the Kruskal – Wallis test is that the mean ranks from the populations are the same. For this study, if the probability of finding a test statistic as extreme as **Z** is less than 0.05, the result is considered significant. In this case the p-value is 0.0005 indicating that there is a significant difference in speed between cats walking on slats under binocular vs. monocular conditions. Similar analyses were conducted for speed, stride length, stride duration, minimum shoulder height, protraction, retraction, and excursion. The results from these analyses are reported in summary Tables 2 through 15.

The tables are broken up into groups by variable and by continuous vs. discontinuous substrates. In each table the species (cat, rat, lemur), substrate (board, pole, slat, rung), sample size, variable value for the binocular and monocular condition, standard deviation for the binocular and monocular, test statistic, and p value are reported. For example Table 3 summarizes the difference in mean horizontal shoulder velocity under binocular vs. monocular conditions for cats, lemurs, and rats on discontinuous substrates. Lemurs will appear in each table twice as they were the only species to traverse the pole and rung substrates. Rats are absent from all tables involving angles as data was not collected for the location of the shoulder, hip, elbow, and knee for this species.

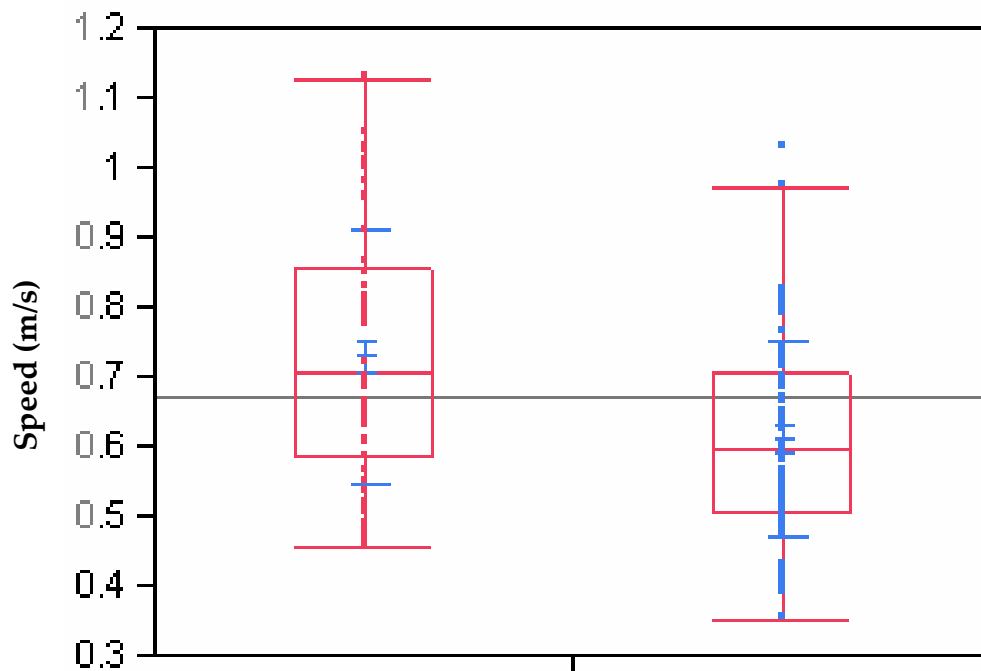


Figure 17: Binocular vs. monocular speed for cats on slats

**Wilcoxon / Kruskal-Wallis Tests (Rank Sums)**

Level	Count	Score Sum	Score Mean	(Mean-Mean0)/Std0
Binocular	60	4293.00	71.5500	3.477
Monocular	60	2967.00	49.4500	-3.477

**2-Sample Test, Normal Approximation**

S	Z	Prob> Z
2967	-3.47722	0.0005



**Table 2: Average binocular vs. monocular differences in average horizontal shoulder velocity on continuous substrates**

Species	Substrate	p	Speed Binoc (m/s)	Speed Monoc (m/s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.566	0.692	0.675	0.157	0.176	0.574	60	60
rat	board	0.561	0.884	0.874	0.075	0.076	-0.582	52	53
lemur	board	0.517	0.751	0.764	0.098	0.116	0.648	60	59
lemur	pole	0.459	0.668	0.669	0.080	0.108	-0.740	60	60

**On continuous substrates none of the three species examined show a significant difference in speed under binocular vs. monocular conditions.** Under binocular conditions cats walked on flat surfaces at 0.692 m/s which was 0.017 m/s faster than their performance under monocular conditions. Rats tended to move the fastest of all three species at 0.884 m/s under binocular conditions which was 0.010 m/s faster than their performance under monocular conditions. Under binocular conditions, lemurs walked faster on boards (0.751 m/s) than on poles (0.668 m/s) and in both cases monocular performances were marginally faster.

**Table 3: Average binocular vs. monocular differences in average horizontal shoulder velocity on discontinuous substrates**

Species	Substrate	p	Speed Binoc (m/s)	Speed Monoc (m/s)	Std Dev Binocular	Std Dev Monocular	Z	N B	N M
cat	slat	0.001	0.728	0.610	0.181	0.141	-3.477	60	60
rat	slat	0.513	0.643	0.641	0.087	0.105	-0.653	60	60
lemur	slat	0.002	0.655	0.601	0.103	0.105	-3.110	60	60
lemur	rung	0.000	0.642	0.584	0.097	0.103	-3.703	60	60

**Cats and lemurs walk significantly more slowly on discontinuous substrates under monocular conditions, while rats show no significant speed differences between binocular and monocular conditions.** Cats walk the fastest of all three species on slats at 0.728 m/s under binocular conditions and 0.118 m/s slower under monocular conditions ( $p = 0.001$ ). Rats on the other hand walk the slowest at 0.643 m/s under binocular conditions and 0.002 m/s slower under monocular conditions. Under binocular conditions lemurs walk faster on slats (0.655 m/s) than on rungs (0.642 m/s), and in both cases they slow down under monocular conditions. The deficit is 0.053 m/s ( $p = 0.002$ ) on slats and 0.058 m/s on rungs ( $p < 0.001$ ).

**Table 4: Average binocular vs. monocular differences in stride length on continuous substrates**

Species	Substrate	p	Stride length Binoc (m)	Stride length Monoc (m)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.437	0.382	0.376	0.047	0.058	0.777	52	52
rat	board	0.989	0.180	0.179	0.014	0.012	0.013	60	59
lemur	board	0.151	0.473	0.482	0.035	0.037	-1.436	60	60
lemur	pole	0.254	0.482	0.487	0.032	0.030	-1.141	56	55

For all three species on continuous substrates, the stride length, horizontal distance between the point of liftoff and point of touchdown, did not differ significantly between monocular and binocular conditions. These results are expected given that there were also no differences in speed between binocular and monocular conditions on continuous substrates. While walking on boards cats exhibited a stride length of 0.382 meters under binocular conditions and 0.376 meters under monocular conditions ( $p = 0.437$ ). Rats demonstrated a 0.18 stride length under binocular conditions and 0.179 meters under monocular conditions ( $p = 0.989$ ). Under binocular conditions lemurs walked with a stride length of 0.473 meters on boards and 0.482 meters on poles. Neither of these results differs significantly when compared to monocular conditions ( $p = 0.151$  and  $0.254$  respectively).

**Table 5: Average binocular vs. monocular differences in stride length on discontinuous substrates**

Species	Substrate	p	Stride length Binoc (m)	Stride length Monoc (m)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.254	0.419	0.414	0.019	0.025	1.142	60	60
rat	slat	0.341	0.156	0.155	0.006	0.007	0.953	60	60
lemur	slat	0.731	0.556	0.558	0.019	0.027	0.344	60	60
lemur	rung	0.791	0.564	0.563	0.016	0.014	0.265	60	60

**None of the species showed a significant difference in stride length between monocular and binocular conditions on discontinuous substrates.** Cats and lemurs did tend to walk at higher speeds under binocular conditions and might therefore be expected to take longer stride lengths. However, the design of the discontinuous substrates limited placement of the limbs. Stride length could not vary much and is more or less an indicator of the distance between slats and rungs.

**Table 6: Average binocular vs. monocular differences in stride duration on continuous substrates**

Species	Substrate	p	Stride duration Binoc (s)	Stride duration Monoc (s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.658	0.716	0.730	0.119	0.121	-0.442	52	53
rat	board	0.459	0.232	0.235	0.026	0.025	0.740	60	59
lemur	board	0.918	0.733	0.736	0.060	0.079	-0.102	60	60
lemur	pole	0.279	0.815	0.827	0.075	0.100	1.083	56	55

**None of the species showed a significant difference in stride duration on continuous substrates.** Given that speed did not differ on continuous substrates this result is not surprising. While walking on boards cats took 0.716 seconds to complete a stride under binocular conditions, rats 0.232 seconds, and lemurs 0.733 seconds. When compared to their performance on boards lemurs took slightly longer to complete a stride under binocular conditions on poles, 0.815 seconds.

**Table 7: Average binocular vs. monocular differences in stride duration on discontinuous substrates**

Species	Substrate	p	Stride duration Binoc (s)	Stride duration Monoc (s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.001	0.767	0.900	0.194	0.204	3.328	60	60
rat	slat	0.587	0.292	0.295	0.043	0.049	0.544	60	60
lemur	slat	0.001	1.004	1.106	0.150	0.166	3.709	60	60
lemur	rung	0.001	1.004	1.124	0.125	0.179	4.027	60	60

**On discontinuous substrates both cats and lemurs took significantly more time to complete a stride under monocular conditions.** Given that these subjects tended to walk faster under binocular conditions and stride length was relatively fixed, it makes sense that subjects increase stride duration under monocular conditions. Cats on slats required 0.767 seconds to complete a stride under binocular conditions and 0.9 seconds under monocular conditions ( $p < 0.001$ ), and lemurs used 1.004 seconds under binocular vs. 1.106 seconds under monocular ( $p < 0.001$ ). On rungs lemurs required 1.004 seconds under binocular conditions and 1.124 under monocular ( $p < 0.01$ ). Rats took 0.292 seconds to complete a stride under binocular conditions which did not differ significantly from monocular performances ( $p = 0.587$ ).

**Table 8: Average binocular vs. monocular differences in minimum shoulder height on continuous substrates**

Species	Substrate	p	Min Shoulder Height Binoc (m)	Min Shoulder Height Monoc (m)	Std Dev Binocular	Std Dev Monocular	Z	N B	N M
cat	board	0.926	0.154	0.153	0.014	0.017	-0.093	52	53
rat	board	0.001	0.075	0.070	0.004	0.005	-5.009	60	59
lemur	board	0.061	0.154	0.152	0.006	0.007	-1.871	60	60
lemur	pole	0.830	0.127	0.126	0.007	0.007	-0.215	56	55

**On continuous substrates rats show a significant decrease in minimum shoulder height under monocular conditions while cats and lemurs show no significant differences.** Rats tend to crouch more on boards under binocular conditions with a minimum shoulder height of 0.075 meters under binocular conditions and 0.007 meters under monocular conditions ( $p < 0.001$ ). Lemurs and cats on boards exhibit a minimum shoulder height of 0.154 meters under binocular conditions, while lemurs have a minimum shoulder height of 0.127 meters on poles. These values are not significantly different from those seen in monocular conditions.

