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Functional Correlates of Rodent Visual Cortex Organization:

A Behavioral and Neuroanatomical Study

of Individual Differences in the Gerbil Visual System

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An abstract of

A thesis submitted to the Faculty of the Graduate School of Emory University

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Abstract

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By Magdalena Krysiak

Rodents are ideal subjects for the study of comparative relationships between brain and behavior, particularly in comparison to Primates. They are small, easily obtainable and trainable, and inhabit a wide range of ecological niches. In this project, we characterized the visual behavior of individual Mongolian gerbils (*Meriones unguiculatus*) using two kinds of tests – measuring both depth perception and acuity - and asked whether these functional measures correlate with measurements of the structural complexity of the visual system. Gerbil posterior cortex contained a distinct primary visual cortex (V1) and a heavily myelinated area similar in location to ground squirrel TP, which is involved in visual motion perception. As expected, the relative expanse of V1 was positively correlated with acuity, and the relative expanse of proto-TP was positively correlated with speed of performance on the jumping stand, implying a role in depth perception and strengthening the case for an evolutionarily conserved visuomotor region. Contrary to our expectations, lower light levels did not decrease performance on the acuity task, and significantly decreased latency on the jumping stand (a trend driven by less day-active animals). Better performance in low light suggests that the cone system in this species is not as well defined and/or behaviorally relevant as previously thought. It is suggested that future behavioral studies performed on nocturnal species should consider how light preference could affect performance. Overall, the results support the value of a comparative approach utilizing within-species individual differences to help understand brain-behavior relationships.

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Functional Correlates of Rodent Visual Cortex Organization

Overview

Our understanding of the human visual system stems largely from research done on non-human primates (such as macaque monkeys) and rodents (such as rats, mice, and hamsters). Animals are often utilized to provide manipulable models of the human brain, however animal studies can also inform evolutionary trends in brain organization. Adaptations driving visual system organization must be studied in a comparative framework as there is no fossil record for the brain, and this paper will argue that a systematic analysis of within-species individual differences can hint at mechanisms of functional specializations. This kind of research can utilize rodent models more easily than primates, both of which show great ecological variability – a characteristic which makes them ideal for comparative studies.

Our lab has examined the neuroanatomical organization of visual cortex in two rodent species: the ground squirrel (*Spermophilus beecheyi*) and the hamster (*Mesocricetus auratus*) (Rodman et al., 1992; Hodson al., 1998**;** Krysiak et al., 2007**)**. Ground squirrel cortex shows a pattern of overall organization that differs markedly from that found in other rodents, including the hamster. For example, in cortical flatmounts treated with stains for myelin or the enzyme cytochrome oxidase, ground squirrel primary visual cortex (V1) contains a conspicuously compartmentalized binocular zone (V1b), which integrates information from the two eyes. Extrastriate cortex of the ground squirrel is large and visibly differentiated, and contains a unique extrastriate area termed TP (temporal posterior area), which plays a role in visual motion processing **(**Paolini & Sereno, 1998). In contrast, V1 in hamster flatmounts does not show a clear binocular zone, and extrastriate cortex appears generally uniform, with perhaps a near lateral and far lateral tier (Krysiak et al., 2007) (see Figure 1).

Constructing an understanding of visual cortical function assumes that behavioral differences involving perceptual abilities and visually guided movements correlate functionally to visual cortex organization. Rodents' differing ecologies naturally result in differences in the selective pressures placed on behavior, which in turn exploit incipient tendencies toward specific sensory and neural adaptations. A few examples of differing ecologies include terrain, predators, social structure, and activity pattern. It is likely that the differences we have observed in visual cortex organization between ground squirrels and hamsters are functionally related to between-species differences in habitat and behavior. For example, ground squirrels are known to be diurnal, while hamsters are classically nocturnal creatures. Visual constraints at various light levels require different optics and neural processing for proper visibility. Tree squirrels (found to have a similar brain organization to that of ground squirrels (Hall et al., 1971)) require visual systems that allow them to jump between branches with great adeptness. Another between-species difference is social behavior. Hamsters are very solitary compared to both ground- and tree squirrels, and may not be as attuned to visible social signals. At the same time, some rodent species may be less dependent on vision in general than others, relying more strongly on their other senses.

This project uses the Mongolian gerbil (*Meriones unguiculatus)* in an integrated behavioral and neuroanatomical program. Well established behavioral tasks were used to probe individual differences in visuomotor abilities: an acuity test to quantify visual discrimination and a jumping stand to quantify jumping ability and depth perception.