**Table 9: Average binocular vs. monocular differences in minimum shoulder height on discontinuous substrates**

Species	Substrate	p	Min Shoulder Height Binoc (m)	Min Shoulder Height Monoc (m)	Std Dev Binocular	Std Dev Monocular	Z	N B	N M
cat	slat	0.015	0.156	0.151	0.009	0.013	-2.422	60	60
rat	slat	0.002	0.079	0.075	0.005	0.006	-3.047	60	60
lemur	slat	0.015	0.145	0.142	0.006	0.008	-2.443	60	60
lemur	rung	0.034	0.146	0.142	0.008	0.008	-2.118	60	60

**All three species have significantly lower minimum shoulder heights under monocular conditions on discontinuous substrates.** On slats cats dip their shoulder to 0.156 meters above the substrate, rats to 0.079 meters, and lemurs to 0.145 meters, while on rungs lemurs have a minimum shoulder height of 0.146 meters. Under monocular conditions values range from 3-5mm lower.



**Table 10: Average binocular vs. monocular differences in protraction angle on continuous substrates**

Species	Substrate	p	Protraction Binoc (°)	Protraction Monoc (°)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.046	125.071	125.929	2.742	3.937	1.993	52	52
lemur	board	0.700	137.691	137.655	3.831	3.299	0.386	60	60
lemur	pole	0.107	141.800	142.326	2.279	2.256	1.613	56	55

**For both species there is little difference between binocular and monocular protraction angles on continuous substrates.** Under binocular conditions cats have a protraction angle of 125.1° and lemurs of 137.7°, while lemurs on poles are at 141.8°. Cats show a significant though marginal increase of 0.8° under monocular conditions (p = 0.046).

**Table 11: Average binocular vs. monocular differences in protraction angle on discontinuous substrates**

Species	Substrate	p	Protraction Binoc (°)	Protraction Monoc (°)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.222	130.234	131.365	5.278	4.968	1.220	60	60
lemur	slat	0.102	140.944	142.592	3.683	3.227	1.635	60	60
lemur	rung	0.108	144.609	145.322	2.645	2.945	1.609	60	60

**On discontinuous substrates cats and lemurs show a non significant trend towards increasing protraction under monocular conditions.** Protraction angles on slats under binocular conditions are 130.2° for cats and 140.9° for lemurs, while lemurs

on rungs are at 144.6°. Monocular protraction angles range from 0.7° to 1.6° larger with  $p < 0.11$  for lemurs.

**Table 12: Average binocular vs. monocular differences in retraction angle on continuous substrates**

Species	Substrate	p	Retraction Binoc (°)	Retraction Monoc (°)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.537	51.039	50.313	4.089	4.228	-0.617	52	51
lemur	board	0.329	58.103	57.815	1.572	1.742	-0.975	60	59
lemur	pole	0.063	57.136	58.150	2.882	3.653	1.857	56	54

Neither species shows a significant difference in the retraction angle on continuous substrates. Under binocular conditions cats on boards retract the forelimb at 51.0° and lemurs at 58.1°. Lemurs on poles approach significance at  $p = 0.063$  with binocular retraction at 57.1° and monocular at 58.1°.

**Table 13: Average binocular vs. monocular differences in retraction angle on discontinuous substrates**

Species	Substrate	p	Retraction Binoc (°)	Retraction Monoc (°)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.002	52.916	51.214	3.293	3.386	-3.026	60	60
lemur	slat	0.068	60.370	59.520	2.661	3.119	-1.824	60	60
lemur	rung	0.081	62.983	62.029	2.243	2.767	1.746	59	60

Cats and lemurs on discontinuous substrates show a trend towards less retraction under monocular conditions. Less retraction indicates that the arm is closer

to the body at liftoff. Under binocular conditions the retraction angle for cats on slats is 52.9° and the retraction angle is 60.4° for lemurs, while lemurs on rungs are at 63.0°. When walking on slats cats exhibit the only significant difference with 1.7° less retraction under monocular conditions ( $p = 0.002$ ).

**Table 14: Average binocular vs. monocular differences in excursion angle on continuous substrates**

Species	Substrate	p	Excursion Binoc (°)	Excursion Monoc (°)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.171	74.032	75.862	5.041	5.917	1.369	52	50
lemur	board	0.370	79.588	79.844	3.930	3.336	0.896	60	59
lemur	pole	0.371	84.664	84.105	3.059	4.838	-0.894	56	54

**Neither species shows a significant difference in excursion on continuous substrates.** On boards cats increase excursion from 74.0° to 75.8° from binocular to monocular conditions and lemurs go from 79.6° to 79.8°. While walking on poles lemurs decrease excursion from 84.7° to 84.1°.

**Table 15: Average binocular vs. monocular differences in excursion angle on discontinuous substrates**

Species	Substrate	p	Excursion Binoc (°)	Excursion Monoc (°)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.006	77.318	80.151	5.369	5.392	2.737	60	60
lemur	slat	0.001	80.573	83.072	3.580	4.073	3.241	60	60
lemur	rung	0.010	81.578	83.292	3.000	3.662	-2.586	59	60

**On discontinuous substrates both species show a significant increase in excursion under monocular conditions.** Subjects are in effect increasing the overall degree to which they are extended on touch down and liftoff. Under binocular conditions cats on slats exhibit 77.2° of excursion and lemurs show 80.6°, while lemurs on rungs have 81.6°. Across these three conditions monocular excursion is 1.7° – 2.8° larger ( $p < 0.01$  in all conditions).

### ***3.2 Placement of the forelimb***

Section two of the results focuses on the path of the wrist during swing phase. Given that the majority of the advantages associated with binocular vision are related to increases in the ability to discriminate depth, it seems reasonable to examine the placement of the wrist in more detail. To this end, the path of the wrist during swing phase has been broken into four subphases, and kinematic variables including duration, horizontal and vertical wrist velocity, and horizontal and vertical distance were

calculated for each phase. Before exploring these variables further, I will first examine some basic characteristics of these phases.

Additionally, I will discuss several variables related to swing phase of the forelimb as a whole. Monocular reaches tend to take more time, occur more slowly, and have higher maximum wrist heights. Initial analyses demonstrated that these variables are also significantly different in each of the phases. For example monocular reaches tend to take more time in all four phases. Therefore, these variables are presented as percentages of the total time and movement. Stride length did not differ between monocular and binocular conditions, and will be presented as a direct measurement rather than a percentage of the total movement. Furthermore, I will save a discussion of wrist speed until variation due to average speed has been removed.

### 3.2.1 Kinematics of the wrist

**Table 16: Average binocular vs. monocular differences in swing time of the left forelimb on continuous substrates**

Species	Substrate	p	Swing Time Binoc (s)	Swing Time Monoc (s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.482	0.239	0.236	0.030	0.024	0.703	52	53
rat	board	0.668	0.120	0.121	0.017	0.014	0.430	60	59
lemur	board	0.456	0.297	0.301	0.027	0.027	0.746	60	60
lemur	pole	0.960	0.327	0.327	0.043	0.043	0.050	56	55

**None of the species show significant differences in swing time on continuous substrates.** This result is consistent with the fact that there were no differences between speed under binocular and monocular conditions on continuous substrates. Under binocular conditions cats required 0.239 seconds to move their left forelimb from liftoff to touchdown, rats required 0.120 seconds, and lemurs took 0.297 seconds. Lemurs on poles used 0.327 seconds.

**Table 17: Average binocular vs. monocular differences in swing time of the left forelimb on discontinuous substrates**

Species	Substrate	p	Swing Time Binoc (s)	Swing Time Monoc (s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.002	0.309	0.353	0.083	0.084	3.167	60	60
rat	slat	0.973	0.140	0.141	0.019	0.022	0.034	60	60
lemur	slat	0.007	0.541	0.589	0.101	0.108	2.676	60	60
lemur	rung	0.035	0.551	0.593	0.086	0.112	2.103	60	60

**Cats and lemurs on discontinuous substrates required less time to swing their left forelimb under binocular conditions.** This result is consistent with the fact that cats and lemurs moved faster on discontinuous substrates and had lower stride durations under binocular conditions. Cats on slats increased swing time from 0.309 under binocular conditions to 0.353 ( $p = 0.002$ ) seconds under monocular conditions, lemurs increased from 0.541 to 0.589 ( $p = 0.007$ ), and lemurs on rungs increased from 0.551 to 0.593 ( $p = 0.035$ ). Rats on slats did not take significantly longer to complete swing phase under binocular conditions, which is consistent with their lack of significant differences for speed.

**Table 18: Average binocular vs. monocular differences in maximum wrist height on continuous substrates**

Species	Substrate	p	Max Wrist Height Binoc (m)	Max Wrist Height Monoc (m)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.571	0.074	0.075	0.007	0.010	-0.567	52	53
rat	board	0.696	0.015	0.015	0.002	0.002	-0.391	60	59
lemur	board	0.302	0.069	0.070	0.006	0.005	1.031	60	60
lemur	pole	0.834	0.039	0.040	0.007	0.006	0.209	56	55

None of the species showed a significant difference in maximum wrist height on continuous substrates. Under binocular conditions cats on boards raised their wrist to a maximum height of 0.074 meters, rats to 0.015 meters, and lemurs to 0.069 meters. Lemurs on poles raised their wrist to 0.039 meters. Cats and lemurs exhibited a non significant increase of 1 mm under monocular conditions.

**Table 19: Average binocular vs. monocular differences in maximum wrist height on discontinuous substrates**

Species	Substrate	p	Max Wrist Height Binoc (m)	Max Wrist Height Monoc (m)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slat	0.069	0.119	0.121	0.008	0.010	1.819	60	60
rat	slat	0.513	0.020	0.020	0.001	0.001	-0.653	60	60
lemur	slat	0.497	0.105	0.106	0.009	0.009	0.680	60	60
lemur	rung	0.027	0.093	0.096	0.008	0.009	2.212	60	60

**Lemurs on rungs raise their wrist significantly higher under monocular conditions.** When walking on rungs lemurs tend to raise their wrist to 0.093 meters



under binocular conditions and 0.096 meters under monocular conditions ( $p = 0.027$ ).

Cats and lemurs on slats raise their wrists an additional 1 – 2 mm, but the difference is not significant. Rats have an average maximum wrist height of 0.020 meters under both binocular and monocular conditions.

**Table 20: Average binocular vs. monocular differences in horizontal wrist velocity during swing phase on continuous substrates**

Species	Substrate	p	Wrist Velocity Binoc (m/s)	Wrist Velocity Monoc (m/s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	board	0.972	1.617	1.599	0.293	0.278	0.035	52	53
rat	board	0.696	1.504	1.490	0.141	0.120	-0.391	60	59
lemur	board	0.696	1.592	1.599	0.150	0.178	0.391	60	60
lemur	pole	0.775	1.484	1.504	0.213	0.243	0.286	56	55

**None of the species show a significant difference in horizontal wrist velocity on continuous substrates.** This result makes sense given that speed did not differ on continuous substrates. Under binocular conditions cats on boards move their wrist at 1.617 m/s, rats at 1.504 m/s, and lemurs at 1.592 m/s, while lemurs on poles move their wrist at 1.484 m/s.

**Table 21: Average binocular vs. monocular differences in horizontal wrist velocity during swing phase on continuous substrates**

Species	Substrate	p	Wrist Velocity Binoc (m/s)	Wrist Velocity Monoc (m/s)	Std Dev Binoc	Std Dev Monoc	Z	N B	N M
cat	slats	0.002	1.452	1.246	0.368	0.302	-3.110	60	60
rat	slats	0.639	1.123	1.114	0.134	0.149	-0.470	60	60
lemur	slats	0.017	1.059	0.976	0.199	0.193	-2.391	60	60
lemur	rungs	0.029	1.046	0.979	0.180	0.192	-2.186	60	60

**Cats and lemurs on discontinuous substrates move their wrists faster during swing phase under binocular conditions.** Cats also move faster and have shorter stride durations under binocular conditions which fits well with this data. When walking on slats cats decrease horizontal wrist velocity from 1.452 m/s under binocular conditions to 1.246 m/s ( $p = 0.002$ ) under monocular conditions, lemurs decrease from 1.059 m/s to 0.976m/s ( $p = 0.017$ ), and rats exhibit a non significant decrease from 1.123 m/s to 1.114 m/s ( $p = 0.639$ ). Lemurs on rungs decrease significantly from 1.046 m/s to 0.979 m/s ( $p = 0.029$ ).

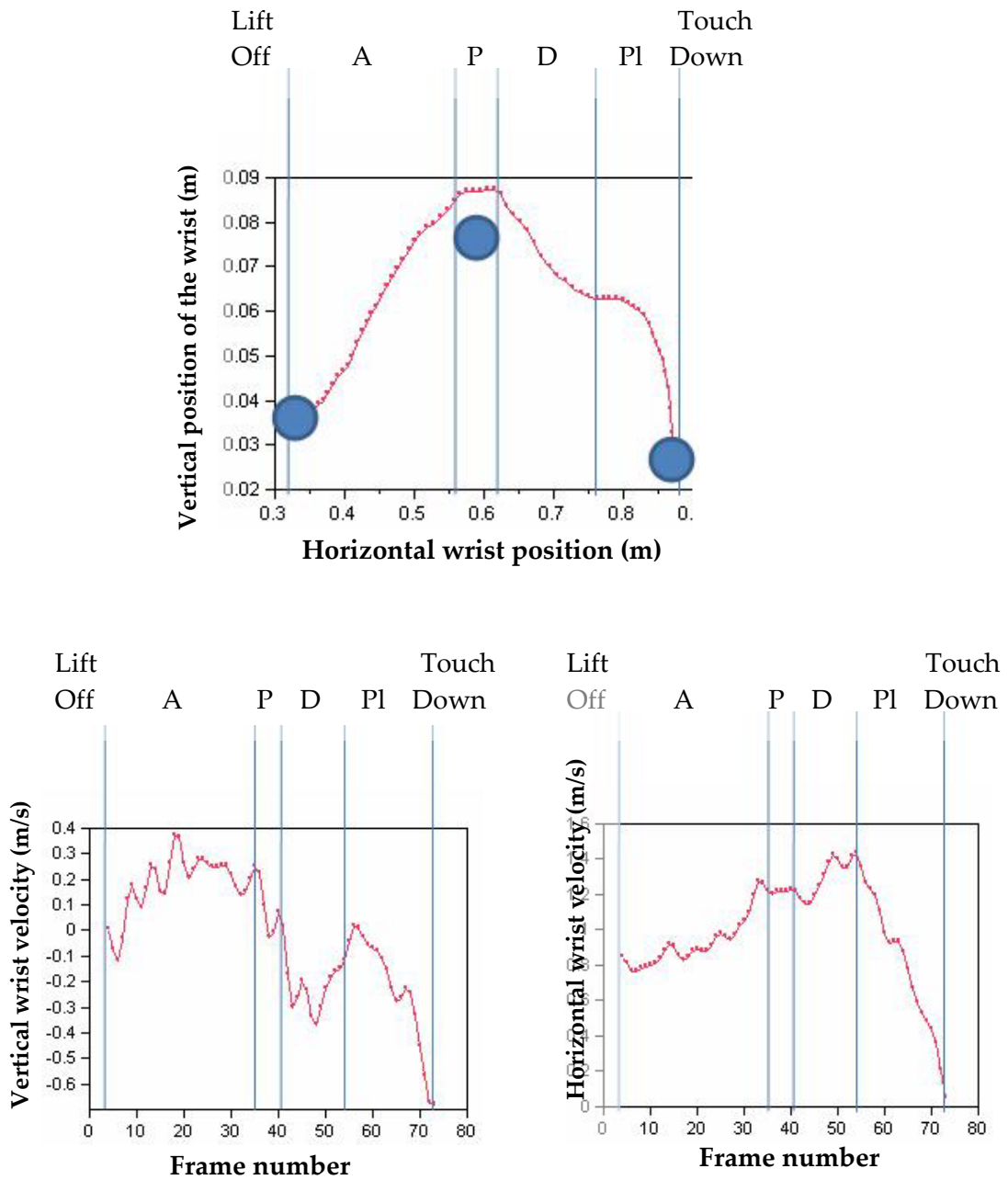


Figure 18: Wrist trajectory, vertical wrist velocity, and horizontal wrist velocity for a lemur walking on rungs. The trajectory and velocities are broken up into four phases, (A)scent, (P)lateau, (D)escent, and (Pl)acement

### 3.2.2 General phase characteristics

The trajectory of the wrist was broken up into four phases. Though the patterns were similar on continuous and discontinuous substrates, the differences were large enough to warrant modified phases. Wrist trajectories on continuous substrates begin with a **separation phase** characterized by low horizontal and vertical velocities and high horizontal acceleration, and then move into an **ascent phase** with high horizontal and vertical velocities, Figure 15. The wrist then reaches a **plateau phase** in which it moves in a more or less horizontal trajectory at high velocity. Finally the wrist drops during the **descent phase** with high negative vertical velocity and low horizontal velocity.

On discontinuous substrates there is no **separation phase** as the wrist usually begins its ascent immediately, Figure 16. The **descent phase** differs in that the wrist continues moving at a high horizontal velocity while dropping. There is an additional **placement phase** in which the wrist decelerates rapidly in the horizontal direction before reaching the substrate. An example of the wrist trajectory for a lemur walking on rungs is provided in Figure 18 along with the horizontal and vertical wrist velocities.

Tables 22 – 25 summarize the horizontal and vertical velocities of the wrist in each phase. Only binocular speeds have been provided, because here the primary

concern is the pattern of speed variation between phases, which is similar under both conditions.

**Table 22: Horizontal wrist speed by phase under binocular and monocular conditions on continuous substrates.**

Phase	Species	Substrate	Horizontal Wrist Velocity Binoc	N B	Std Dev Binoc
separation	cat	board	1.766	51	0.348
ascent	cat	board	2.116	52	0.386
plateau	cat	board	1.682	52	0.323
descent	cat	board	0.949	52	0.200
separation	rat	board	1.586	49	0.183
ascent	rat	board	1.752	49	0.179
plateau	rat	board	1.630	49	0.208
descent	rat	board	1.023	49	0.207
separation	lemur	board	1.669	60	0.187
ascent	lemur	board	2.143	60	0.256
plateau	lemur	board	1.906	60	0.272
descent	lemur	board	1.119	60	0.136
separation	lemur	pole	1.523	56	0.243
ascent	lemur	pole	1.924	56	0.379
plateau	lemur	pole	1.348	56	0.338
descent	lemur	pole	0.589	56	0.239

In Table 26, the horizontal velocity starts out at a moderate pace, peaks during the ascent phase, and then decreases during the plateau and descent phase. The lowest

horizontal velocities are seen in the descent phase. This trend holds for all species. As an example under binocular conditions, cats on boards separate at 1.766 m/s, move through the ascent phase at 2.116 m/s, the plateau phase at 1.682 m/s, and finally the descent phase at 0.949 m/s.

**Table 23: Horizontal wrist speed by phase under binocular and monocular conditions on discontinuous substrates**

Phase	Species	Substrate	Horizontal Wrist Velocity Binoc	N B	Std Dev Binoc
ascent	cat	slat	1.891	60	0.334
plateau	cat	slat	1.566	60	0.486
descent	cat	slat	1.391	46	0.434
placement	cat	slat	0.786	60	0.253
ascent	rat	slat	1.077	60	0.164
plateau	rat	slat	1.351	60	0.203
descent	rat	slat	1.294	41	0.202
placement	rat	slat	0.779	60	0.140
ascent	lemur	slat	0.981	60	0.221
plateau	lemur	slat	1.307	60	0.309
descent	lemur	slat	1.447	60	0.237
placement	lemur	slat	0.713	60	0.124
ascent	lemur	rung	0.962	60	0.205
plateau	lemur	rung	1.279	60	0.278
descent	lemur	rung	1.428	60	0.209
placement	lemur	rung	0.790	60	0.129

The pattern of horizontal wrist velocity across phases is more variable on discontinuous substrates. The general trend is to have moderate ascent phase, followed by a fast plateau and descent phase, with a slow placement phase. For example lemurs on rungs under binocular conditions move the wrist at 0.962 m/s during ascent, 1.279 m/s during the plateau, 1.428 m/s during descent, and 0.790 m/s during placement. In some cases the plateau phase is the fastest in others the descent phase is the fastest. Cats break this trend somewhat with a very fast ascent of 1.891 m/s, a moderate plateau phase of 1.566 m/s, a descent phase of 1.391 m/s, and a placement phase of 0.786 m/s. In all cases placement phase is by far the slowest.