Both tasks were performed under three luminance levels - akin to low daylight, dim light, and moonlight - used to probe vision thresholds. Following behavioral testing, brain tissue was stained and analyzed for the relative complexity and size of areas within the visual cortex. Brain-behavior interactions were analyzed with the expectation that the complexity and/or expanse of V1 and areas in extrastriate cortex are correlated with specific aspects of visual behavior. Specific predictions are described below.

Impetus and Implications

Studies of brain evolution are especially provocative when implications are formed regarding the organization of the human brain. In comparing the visual cortex of humans to that of nonhuman primates, for example, it is known that the early visual areas V1, V2 and V3, as well as the motion area MT are conserved. Beyond these areas, differences between human and monkey functional organization are increasingly evident (Orban et al., 2004). To establish how these unique areas developed in the human brain, comparative analyses of many primate species with various ecological specializations would be desirable. While some such work has been done (e.g. Barton, 1998), primate comparative work is complicated for numerous reasons, including difficulties obtaining a large number of animals and the overall scarcity and endangered status of species of particular interest.

The rodent taxon includes a wide variety of species with ecological diversity that parallels that of primates, and rodents are much more practical to obtain and work with in the laboratory. Extensive comparative analyses of rodent visual specializations may be more feasible than that of primates, the implications of which may be applicable to mammals as a whole. Rodents are the most diverse mammalian order in terms of number of species, and probably also in terms of the variety of niches they occupy. There are about 2,277 species of rodents (Wilson and Reeder, 2005), with over 40 percent of mammalian species belonging to the order. Rodents have evolved numerous independent neural solutions to the problems posed by a variety of visual environments; for example, in the major rodent subgroups, visual and visuomotor adaptations to diurnal, arboreal, aquatic and burrowing niches have been invented independently (Finlay and Sengelaub, 1981)

Thus far, rats, mice, and hamsters have served as the prototypical rodent species of interest, and have been used as convenient rodent "models" of the human visual system (e.g. Gordon & Stryker, 1996). However, all of these species are nocturnal, relying less heavily on vision than diurnal species. Diurnal rodent models, such as squirrels, have recently been gaining interest (reviewed in Van Hooser & Nelson, 2006). As described above, these animals appear to have a substantially more complex visual cortical organization than their nocturnal relatives. At the same time, squirrels have visual specializations all their own. They can be described as a hyper-visual species, being able to see in detail up close, use binocular vision for jumping through trees, as well as having a wide field of view which allows them to spot predators. Clearly, the use of any animal model should be considered carefully with regard to its ecology. For reasons detailed below, we propose that the gerbil will be a valuable addition to such research.

Comparative Analysis and the Case for Studying Individual Differences

One way of going about a comparative analysis is to examine a wide variety of species. For example, Refinetti (2006) studied seven species of diurnal and nocturnal rodents to investigate the effects of prolonged dark adaptation on circadian photoresponsiveness. Roll et al. (2006) carried out a literature survey of the activity patterns of 700 rodent species to ask whether the diel activity patterns of animals reflect their phylogenies. Such extensive analyses are not always feasible. A small number of target species could be used to answer specific questions if they are chosen carefully.

There are two main ways to isolate a variable of interest in a more limited comparative analysis. One is to compare related species in dissimilar environments as examples of divergent evolution; the other is to compare distant species in similar environments as examples of convergent evolution (Finlay & Sengelaub, 1981). There are several environmental variables that potentially drive specializations in visual cortex organization, such as activity pattern, locomotor requirements, or social behaviors. These can be broken down even further: the environment of terrestrial rodents can vary in terrain, competition for resources, and predatory threat. Climbing animals may vary in their preferred altitude and jumping tendencies. In order to isolate any one environmental factor, ideally the target species would either differ or compare only in terms of that one factor.

Individual differences within the same species can also hint at functional evolutionary trends. The benefit of this kind of analysis is that the animals in question will be similar in many respects. The source of any variability can be identified more easily. When comparing different species, there are many more physical and environmental differences to control for. In this project, we are examining individual differences in gerbil brain and behavior which might have implications for the functional significance of specific patterns of organization in the rodent visual cortex. Because the gerbils had little variability in their visual experience before we obtained them, we assume *a priori* that any differences are most likely innate rather than being the result of differential experience. It is also known that the visual system has a short critical period – within the first few months of life in kittens (Hubel and Weisel, 1970) – after which few changes occur with experience. However, it is possible that different visual structures have varying sensitive periods and are differentially modifiable by experience. Therefore, care must be taken in interpreting these data. Future studies could build upon our findings by taking a developmental focus and determining the specific effects of experience.