**Table 24: Vertical wrist speed by phase under binocular and monocular conditions on continuous substrates**

Phase	Species	Substrate	Vertical Wrist Velocity Binoc	N B	Std Dev Binoc
separation	cat	board	-0.068	51	0.088
ascent	cat	board	0.263	52	0.106
plateau	cat	board	0.059	52	0.042
descent	cat	board	-0.319	52	0.101
separation	rat	board	-0.130	49	0.034
ascent	rat	board	0.110	49	0.050
plateau	rat	board	0.017	49	0.014
descent	rat	board	-0.251	49	0.064
separation	lemur	board	-0.076	60	0.048
ascent	lemur	board	0.148	60	0.053
plateau	lemur	board	0.032	60	0.030
descent	lemur	board	-0.276	60	0.062
separation	lemur	pole	-0.169	56	0.068
ascent	lemur	pole	0.208	56	0.055
plateau	lemur	pole	0.042	56	0.037
descent	lemur	pole	-0.328	56	0.076

Changes in vertical wrist velocity across phases are generally consistent for all species on continuous substrates. The separation and plateau phases are periods of low velocity and can show a moderate rise, positive vertical velocity, or fall, negative vertical velocity. The ascent phase shows a moderate positive vertical velocity and the descent phase shows the largest magnitude velocity and is always negative. Under binocular



conditions lemurs on poles drop the wrist at 0.169 m/s during separation, raise the wrist at 0.208 m/s during the ascent phase, raise the wrist slightly during the plateau phase at 0.042 m/s, and the drop the wrist rapidly at 0.328 m/s during the descent phase.

**Table 25: Vertical wrist speed by phase under binocular and monocular conditions on discontinuous substrates**

Phase	Species	Substrate	Vertical Wrist Velocity Binoc	N B	Std Dev Binoc
ascent	cat	slat	0.430	60	0.052
plateau	cat	slat	0.051	60	0.041
descent	cat	slat	-0.458	46	0.227
placement	cat	slat	-0.558	60	0.176
ascent	rat	slat	0.186	60	0.056
plateau	rat	slat	0.009	60	0.012
descent	rat	slat	-0.142	41	0.040
placement	rat	slat	-0.281	60	0.065
ascent	lemur	slat	0.185	60	0.047
plateau	lemur	slat	0.017	60	0.010
descent	lemur	slat	-0.335	60	0.080
placement	lemur	slat	-0.323	60	0.053
ascent	lemur	rung	0.189	60	0.043
plateau	lemur	rung	0.020	60	0.014
descent	lemur	rung	-0.279	60	0.068
placement	lemur	rung	-0.299	60	0.090

The phase profile for vertical wrist velocity on discontinuous substrates also shows a consistent pattern for all species. The magnitude of the descent and placement

phase is always greater than the magnitude of the ascent phase. In general, the fastest drop occurs during the placement phase. The plateau phase always shows a vertical velocity close to zero. As an example under binocular conditions lemurs on rungs raise the wrist at 0.189 m/s during ascent, keep the wrist relatively flat during the plateau at 0.020 m/s, drop the wrist at 0.279 m/s during descent, and at 0.299 m/s during placement.

### **3.2.3 Phase variables**

A number of variables including horizontal and vertical displacement, horizontal and vertical speed, duration of phases, and angle of approach relative to the horizontal, were examined in an attempt to characterize differences in placement of the wrist during binocular vs. monocular performances on continuous and discontinuous substrates. Significant differences were most common and most consistent for variables related to vertical displacement and duration of phases, and there were very few significant differences on continuous substrates. Therefore, only percent duration and percent vertical displacement will be considered in this section. Additionally, most of the significant results were found in the descent and placement phase, and these areas will be focused on for further discussion. Finally, horizontal and vertical wrist velocities will be discussed after removing the effects of speed.

**Table 26: Binocular vs. monocular differences in percent of swing phase covered during the descent phase on discontinuous substrates**

Phases	Species	Substrate	p	Percent Duration Binoc	Percent Duration Monoc	N B	N M	Std Dev B	Std Dev M	Z
descent	cat	slat	0.159	0.161	0.174	46	58	0.085	0.069	-1.407
descent	rat	slat	0.827	0.174	0.178	41	42	0.077	0.080	-0.219
descent	lemur	slat	0.239	0.169	0.167	60	60	0.033	0.055	-1.178
descent	lemur	rung	0.046	0.137	0.128	60	60	0.037	0.047	-1.997

**Lemurs on rungs spend significantly more time in the descent phase under binocular conditions.** When walking on rungs, lemurs spend 13.7% of swing phase in the descent phase under binocular conditions and 0.9% less swing time under monocular conditions ( $p = 0.046$ ). Under binocular conditions lemurs on slats spend 16.9% of swing phase in the descent phase and an insignificant 0.2% less under monocular conditions. Under binocular conditions cats on slats spend 16.1% of swing phase in the descent phase, and rats spend 17.4%. Both of these species spend slightly more time under monocular conditions, but the difference is not significant.

**Table 27: Binocular vs. monocular differences in percent of swing phase covered during the placement phase on discontinuous substrates**

Phases	Species	Substrate	p	Percent Duration Binoc	Percent Duration Monoc	N B	N M	Std Dev B	Std Dev M	Z
placement	cat	slat	0.525	0.251	0.237	60	60	0.085	0.069	-0.635
placement	rat	slat	0.956	0.191	0.193	60	60	0.041	0.037	0.055
placement	lemur	slat	0.006	0.239	0.247	60	60	0.025	0.045	2.770
placement	lemur	rung	0.001	0.222	0.239	60	60	0.032	0.037	3.236

**Lemurs on discontinuous substrates spend significantly less of swing phase in the placement phase under binocular conditions.** When walking on slats lemurs spend 23.9% of swing phase in the placement phase under binocular conditions and 0.8% more time under monocular conditions ( $p = 0.006$ ), and lemurs on rungs spend 22.2% under binocular conditions and 1.7% more time under monocular conditions ( $p = 0.001$ ). Cats spend 25.1% of swing time in the placement phase under binocular conditions and an insignificant amount less under monocular conditions, while rats spend 19.1% under binocular conditions and an insignificant amount more under monocular conditions.

**Table 28: Binocular vs. monocular differences in percent of total vertical wrist displacement covered during the descent phase on discontinuous substrates**

Phases	Species	Substrate	p	Percent Height Binoc	Percent Height Monoc	N B	N M	Std Dev B	Std Dev M	Z
descent	cat	slat	0.997	0.325	0.322	46	58	0.116	0.126	0.003
descent	rat	slat	0.341	0.313	0.280	41	42	0.145	0.120	0.952
descent	lemur	slat	0.003	0.409	0.359	60	60	0.086	0.090	-2.989
descent	lemur	rung	0.003	0.355	0.304	60	60	0.094	0.103	-2.963

**During the descent phase lemurs on discontinuous substrates drop the wrist a larger percentage of the total vertical wrist displacement under binocular conditions.**

When walking on slats, lemurs drop 40.9% of the total vertical wrist displacement under binocular conditions and 5% less under monocular conditions ( $p = 0.003$ ), and drop 35.5% on rungs under binocular conditions with 5.1% less occurring under monocular conditions ( $p = 0.003$ ). Cats on slats drop 32.5% under binocular conditions and an insignificant amount less under monocular, and rats drop 31.3% under binocular conditions with an insignificant amount less under monocular.

**Table 29: Binocular vs. monocular differences in percent of total vertical wrist displacement covered during the placement phase on discontinuous substrates**

Phases	Species	Substrate	p	Percent Height Binoc	Percent Height Monoc	N B	N M	Std Dev B	Std Dev M	Z
placement	cat	slat	0.205	0.696	0.640	60	60	0.198	0.142	-1.268
placement	rat	slat	0.620	0.745	0.767	60	60	0.206	0.181	0.496
placement	lemur	slat	0.004	0.567	0.617	60	60	0.085	0.092	2.874
placement	lemur	rung	0.003	0.617	0.670	60	60	0.097	0.101	2.958

**During the placement phase lemurs drop their wrists a significantly smaller percentage of the total vertical wrist displacement under binocular conditions.** When walking on slats lemurs drop 56.7% of the total vertical wrist displacement under binocular conditions and 61.7% under monocular conditions ( $p = 0.004$ ), and on rungs the wrist drops 61.7% under binocular conditions and 67.0% under monocular conditions ( $p = 0.003$ ). On slats cats drop their wrists 69.6% under binocular conditions and an insignificant amount less under monocular conditions, while rats drop their

wrists 74.5% under binocular conditions and an insignificant amount more under monocular conditions.

### ***3.3 Removing the effects of speed***

Preliminary analyses showed that almost every variable was correlated with speed for at least one condition, and most were highly correlated in many conditions. Some of these correlations are straightforward relationships such as the reduction of stride duration as speed increases. In other cases such as speed slowing down as animals spend more time in the placement phase are not quite as obvious. To be consistent all variables that had a correlation with speed were analyzed using a multiple regression to remove variation due to the effects of speed. Significance is reported under the 'p' column, while the difference between binocular and monocular variables after removing variation due to speed is reported under the 'B – M Estimate' column.

### 3.3.1 Removing speed from whole body and forelimb variables

**Table 30: Binocular vs. monocular differences in contact time of the left forelimb after removing variation due to speed**

species	Substrate	p	B - M Estimate (s)	Std Error	t Ratio	N B	N M
cat	slat	0.526	-0.003	0.004	-0.636	60	60
rat	slat	0.439	-0.001	0.001	-0.776	60	60
lemur	slat	0.001	-0.012	0.003	-3.553	60	60
lemur	rung	0.001	-0.020	0.006	-3.659	60	60

**After removing variation due to speed, lemurs on discontinuous substrates spend significantly more time with their left forelimb in contact with the substrate under monocular conditions.** Lemurs on slats spend 0.012 more seconds in contact with the substrate under monocular conditions ( $p = 0.001$ ), and lemurs on rungs spend 0.020 more seconds ( $p = 0.001$ ). Cats and rats spend an insignificant 0.003 and 0.001 seconds more in contact with the substrate under monocular conditions.



**Table 31: Binocular vs. monocular differences in minimum shoulder height on continuous substrates after removing variation due to speed**

species	Substrate	p	B - M Estimate (m)	Std Error	t Ratio	N B	N M
cat	board	0.735	0.001	0.002	0.339	52	53
rat	board	0.001	0.002	0.000	5.744	60	59
lemur	board	0.066	0.001	0.001	1.854	60	60
lemur	pole	0.600	0.001	0.001	0.526	56	55

**Rats on continuous substrates exhibit a significant decrease in minimum shoulder height under monocular conditions after removing variation due to speed.**

Cats and lemurs maintain a non significant drop in minimum shoulder height of 1 mm.

Rats still drop minimum shoulder height by 2 mm even after removing variation due to speed ( $p = 0.001$ ).

**Table 32: Binocular vs. monocular differences in minimum shoulder height on discontinuous substrates after removing variation due to speed**

species	Substrate	p	B - M Estimate (m)	Std Error	t Ratio	N B	N M
cat	slat	0.286	0.001	0.001	1.072	60	60
rat	slat	0.001	0.002	0.000	3.680	60	60
lemur	slat	0.001	0.002	0.001	3.507	60	60
lemur	rung	0.197	0.001	0.001	1.297	60	60

After removing variation due to speed rats and lemurs on slats show a significant decrease in minimum shoulder height under monocular conditions. Rats and lemurs both drop minimum shoulder height by 2 mm under monocular conditions ( $p = 0.001$  for both species). Cats on slats and lemurs on rungs show an insignificant drop of 1 mm under monocular conditions.