The comparative framework fits with the logic of experimental analysis, the difference being that the variables of interest are not manipulated by the experimenter; the manipulation lies in an informed choice of target species and the exploration of individual differences within these species. In truth, scientists could never recreate millions of years of speciation. However, the results of such an analysis potentially have very wide implications about the evolutionary processes governing species differences.

Visual Cortex

Visual cortex, the region of the cortex that gives rise to visual perception, is located in the occipital lobe in the posterior (back) part of the brain, and in visually dependent species comprises a large proportion of total cortical area. The main pathways by which light information travels to visual cortex are the same across all mammals (Jones, 1985; Kaas and Huerta, 1988). In the geniculostriate pathway, information is processed sequentially from the retina through the lateral geniculate nucleus (LGN) of the thalamus to the primary (or striate) visual cortex (V1). The tectopulvinar system controls eye movements in response to visual stimuli. It arises from axons in the optic tracts that bypass the LGN and continue into the midbrain where they synapse in the optic tectum, primarily in a structure called the superior colliculus. The superior colliculus sends some of this information to the pulvinar nucleus of the thalamus, which then relays it to the secondary visual or extrastriate cortex.

The extrastriate cortex surrounds V1, receiving much information from V1 as well as the tectopulvinar system. Extrastriate cortex is subdivided into a number of areas, each defined at the most fundamental level as containing an independent representation of visual space or a portion of visual space (Van Essen & Zeki, 1978). Each extrastriate area is thought to perform a different level of perceptual analysis, and/or processing within one perceptual category, such as color or motion. Relatively little is known at all about the organization of extrastriate cortex in rodent species compared with primates.

Cross-Species Neuroanatomical Comparisons

Functionally equivalent areas can either be homologous (arising from a common ancestor) or can result from convergent evolution. As there is no fossil record of brain organization, extant (currently living) species are examined to find answers to questions of evolutionary progression. For example, Rosa and Krubitzer (1999) carefully reviewed evidence supporting both sides of a controversy surrounding the evolution of extrastriate area V2 in mammals, examining the cortical organization of diverse species – from marsupials, insectivores, and rodents, to carnivores, ungulates, and primates.

In addition to retinotopic organization, one or more of the following 3 criteria have also been used to identify cortical areas: (1) cyto- and chemoarchitecture, such as staining of myelin patterns, (2) connectivity, and (3) function, as revealed by single-cell, lesion, neuroimaging analyses, and behavior (Orban et al., 2004). The current project combines cytoarchitecture with behavior in order to better distinguish cortical visual areas in the gerbil. By performing our analysis using more than one criterion concurrently, a tighter link can be made between individual differences in behavior and neuroanatomy, pointing more strongly to the functional underpinnings of visual behavior.

Gerbil Ecology

The gerbil subfamily includes about 110 species of African, Indian, and Asian rodents, including sand rats and jirds, all of which are adapted to arid habitats. For the most part, gerbillines are diurnal rodents, but some species are nocturnal, crepuscular, or active both day and night (Nowak, 1999). The Mongolian gerbil (*Meriones unguiculatus)* originally appeared, and still lives, on the semi-deserts and steppes of Mongolia. It is a gentle and hardy animal that has become a popular pet. It was first brought to the United States in 1954 by Dr. Victor Schwentker for use in research (Schwentker, 1963).

In the wild, Mongolian gerbils live in groups generally consisting of one parental pair and the last few litters, in which only the dominant female and male produce pups. A group lives in a central burrow with 10-20 exits. The gerbil’s main predators are birds of prey, snakes, weasels and wolves; from which they jump away on their long hind legs. Wild Mongolian gerbils are omnivorous rodents, whose naturally curious nature rewards them with several different sources of foodstuffs in the harsh landscape where they live. Technically gerbils are classed as a hoarding rodent, and around August gerbil communities begin gathering seeds and other foodstuffs to last them through the adverse weather periods that are common to the region (Agren et al, 1989).

One interesting fact about Mongolian gerbils which sets them apart from many well-studied rodent species is that they exhibit inter-species variability in activity pattern. In a controlled laboratory setting in which circadian rhythms were monitored continuously, Refinetti (2006) found that individual gerbils could be separated into two groups based on their activity pattern, some described primarily as diurnal, others as nocturnal. This finding inspired the idea of systematically studying such individual differences in this species. Perhaps specific brain mechanisms are involved in these differences, and correlate with behavior in a non-random way.