**Table 33: Binocular vs. monocular differences in excursion, minimum elbow angle, protraction, and retraction in lemurs on slats after removing variation due to speed**

Variable	species	Substrate	p	B - M Estimate (°)	Std Error	t Ratio	N B	N M
excursion	lemur	slat	0.001	-1.224	0.363	-3.372	60	60
protraction	lemur	slat	0.028	-0.724	0.326	-2.222	60	60
retraction	lemur	slat	0.070	0.500	0.273	1.831	60	60

Lemurs on slats show a strong trend towards a more crouched posture as demonstrated by several angular variables of the forelimb. Protraction increases

significantly by  $0.724^\circ$  under monocular conditions ( $p = 0.028$ ), meaning animals are more extended at touch down. Retraction decreases under monocular conditions by  $0.5^\circ$  ( $p = 0.070$ ), meaning subjects are more flexed at liftoff. Excursion increases by  $1.224^\circ$  under monocular conditions ( $p = 0.001$ ), meaning animals are in contact with the substrate for a larger angular extent during stance phase. Cats on slats and lemurs on rungs exhibit a similar trend in binocular – monocular differences for these variables with a few significant results.

### 3.3.2 Removing speed from kinematics of the wrist

**Table 34: Binocular vs. monocular differences in maximum wrist height after removing variation due to speed**

Species	Substrate	p	B – M Estimate (m)	N B	N M	Std Error	t Ratio
cat	slat	0.410	-0.001	60	60	0.001	-0.826
rat	slat	0.516	0.001	60	60	0.000	0.652
lemur	slat	0.651	0.001	60	60	0.001	0.453
lemur	rung	0.001	-0.003	60	60	0.001	-3.297

**After removing variation due to speed lemurs on rungs move the wrist higher under monocular conditions.** When walking on rungs lemurs have a maximum wrist height 3 mm higher under monocular conditions ( $p = 0.001$ ), and cats on slats move the wrist an insignificant 1 mm higher. Lemurs and rats on slats both move the wrist a non significant 1 mm lower under monocular conditions.

**Table 35: Binocular vs. monocular differences in vertical wrist velocity during the placement phase after removing variation due to speed**

Phases	Species	Substrate	p	B - M Estimate (m/s)	N B	N M	Std Error	t Ratio
placement	cat	slat	0.189	0.017	60	60	0.013	1.320
placement	rat	slat	0.268	0.006	60	60	0.005	1.113
placement	lemur	slat	0.002	0.015	60	60	0.005	3.169
placement	lemur	rung	0.001	0.023	60	60	0.006	4.154

**After removing variation due to speed, lemurs on discontinuous substrates exhibit an increase in the vertical velocity of the wrist under monocular conditions during the placement phase.** Since values for descending velocities are negative, the 1.5 cm/s difference for lemurs on slats represents a larger magnitude descent under monocular conditions ( $p = 0.002$ ). Similarly, lemurs on rungs have a wrist velocity that is 2.3 cm/s more negative under monocular conditions ( $p = 0.001$ ). Cats and rats exhibit a non significant difference of 1.7 cm/s and 0.6 cm/s respectively.

**Table 36: Binocular vs. monocular differences in proportion of total vertical wrist displacement during the descent phase after removing variation due to speed**

Phases	Species	Substrate	p	B - M Estimate	N B	N M	Std Error	t Ratio
descent	cat	slat	0.433	0.010	46	58	0.013	0.788
descent	rat	slat	0.265	0.016	41	42	0.014	1.122
descent	lemur	slat	0.002	0.026	60	60	0.008	3.094
descent	lemur	rung	0.022	0.022	60	60	0.009	2.322

**After removing variation due to speed, lemurs on discontinuous substrates move a smaller proportion of the total vertical wrist displacement under monocular conditions during the descent phase.** Lemurs on rungs spend 2.2% less of the vertical displacement in descent under monocular conditions ( $p = 0.022$ ), and lemurs on slats spend 2.6% less ( $p = 0.002$ ). Cats spend an insignificant 1% less and rats spend 1.6% less under monocular conditions.

**Table 37: Binocular vs. monocular differences in proportion of total vertical wrist displacement during the placement phase after removing variation due to speed**

Phases	Species	Substrate	p	B - M Estimate	N B	N M	Std Error	t Ratio
placement	cat	slat	0.121	0.026	60	60	0.017	1.561
placement	rat	slat	0.505	-0.012	60	60	0.017	-0.668
placement	lemur	slat	0.005	-0.024	60	60	0.008	-2.880
placement	lemur	rung	0.041	-0.019	60	60	0.009	-2.063

After removing variation due to speed, lemurs on discontinuous substrates move a larger proportion of the total vertical wrist displacement under monocular conditions during the placement phase. When walking on slats lemurs move the wrist through 2.4% more of the total vertical displacement under monocular conditions ( $p = 0.005$ ), and 1.9% more when walking on rungs ( $p = 0.041$ ). Cats move the wrist through 2.6% less under monocular conditions, while rats displace 1.2% more.

**Table 38: Binocular vs. monocular differences in horizontal wrist velocity during the descent phase after removing variation due to speed**

Phases	Species	Substrate	p	B - M Estimate (m)	N B	N M	Std Error	t Ratio
descent	cat	slat	0.040	-0.031	46	58	0.015	-2.077
descent	rat	slat	0.167	0.018	41	42	0.013	1.395
descent	lemur	slat	0.744	-0.003	60	60	0.011	-0.327
descent	lemur	rung	0.455	-0.009	60	60	0.012	-0.749

**After removing variation due to speed cats on slats exhibit higher horizontal wrist velocities under monocular conditions during the descent phase.** Cats move the wrist significantly faster, 3.1 cm/s, under monocular conditions ( $p = 0.040$ ), while lemurs on discontinuous substrates show a non significant increase under monocular conditions. Rats on the other hand show a non significant decrease of 1.8 cm/s under monocular conditions.

**Table 39: Binocular vs. monocular differences in horizontal wrist velocity during the placement phase after removing variation due to speed**

Phases	Species	Substrate	p	B - M Estimate (m)	N B	N M	Std Error	t Ratio
placement	cat	slat	0.011	0.041	60	60	0.016	2.596
placement	rat	slat	0.253	-0.012	60	60	0.011	-1.148
placement	lemur	slat	0.537	0.006	60	60	0.009	0.620
placement	lemur	rung	0.824	-0.002	60	60	0.010	-0.224

**After removing variation due to speed cats on slats exhibit lower horizontal wrist velocities under monocular conditions during the placement phase.** Cats on slats move the wrist 4.1 cm/s slower under monocular conditions during the placement phase ( $p = 0.011$ ), and lemurs on slats move the wrist an insignificant 0.6 cm/s slower. Lemurs on rungs move the wrist a non significant 0.2 cm/s faster under monocular conditions, while rats move the wrist 1.2 cm/s faster.



## 4. Discussion

The primary focus of this dissertation is to discover an underlying functional explanation as to why primates have eyes that point in the same direction. Does this extreme morphological condition require a unique functional explanation? The bulk of the anatomical and physiological data points to an increase in the region of space over which binocular cues are available as the most likely advantage to extreme convergence. These binocular cues increase the accuracy with which animals can estimate distance to surrounding objects.

The praxic hypothesis offers a simple explanation as to why some animals like rats have a small binocular field, and other animals like cats and lemurs have extensive binocular fields. The praxic hypothesis states that the size of an animal's binocular field is correlated with the region over which it must make precise visually guided movements without reorienting (Hughes 1977). Praxis has two assumptions which can be tested experimentally: 1) The visual system can extract cues from the binocular visual field that are useful for guiding precise movements and are not available in the monocular visual field, and 2) Increasing the binocular visual field is advantageous to animals that must make visually guided movements over a wide area.

For this dissertation, I tested Assumption 1 by training cats, rats, and lemurs to walk across simple continuous and complex discontinuous substrates. I used an eye

patch to occlude vision on the right side, thereby removing all binocular cues. I predicted that for all three species the loss of distance cues would disrupt locomotor performances on the discontinuous substrates. Monocular cues were predicted to provide subjects with enough distance information to navigate boards and poles without altering performance.

If the assumption holds, then the praxic hypothesis offers a potential functional explanation as to why primates have forward facing eyes. On the whole a review of the data presented in this dissertation upholds Assumption 1 of the praxic hypothesis. I will first discuss potential ramifications of binocular – monocular differences in the kinematic variables presented here, and then consider the meaning for theories of primate origins.

#### ***4.1 Whole body kinematics***

The most basic finding is that cats and lemurs slow down when walking on discontinuous substrates under monocular conditions, but move at the same speed when walking on continuous substrates. Monocular information seems to provide enough information to avoid a change in behavior on poles and boards. Loss of binocular vision does not cause rats on slats to slow down. On the other hand, locomotion on slats and rungs, where a precise estimate of distance and shape is required with each step, causes cats and lemurs to slow down. Reducing speed directly

reduces an animal's momentum and kinetic energy, which in turn would make it easier to reduce trauma and recover from any unintended collisions. Additionally, a lower speed makes it easier to decelerate when stopping or changing direction.

A reduction in speed is also associated with some combination of a reduction in stride length and an increase in stride duration. There were no differences seen between monocular and binocular stride lengths. On continuous substrates there were no differences in speed, while on discontinuous substrates stride length was restricted to a narrow range due to the design of the slats and rungs. In contrast, stride duration increased under monocular conditions for all species demonstrating changes in speed – cats and lemurs on slats, and lemurs on rungs. Increasing the time required to complete a movement gives subjects additional opportunities to survey the environment and make decisions based on this input. Such a benefit might be useful when dealing with a cue – deprived visual scene. Moreover, increasing stride duration is equivalent to decreasing stride frequency which is associated with a reduction in oscillation of flexible substrates (Demes et al. 1990).

All three species show significant differences in variables related to crouching such as minimum shoulder height, protraction, retraction, and excursion. Crouching is a means to increase stability by lowering the center of mass (Cartmill 1985). Increasing stability is particularly important for primates because the use of grasping hands on

small substrates is an inherently unstable form of locomotion. Primates require relatively long mobile limbs for locomotion in a complex discontinuous environment. Crouching leads to an increase in limb loads which the gracile and mobile limbs of primates are not designed to withstand. Primates use a specific strategy, compliance, to lower center of mass which includes greater protraction at touchdown, retraction at lift off, elbow yield, and overall angular excursion which all serve to increase stride length, increase contact time, and decrease stride frequency (Schmitt 1999). These changes tend to reduce load on primate limbs and reduce oscillation in flexible substrates. While subjects in my study did not exhibit greater elbow yield and could not increase stride length on discontinuous substrates, changes in kinematic variables under monocular conditions would serve to increase stability while decreasing the negative impacts associated with this change in posture.