According to the somewhat debated taxonomy of the Order Rodentia, it is clear that gerbils are more closely related to hamsters than either are to ground squirrels. Ground squirrels belong to the subgroup Sciuromorpha, which contains the squirrel species, while gerbils and hamsters belong to the subgroup Myormopha, which contains the mouse-like species, including rats. In fact, gerbils used to be classified with hamsters into the family Cricetidae (Finlay and Sengelaub, 1981), a classification that now only applies to hamsters. The Myomorph and Sciuromorph species are two consistently distinct groups within an order that has been divided into 3 or 5 suborders, including the diverged group of South American rodents such as guinea pigs. Gerbils may be especially good rodent models of the primate visual system, because they are closely related to commonly studied Myomorph rodents while differing in their diurnal habits and consequently on their reliance on vision.

Previous Studies of Gerbil Visual Behavior

This project utilizes a behavioral paradigm that has been previously used in the literature on gerbil visual behavior: the jumping stand. This technique capitalizes on the gerbils' natural jumping abilities. Karl Lashley invented the jumping stand in the 1930's to study visual discrimination in rats. It comprises a platform on which a rat or other rodent is placed, and two vertical cards, each containing a visual stimulus, towards which the animal jumps. If the rat chooses the correct card, then a door swings open and the rat lands in a chamber and receives a food reward; if it chooses incorrectly, it bumps against a fixed door and falls into a net below. While the negative consequence provided by the bump into the closed door and subsequent fall may increase the animals' learning curve, gerbil researchers have modified the jumping stand to include platforms underneath the stimulus cards onto which the animals can land. The food reward is typically a favorite treat of gerbils: a sunflower seed. The jumping stand has also been modified further by eliminating the discrimination. Instead, two raised platforms can be used to test distance estimation by varying their relative positions. In the current study, the term "jumping stand" refers to the later variation, which does not include a discrimination. The term "acuity apparatus" is used to describe the more traditional jumping stand used to measure visual acuity.

Our acuity apparatus is based off of that used by Baker and Emmerson (1983) (see Figures 5 and 6). By using a visual discrimination paradigm in which gerbils were trained to jump toward gratings with increasing spatial frequencies, the authors determined the acuity of the gerbil to be about 1.5- 2.0 cycles/degree at 70cd/m2, using 70% and 80% correct levels of performance as criteria for defining acuity. This value is higher than the acuity of the hamster by a factor of about 2.5. Horizontal, vertical, and oblique gratings were presented, with the best resulting performance corresponding to horizontal gratings. In the current study, vertical gratings were used so as to minimize the chance that gerbils might enhance their vision with vertical movements of the head. Acuity was also found to increase with luminance in the previous study, which the authors interpret as suggesting the existence of a functional cone system.

What is called the “jumping stand” in our study has been simply referred to as a “jumping task” by previous researchers. In this task, the animals are trained to jump a gap of varying distances between two raised platforms, with no discrimination task upon landing (see Figures 2 and 3). This paradigm has been used with gerbils to study the factors involved in distance estimation. In order to successfully clear a jump positioned at an unknown distance, depth perception is clearly required. However, there are a few different cues that can be utilized to achieve an estimate of depth (such as retinal image size, binocular disparity, and motion parallax), which may be selectively processed by means of specific brain mechanisms.

Retinal image size corresponds to a representation of the width of the front edge of the landing platform, which projects onto a smaller portion of the retina when it is further away. It has been shown that this cue is readily utilized by gerbils. Ellard et al. (1991) tested gerbils with probe trials in which the landing platforms differed in width from that used in training. It was found that the animals had learned to calibrate the retinal image size of the landing platform with its distance. The presentation of smaller probe platforms resulted in overjumps relative to control performance, and the presentation of larger probe platforms produced relative underjumps

Motion parallax is a cue that results from movements of the head or body. Gerbils have been observed to perform a series of “head bobs” prior to jumping, the amplitude and velocity of which have been found to be related to the gap distance and to each animal’s accuracy (Ellard et al. 1984). Gerbils use this as a cue for distance by combining information about the velocity or amplitude of their head bobs with information about the velocity or displacement of the moving image of the landing platform. In fact, it has been demonstrated that computation of the distance to be jumped is dependent on both image size and retinal motion (Goodale et al., 1990). When image size is not a reliable cue (on trials when probe platforms of differing widths were introduced), the animals produce more head bobs.

The Current Experiment

This experiment consists of two parts: 1) behavioral tasks designed to quantify visual ability, and 2) neuroanatomical analysis of visual cortex organization. This combination of data will serve to inform us about possible functional correlates of visual cortex organization in rodents, and more generally in mammals.