Rats on boards and all three species on discontinuous substrates lower minimum shoulder height under monocular conditions. Lowering minimum shoulder height under monocular conditions might provide several benefits to subjects deprived of important visual information. First, lowering height above the substrate decreases a subject's center of mass (Cartmill 1985). Crouching might also make it easier to accelerate, decelerate, and change direction (Biewener 1983, 1989). Finally, while not

related to theories of binocular vision, subjects could crouch to lower their profile as part of a stereotyped defense mechanism.

The fact that rats crouch on boards and slats is somewhat puzzling. While my initial predictions were that rats would show some changes in behavior associated with a loss of binocular cues, crouching is the only demonstrable change. It is even more unusual that rats crouch more even when moving across a flat surface. One possibility is that rats might lower their bodies to bring their whiskers more directly in contact with the substrate. Many authors have demonstrated the ability of rats to make fine discriminations using vibrissae (Brecht et al. 2006, Horev et al. 2007, Ahissar and Knutsen 2008). I also observed that during locomotion on slats rats frequently made an unusual drop in head height just low enough to brush the vibrissae against the upcoming slat. When walking on flat surfaces, rats may still attempt to increase tactile cues via the vibrissae as part of a generalized behavior to make up for the loss of visual information.

Cats on boards show a significant increase in protraction under monocular conditions, and cats and lemurs show a non significant trend towards increasing protraction under monocular conditions. An increased protraction angle means that the animals have a more extend forelimb posture at touch down. The protraction angle for cats on boards is one of the few significant results for any animal on a continuous

substrate. Given the isolated nature of the result it is difficult to interpret. This was also one of the weaker results in this study with a difference of  $0.86^\circ$  ( $p = 0.046$ ).

Increased protraction serves to align the scapula and humerus increasing effective stride length (Alexander et al. 1979) and may increase the angle of attack as the forelimb approaches the substrate thereby lowering vertical forces (McMahon et al. 1987). Additionally increased protraction helps to increase crouching at touch down which lowers center of mass and potentially helps lower oscillations in the center of mass generating an increase in stability (Schmitt 1999, Larson et al 2001).

While there are no differences between retraction angles on continuous substrates, cats and lemurs show a trend towards smaller retraction angles under monocular conditions on slats and rungs. Differences were under  $2^\circ$  and only significant for cats on slats. Lower retraction angles mean that subjects are more flexed at the shoulder joint at lift off. Increased flexion at lift off helps to lower the center of mass and oscillations in the center of mass.

Excursion angles are similar under binocular and monocular conditions on continuous substrates. However, on discontinuous substrates excursion angles are significantly larger under monocular conditions. Differences were  $2-3^\circ$  and highly significant in all three conditions. A larger excursion angle means that monocular animals spent a larger portion of the angular extent of the stride in contact with the

ground. Increases in excursion are most likely related to the need to increase contact time – the benefits of which are described below.

## ***4.2 Placement of the forelimb***

While none of the species shows a difference in swing time between monocular and binocular conditions on continuous substrates, cats and lemurs required more time to swing the left forelimb under monocular conditions when walking on discontinuous substrates. Given that stride duration is longer under monocular conditions it stands to reason that swing time is also longer. Having more time to swing the forelimbs also means that the subject has additional time to gather information and make decisions about placing the manus.

Maximum wrist height tends to be higher under monocular conditions, but only for lemurs walking on rungs with other species showing no significant differences. The increase in maximum wrist height means that the wrist has more clearance as the forelimb passes over the middle rung. The high stepping seen here might allow a cushion to help avoid collision with the substrate under uncertainty about distance to the rung produced by the cue deprived monocular condition.

While none of the species show a significant difference in horizontal wrist velocity on continuous substrates, cats and lemurs move their wrists more slowly on discontinuous substrates under monocular conditions. As with considerations of the

entire body, a lower velocity of the wrist engenders a decrease in momentum and kinetic energy which lower the severity of a collision with the substrate and might help prevent slipping.

#### **4.2.1 Phase variables**

To better understand placement of the forelimb, swing phase was divided into four distinct phases and a number of kinematic variables were calculated for each phase. Significant results were found for cats and lemurs walking on discontinuous substrates. There were two variables, percent of vertical wrist displacement and percent of swing phase, that were consistently significant. These variables were significant in the descent and placement phase. Percentages were used because swing time is generally longer under monocular reaches and wrist height is higher under monocular reaches yielding significantly more time and vertical displacement in many phases. Percentages were used as a more conservative measure of the importance of phases. In all cases when a percent is reported as significant the raw data was also significant.

Lemurs on discontinuous substrates spend a significantly larger percentage of swing phase in the descent phase under monocular conditions, and less time in the descent phase though only significantly less on rungs. The significant increase in the placement phase is generated by taking smaller and statistically insignificant amounts of

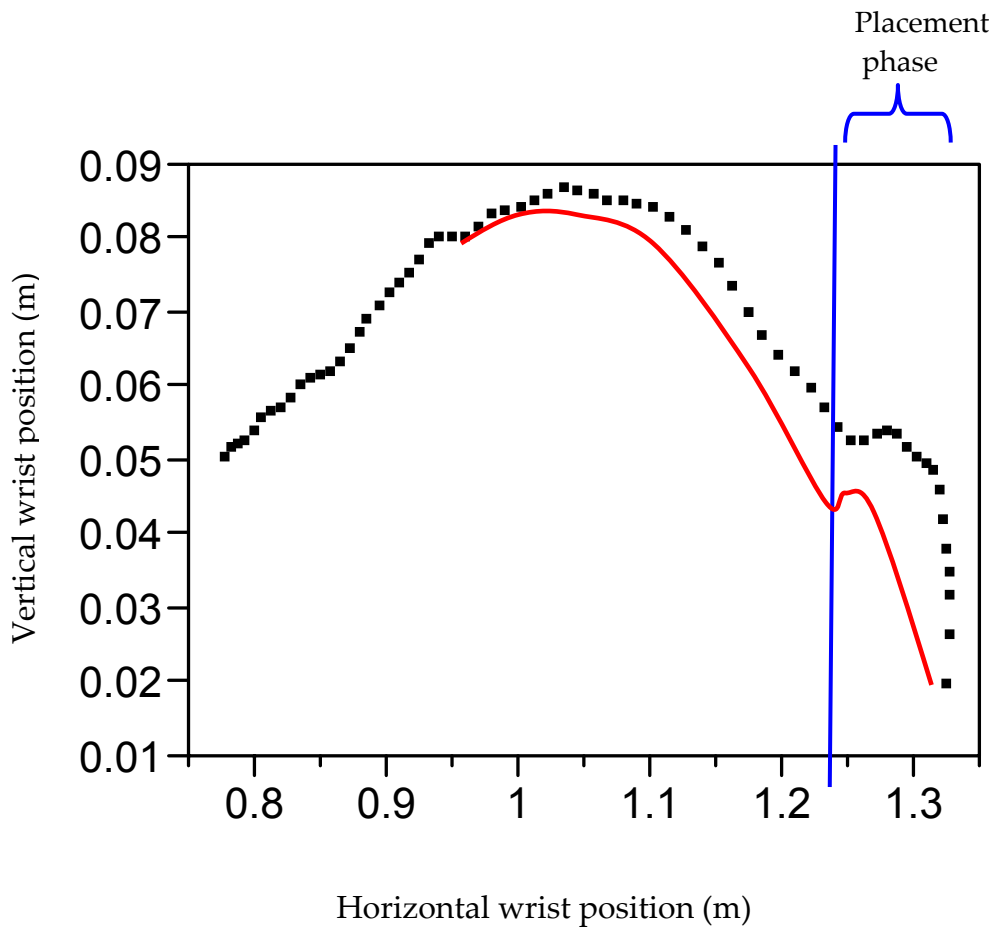


time from the other three phases. The placement phase is a time of high negative vertical velocity and low horizontal velocity.

A similar phenomenon has been reported in studies of human subjects reaching for blocks of wood on flat surfaces. A period of low velocity is accompanied by spikes in the velocity profile. These velocity spikes are interpreted as online corrections to initial mistakes in distance estimation due to a lack of binocular cues (Loftus et al. 2004). The data presented here also show spikes in vertical velocity, which appear as a flat section of the trajectory curve at the beginning of the placement phase. These flat regions, correction phases, were highly variable and did not occur with more frequency or in greater magnitude in monocular vs. binocular conditions. They do tend to support the notion that the placement phase is a time when subjects make last minute adjustments to correctly place the forelimb. Animals under monocular conditions might alter reaches to spend significantly more time in this phase due to a need to make online corrections.

Under monocular conditions lemurs on discontinuous substrates also show a significant decrease in the percent of vertical wrist displacement that occurs during the descent phase. Conversely the percent of displacement is much larger during the placement phase under monocular conditions. The effects on the shape of the curve are

presented in Figure 19. Essentially a larger vertical distance is covered during a time of extremely low horizontal velocity.



**Figure 29: Trajectory of the wrist for a lemur walking on rungs. The dashed line is an actual monocular walk, and the red line is an idealized schematic based on experimental data of what the same walk would look like under binocular conditions.**

### **4.3 Removing speed**

Given that speed was highly correlated with most of the kinematic variables a multiple regression was used to remove variation due to speed. After removing this variation significance was still observed in contact time, minimum shoulder height, protraction, retraction, excursion, and maximum wrist height. Of the variables related to placement of the wrist, percent vertical displacement, horizontal velocity of the wrist, and vertical velocity of the wrist, were significant in several conditions.

#### **4.3.1 Removing speed from whole body kinematics**

After removing variation due to speed, lemurs on discontinuous substrates have longer contact times of the left forelimb under monocular conditions. Longer contact times were also present before removing variation due to speed. Given stride duration was greater under monocular conditions this is difficult to interpret. A significant result after the regression demonstrates that monocular lemurs are placing additional value on contact time regardless of speed. Increased contact times serve to lower peak forces by spreading them out over a longer period of time, thereby reducing oscillation of the substrate and lowering loads on forelimbs (Schmitt 1999, Larson et al. 2001). Increased contact times also increase stability by potentially augmenting the time an animal

spends over its support polygon (Cartmil 2001), and increasing the percentage of time spent in a multi limb support phase (McMahon et al. 1987).

Rats exhibit significant decreases in minimum shoulder height under monocular conditions even after removing variation due to speed. The significance is maintained on both continuous and discontinuous substrates. The strength of the result is somewhat surprising, and may as noted above be related to the need to bring the vibrissae in contact with the substrate. Lemurs on slats were the only other species to demonstrate a decrease in shoulder height after removing variation due to speed. Increased crouching by lemurs is most likely related to the lowering of the center of mass.

Lemurs on slats also show a trend towards crouching in several measures of joint angles even after removing variation due to speed. Under monocular conditions lemurs tend to be more extended at touch down, protraction, more flexed at lift off, retraction, and show a larger angular extent of the shoulder joint during the contact phase, excursion.

#### **4.3.2 Removing speed from swing phase kinematics**

When walking on rungs, lemurs exhibit a larger maximum wrist height under monocular conditions even after removing variation due to speed. The increased wrist height provides a margin of error protecting individuals from a collision between the

wrist and substrate. Lemurs on rungs are the only condition exhibiting this trend with or without variation due to speed.

During the placement phase, lemurs on discontinuous substrates exhibit an increased vertical wrist velocity under monocular conditions after removing variation due to speed. This result is surprising given that body speed and wrist speed are generally higher under binocular and not monocular conditions. The seeming paradox arises from the fact that the wrist enters the descent phase much higher under binocular conditions. However, the time allotted to this phase is increased marginally. The downside to this increase in vertical velocity is that the force and momentum transferred to the substrate both increase yielding a potential increase in oscillations of a flexible substrate. It is surprising that subjects do not simply allow more time to place the wrist. There might be some advantage to moving the wrist through such a large portion of the vertical displacement during a phase of low horizontal velocity. Alternatively, this could be a consequence of either trying to keep the wrist away from the center rung as long as possible to avoid contact. It may also be safer to drop the wrist in a more vertical trajectory.

After removing variation due to speed, monocular lemurs on discontinuous substrates spend significantly less percent vertical displacement in the descent phase and significantly more percent vertical displacement in the placement phase. Lemurs

choose to drop the wrist more during a phase with low horizontal velocity and high vertical velocity, placement, than in a phase with high horizontal and vertical velocity, descent.

Some of the major differences in the shapes of the monocular and binocular curves are demonstrated in Figure 19. On rungs the binocular movement begins to drop below the monocular rung in the plateau phase. On slats this drop occurs somewhere in the descent phase. By the beginning of the placement phase the wrist is significantly and proportionally lower. There are however no differences in the horizontal position at which placement begins. Vertical velocities in this portion of the curve are much higher under monocular conditions, while horizontal velocities are similar.

Cats appear to adopt a different strategy in an attempt to cope with placing the wrist under cue deprived conditions. When walking on slats, monocular cats exhibit an increase in horizontal velocity of the wrist during the descent phase and a decrease in horizontal velocity of the wrist during placement phase after removing variation due to speed. The cats might be decreasing velocity during descent so that the wrist is moving more slowly when it approaches the substrate. A decrease in horizontal velocity might help prevent cats from slipping on the slats.

**Table 40: Marked variables demonstrate significance between monocular and binocular conditions. The direction of change under monocular conditions is indicated in the left hand column.**

	Cats on boards	Rats on boards	Lemurs on boards	Lemurs on poles	Cats on slats	Rats on slats	Lemurs on slats	Lemurs on Rungs
Decrease speed					√		√	√
Increase stride duration					√		√	√
Decrease minimum shoulder height		√			√	√	√	√
Increase protraction	√							
Decrease retraction					√			
Increase excursion					√		√	√
Increase swing time					√		√	√
Increase maximum wrist height								√
Decrease wrist speed					√		√	√
Decrease % duration in descent phase							√	√
Increase %duration in placement phase							√	√
Decrease %vertical displacement in descent phase							√	√
Increase %vertical displacement in placement phase							√	√



**Table 41: Marked variables demonstrate significance between monocular and binocular conditions after removing variation due to speed. The direction of change under monocular conditions is indicated in the left hand column.**

	Cats on boards	Rats on boards	Lemurs on boards	Lemurs on poles	Cats on slats	Rats on slats	Lemurs on slats	Lemurs on Rungs
Increase contact time							√	√
Increase duty factor							√	√
Decrease minimum shoulder height		√				√	√	
Increase excursion							√	
Increase protraction							√	
Decrease minimum elbow angle							√	
Increase maximum wrist height								√
Increase vertical wrist velocity in placement phase							√	√
Decrease %vertical displacement in descent phase							√	√
Increase %vertical displacement in placement phase							√	√
Increase horizontal wrist velocity in descent phase					√			
Decrease horizontal wrist velocity in placement phase					√			

#### **4.4 Testing aims**

One of my primary goals was to test the validity of four aims stated in several specific hypotheses. Aim 1 was designed to test the effect of binocular cues on performing locomotion in a simple environment. Aim 2 was designed to test the effect of binocular cues on performing precision reaching in a complex environment. Aim 3 was designed to test the effect of binocular cues on locomotion requiring grasping on a simple substrate. Finally, Aim 4 was designed to test the effect of binocular cues on performing precision grasping on complex substrates.

The hypothesis for Aim 1 is that the loss of binocular information will not reduce performance in simple locomotion tasks. The substrate for this task was a flat board meant to simulate locomotion on even ground or a very large branch. It was assumed that since direction, distance, shape, and size of the substrate were relatively fixed the precise distance and shape information provided by binocular cues would not be needed. While it is certainly possible some binocular information is used for guiding locomotion on flat surfaces, Aim 1 was used primarily as a control. Since binocular cues are probably not particularly useful for this behavior, monocular – binocular differences might indicate a problem with experimental design.

As seen in Table 40, cats on boards exhibit a slight increase in protraction under monocular conditions, but did not show changes in any other variables related to

crouching. Given the isolated nature of this finding and its marginal significance and magnitude it is difficult to interpret this finding. On the other hand rats on boards demonstrated a strong tendency to crouch more, even after removing variation due to speed, Table 41. This finding was unexpected and might be part of a generalized strategy to cope with a loss of binocular information by relying on tactile cues from vibrissae to guide locomotion. While there were some significant differences between monocular and binocular conditions on boards, the findings are not strong enough to reject Hypothesis 1 outright. Further testing is needed to determine why rats crouch under monocular conditions.

The hypothesis for Aim 2 is that the loss of binocular information will significantly reduce performance in precision reaching tasks. The substrates for this aim are a series of slats which were intended to simulate situations when terrestrial animals walk on extremely uneven ground or when arboreal animals walk between larger branches. As seen in Tables 40 and 41, under monocular conditions lemurs tended to walk more slowly, increase stride duration, increase crouching, move the wrist more slowly, keep the wrist at a greater height longer, and spend more time in the placement phase. Cats tended to mirror the changes seen in lemurs though did not alter the kinematics of placement phase, while rats tended to only lower minimum shoulder height.

Decreasing velocity would be detrimental in a number of situations. For example when a lemur is running from a predator or attempting to avoid conspecifics. While crouching lowers the center of mass, increasing stability, it also increases the metabolic cost of locomotion (McMahon 1987). Finally, by keeping the wrist at a greater height without taking too much additional time to complete the placement phase, lemurs are forced to drop the wrist more rapidly under monocular conditions. This has the potential to augment destabilization of the substrate or produce damage to joint tissue over an extended period of time. The loss of binocular cues reduces performance on slats under monocular conditions. Hypothesis 2 cannot be rejected for any of the species.

The hypothesis for Aim 3 is that the loss of binocular information will not reduce performance in simple grasping tasks. The substrate for Aim 3 is a pole which was intended to simulate locomotion on smaller branches. While grasping is important on this substrate it is assumed that monocular cues provide enough information to complete this task without reducing performance. As seen in Tables 40 and 41, there were no significant differences between monocular and binocular conditions when lemurs walked on poles. The loss of binocular information does not appear to disrupt performance on poles. Hypothesis 3 cannot be rejected for *Lemur catta*.

The hypothesis for Aim 4 is that the loss of binocular information will significantly reduce performance in precision grasping tasks. The substrate in Aim 4 is a series of rungs meant to simulate locomotion on a discontinuous set of small branches. Distance, shape, and orientation information are all important for each step, and binocular cues might therefore be highly valuable under these circumstances. As seen in tables 40 and 41, under monocular conditions lemurs walk more slowly, increase stride duration, increase crouching, move the wrist more slowly, keep the wrist at a greater height longer, and spend more time in the placement phase, and reach a greater maximum wrist height. These significant variables are similar to those seen on slats with the inclusion of the variable for maximum wrist height. Locomotion on rungs also differs in that after removing speed, variables associated with crouching lose their significance on rungs but not on slats. Removing binocular cues appears to disrupt performance on rungs. Hypothesis 4 cannot be rejected for *Lemur catta*.

On the whole, the data collected support the four hypotheses proposed here. The praxic hypothesis cannot be rejected from the evidence presented in this dissertation. The only significant discrepancy from predictions is the highly significant and large magnitude drop in minimum shoulder height associated with monocular rats walking on boards. While this information does not reject the hypothesis, it does

suggest either problems with the experimental design or additional uses for binocular cues which might lead to augmentation of the praxic hypothesis.

#### ***4.5 Implications for theories of primate origins***

My data demonstrate that binocular cues are useful in a task involving locomotion on a straight and narrow path. Most theories of primate origins are concerned with whether large binocular fields are better than small binocular fields. Due to methodological concerns outlined earlier this is a difficult place to start testing. As illustrated in the flow diagram, Figure 4, Hypotheses 1 through 4 could possibly have rejected the praxic hypothesis, but could not in and of themselves confirm it. Additional support would require testing in tasks of varying width, and a means of altering visual field overlap instead of removing it outright.

My results suggest that even a narrow binocular field is useful for guiding locomotion on narrow but complex substrates. While this data was collected on locomotor tasks, these findings could be part of a larger benefit from binocular vision in which cues are used to guide action during tasks requiring precise movements. If early primates had the ability to make visuomotor transformations using binocular cues from a small binocular field, it is easy to imagine a co-evolution of increasing task complexity and increasing binocular field size.

The nature of the increasingly complex task cannot be addressed by the data presented here. It is possible that as forelimbs lengthen, joints loosen, and early primates use reaching and grasping to navigate fine branches, binocular cues would be useful for guiding precise movements. Alternatively, the ability to acquire precise distance information over a larger region of space might allow nocturnal predators to more easily catch mobile prey or to ambush stationary prey over a wider range of space.

My data points to one possibility in particular that might have important implications for why primates needed to evolve binocular vision in the first place. Rats on both boards and slats lowered body height under monocular conditions. Personal observations indicated that on slats rats would lower often lower their head just enough to bring the vibrissae in contact with the next slat.

The importance of vibrissae as a sensory tool for guiding locomotion has been underappreciated. Recent advances demonstrate that vibrissae are an incredibly accurate tool for gathering information about an animal's immediate surroundings (Ahissar and Knutsen 2008). At the most basic level individual whiskers sense force transmitted along the shaft as action potentials in a sensory neuron attached to the whisker follicle (Gibson and Welker 1983). Together the five whisker rows can efficiently encode three dimensional localization of nearby objects in a system using three orthogonal axes. Horizontal discrimination is based on the timing of firing of

different neurons, vertical discrimination is based on the identity of individual neurons (Szwed et al. 2003), and radial discrimination is based on the intensity of firing of neurons (Szwed et al. 2006). The accuracy and reliability of distance measurements is enhanced by comparing information across populations of neurons from independent receptors. This encoding system allows rats to discriminate objects less than 1mm apart in the horizontal direction (Knutson et al. 2006), and less than 3mm apart radially (Krupa et al. 2001). It stands to reason that rats and perhaps many other small mammals use vibrissae as an accurate tool for guiding placement of the limbs during locomotion. The sensory information provided by vibrissae probably accounts for the ease with which rats moved across such complex substrates in my experiments.

Unfortunately, the error associated with distance measurement from vibrissae would probably be much higher in primates. First, animals with long forelimbs would need commensurately lengthened vibrissae. Long vibrissae would likely be more susceptible to large perturbations that might be difficult to track. Additionally, as the point of contact of the whisker and substrate gets further from the receptor, the error associated with distance estimates increases. An equivalent change in angular deviation at the receptor is associated with a larger error of estimation at greater distances. A similar result has been noted in distance estimates associated with vergence and retinal disparity (Tresilian et al. 1999, Howard and Rogers 1995).



Another reason vibrissae might not be as accurate for primates, is that an animal only knows whether or not the vibrissae have been disrupted, but not where along the length of the whisker contact occurs. Therefore in a cluttered environment where the whisker might contact several objects at different lengths along the vibrissae, it is difficult to calculate distance to any single object.

Vibrissae are probably less accurate in determining distance to nearby objects for animals with long limbs in cluttered environments. Vibrissae present another problem for primates in that they only provide information about the immediate environment. Animals moving in a complex discontinuous substrate need information about the distance to and shape of objects over a wider area. While poor vision coupled with good olfactory, aural, and tactile cues might be enough to determine a general heading on a flat surface, a more accurate estimate is needed to plan a path on a complex substrate. Binocular cues would allow subjects to quickly determine reasonable handholds for the next few steps, and choose a path through an arboreal environment. The loss of both the accuracy and utility in tactile information from vibrissae may have been a primary driving factor in the evolution of binocular vision in primates.

It should be noted that any test of functional hypotheses cannot rule out an adaptational hypothesis based on comparative anatomy and ecology. As an example, if it were discovered that removing binocular vision did not disrupt a nocturnal predator's

ability to acquire prey, other functional hypotheses could be developed and tested. For example, alignment of the optic and visual axes might be particularly beneficial in scotopic conditions, and would not be disrupted by the loss of the binocular field (Allman 1977, Cartmill 1992). However, a lack of any suitable functional hypothesis after thorough testing could indicate that the initial adaptational hypothesis was based on spurious correlations and should be reconsidered.

#### **4.6 Future work**

Current comparative analyses suggest that there are several different niches associated with forward-facing eyes. The most consistent methods and systematic sampling of species are available from studies of orbit orientation. However, it is important to increase the sample of both the number of species and individuals per species. Such data would go a long way to confirming current hypotheses. A large sample of closely related animals with a known phylogeny that differ in foraging strategy, activity cycle, and locomotor behavior would further increase our confidence in adaptational hypotheses. Such a detailed analysis would be feasible for phalangerids, viverrids, and procyonids.

Finally, there is still much comparative work that needs to be done on other anatomical variables such as visual-field overlap and optic orientation. Such studies would help to substantiate hypotheses based on orbit orientation. Moreover, these

variables are easier to relate to behavior and physiology. If further anatomical analysis cannot resolve ecological categories based on orbital or optical direction alone, it might be possible to make further distinctions based on some other anatomic variables. For instance, species evolving forward-facing eyes to guide grasping need high-resolution spatial information. However, nocturnal species will receive a strong advantage from binocular summation even with very low acuity. Thus, we might predict that in addition to forward-facing eyes, species with a large praxic space also have high visual and stereo-acuity. The relative size of the orbit and optic foramen are a useful osteological proxy for visual acuity (Kay and Kirk 2000), and might help distinguish grasping species from other animals with forward-facing eyes.

If comparative anatomy is to tell us anything about how a given trait is adapted to a certain environment, then there must be a functional link between the two. If not, then it is equally parsimonious to assume that our proposed relationship is based on some other variable correlated with the trait of interest. To date few studies have examined the effect of cues such as disparity, vergence, summation, and optic-flow fields on behavior under ecologically relevant conditions. Future studies should seek to tease apart which binocular cues are useful for specific behaviors under controlled environmental conditions.

It would also be beneficial to expand the tasks associated with these tests. The data presented here demonstrate that binocular cues are useful for guiding locomotion, but they may be beneficial to animals capturing prey at night. Monocular viewing conditions might decrease a subject's ability to detect cryptic objects, estimate distance in low-light conditions, and catch moving objects.

Additional experimentation is also needed to determine the effects of field size on performance. Such studies would be of more direct support for theories of primate origins. Partially occluded contact lenses or a divider placed between the eyes might be feasible methods for occluding only a portion of the binocular field. Simple experiments such as these could help provide a functional link between forward-facing eyes and theories of primate origins.

Future morphological and functional experiments should take into account the unique manner in which primates are arboreal. Primates are not simply arboreal mammals with grasping hands and feet – both of which are ancient mammalian traits. Research in locomotion has demonstrated a suite of unusual primate characteristics including a compliant gait, diagonal sequence walking, large excursion angles, and a crouched posture (Cartmill 1985, Schmitt 1999, Larson et al. 2001, Cartmill et al. 2002). These locomotor specializations appear to be related to the use of long mobile limbs with clawless grasping extremities. Perhaps the fundamental adaptation for crown

primates is arboreality at large body size relative to substrates size regardless of ecological niche. Small primates are able to use long mobile grasping forelimbs to navigate terminal branches more adeptly than most other animals. Larger primates such as orangutans, chimpanzees, and even juvenile gorillas are even able to use arboreal environments to varying degrees as an additional food resource or escape route.

However, most comparative work on binocular vision focuses on arboreality as the environmental factor that might be driving convergence of the orbits and grasping as the key adaptation for primate arboreality. Rather than arboreality *per se* research should be focused on moving in discontinuous environments at a relatively large body size using long mobile grasping forelimbs. In comparative work this means creating finer grained locomotor categories for tests of correlation with morphological traits. In functional work this means designing tasks that test the unique capabilities of primates.

## **4.7 Conclusions**

The data presented here for cats, rats, and lemurs supports the hypothesis that a loss of binocular cues alters locomotion on discontinuous substrates. The alteration in performance is interpreted as a shift to a more conservative kinematic strategy associated with an increase in uncertainty regarding the precise location of the substrate. One interpretation of this finding is that early primates would have had access to visuomotor transformations allowing them to use binocular cues to guide precise movements. As forelimbs lengthened and became more mobile, the binocular visual field also increased to help place the forelimbs on complex discontinuous substrates. These specializations would have allowed early primates to invade arboreal niches at large body sizes relative to other mammals. Determining the specific niche will require additional work in functional morphology, comparative anatomy, and paleontology. The role of forward facing eyes in primate origins remains one of the most intriguing questions in primate biology.

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## Biography

Terence Reid Townsend Mitchell was born October 4<sup>th</sup>, 1976, and at one point or another called Bozeman, Montana, Nashville, Tennessee, and Emerald Isle, North Carolina, home. He graduated with a B.S. in Biology and minor in Computer Science and Chemistry from the University of North Carolina at Chapel Hill in 1999. In 2001, Terry entered a PhD program at Duke University in the Department of Biological Anthropology and Anatomy. In 2009, he graduated from Duke University after completing a research tract involving the relationship of binocular vision to the guidance of precise movements.

### Honors, Awards, Grants, and Fellowships

2007	Katherine Goodman Stern Dissertation Year Fellowship
2005	NSF BCS Dissertation Improvement Grant, Title: <i>The role of binocular vision in primate evolution</i>
2005	LSB Leakey Foundation Dissertation Improvement Grant, Title: <i>The role of binocular vision in primate evolution</i>
2005	Aleane Webb Endowment Fellowship
2003 – 2005	NSF Graduate Research Fellowship
2003,'04,'06,'08	Duke University Conference Travel Grant
2001, '02, '06	Duke University Graduate Fellowship

## Publications

Siddiqui NY, **Mitchell TRT**, Bentley R, Weidner AC. Uterosacral Ligament Suspension and Neural Injury: An Anatomic Study in Female Cadavers. American Urogynecologic Society Annual Mtg, Sept 2009, Hollywood, FL (Accepted as abstract and in preparation as manuscript for American Journal of Obstetrics and Gynecology).

Siddiqui NY, **Mitchell TRT**, Weidner AC. Anatomic pathways of the TVT-SECUR mid-urethral sling. American Urogynecologic Society Annual Mtg, Sept 2009, Hollywood, FL (Accepted as abstract and in preparation as manuscript for American Journal of Obstetrics and Gynecology).

Kivell TL, Doyle SK, Madden RH, **Mitchell TRT**, Sims, EL. An interactive method for teaching anatomy of the human eye for ophthalmology rotations using suid eyes. *American Association of Anatomists*, New Orleans: April, 2009 (Accepted as abstract and in review as manuscript for Anatomical Sciences Education).

**Mitchell TRT**, Bishop KL (2008). The use of binocular cues in feline locomotion – consequences for primate evolution. *Am J. Phys. Anthropol.* 135 (Suppl. 46). pp. 156 – 157.

Kay RF, Fleagle JG, **Mitchell TRT**, Colbert M, Bown T, Powers DW (2008). The anatomy of *Dolichocebus gaimanensis* a stem platyrrhine monkey from Argentina. *J. Hum. Evol.* 54(3) pp. 323 – 382.

**Mitchell TRT**, Schmitt D, Kay RF (2006). The role of binocular vision in primate locomotion. *Am J. Phys. Anthropol.* 129 (Suppl. 42). pp. 132 – 133.

**Mitchell TRT**, Kay RF, Colbert MW, Rowe TB (2004). The interorbital region of *Dolichocebus gaimanensis* (Platyrrhini, early Miocene, Argentina) based on high resolution X-ray CT imaging – phylogenetic implications. *Am J. Phys. Anthropol.* 123 (Suppl. 38). p. 148

Kay RF, **Mitchell TRT** (2003). Cranial evidence for the timing of the platyrrhine-catarrhine divergence. *Am. J. Phys. Anthropol.* 120 (Suppl. 36). p. 127.

**Mitchell TRT** (1999). Do roadside breeding bird surveys provide accurate estimates of avian populations? Senior Honors Thesis: University of North Carolina, Chapel Hill.