Two behavioral tasks were employed to characterize the animals’ visual abilities: a jumping stand and an acuity apparatus. These tests were conducted at three luminance levels: akin to low daylight, dim light, and moonlight. The jumping stand was designed to quantify depth perception and jumping ability as it produced measures of accuracy and latency to jump across a gap of varying distances. The acuity apparatus was used as a precise measure of the animals’ visual discrimination ability. These two tasks potentially tap into two types of visual processing: pattern perception (acuity task) vs. visuomotor perception (jumping stand), known to be subserved by different brain circuits, at least in primates (Ungerleider & Mishkin, 1982), and potentially different brain areas in rodents. The variability in luminance serves to define thresholds for visual perception as well as each animal’s luminance preference.

After the behavioral tests were completed, the animals were euthanized and their brains were fixed, sliced, and processed with a Myelin stain, which is optimal for revealing cortical subdivisions. The relative size of each area of interest was calculated and standardized. In addition to relative area measures, the degree of compartmentalization or distinctiveness of particular areas were quantified by observing the relative intensity of staining in adjacent areas.

Predictions

The overall hypothesis was that there would be individual differences on behavioral measures that would be reflected in individual differences in cortical organization, which in turn could help explain both visual behavior and the functional organization of visual cortex. Some variability is always expected in a psychological study. Sometimes, it is overlooked, and data is collapsed across subjects. On the contrary, in this study we set out to exploit individual differences as well as the opportunity to use group data. Specific predictions based on prior research and theoretical assumptions were as follows:

1) We hypothesized that jumping accuracy would decrease with increasing gap distance. Because training occurred in dim light, we predicted that accuracy at this luminance level would be highest, although high accuracy was also expected under bright light. Due to constraints on vision, accuracy was expected to be lowest in very dim light, if there were to be jumps at all.
2) Latency was expected to increase with increasing distance. At short distances, due to familiarity, dim light was expected to result in the shortest jump latencies. At longer distances, however, latency was expected to be shorter in bright light

due to visual constraints in the dim condition. The highest latencies were expected at the darkest light level.

3) Acuity was expected to increase with increasing luminance due to the increase in light stimulation on the retina, consistent with the results of Baker & Emmerson (1983).
4) Gerbils that performed poorly on the jumping stand task were expected to either a) have poor vision overall, and were thus also expected to perform poorly on the acuity task, or b) show evidence of a tradeoff between the functions of depth perception and acuity, which we believe to be subserved by different brain areas.
5) We also expected that animals that performed poorly on the jumping stand (as evidenced by low accuracy and high latencies) to have a smaller expanse and less differentiation of extrastriate areas devoted to depth and motion processing. Specifically, we predicted that gerbils with better depth perception would have a larger and/or more clearly defined binocular zone in primary visual cortex, as seen in the ground squirrel. We also predicted that these animals would have a larger and/or more clearly defined area comparable to TP of the ground squirrel, if present.
6) As primary visual cortex is associated with the processing of basic contrast and form information, gerbils with poor acuity were expected to have a smaller expanse of primary visual cortex.

In addition, we originally proposed that individual differences in activity pattern would also factor into the analysis. Although we were unable to measure circadian rhythms systematically, as outlined in the original proposal, we did record observations of activity level more crudely (see Methods). While no clear assumptions can be made in terms of categorizing animals as “nocturnal” or “diurnal”, we did have several predictions regarding activity pattern that we tested using our modified measure.

7) Diurnal gerbils were expected to have better visual acuity and jumping accuracy under bright luminance conditions, than their nocturnal counterparts. Nocturnal gerbils were expected to perform better, however, under low luminance conditions, as diurnal gerbils should not be as accustomed to seeing in the dark, and nocturnal gerbils may prefer to be active in dimmer light.
8) Diurnal gerbils were expected to have a distinctly compartmentalized binocular zone within V1 (V1b), and more highly differentiated extrastriate areas than their nocturnal counterparts, as they should be more reliant on vision in general.

Methods

Overview

Animals were given the following manipulations in order: acclimation to housing (1 week) → food restriction (1 week) → jumping stand training and testing (2 weeks) → acuity apparatus training and testing (2 weeks) → euthanasia and anatomical analyses, as described below. Three to four animals were run through this sequence at a time.

Animals

16 male Mongolian gerbils (*Meriones unguiculatus*) were obtained from Charles River Laboratories. Females were not used to minimize the effects hormonal fluctuations may have on our variables of interest. Two of the obtained animals could not be tested. One would not allow himself to be handled, and was dangerous to work with. The other refused to jump during training, and was uninterested in any food reward, even after

being food deprived. As a result, 14 gerbils were included in the analysis. Animals were singly housed on a strict light-dark cycle (lights on at 0600, off at 1800), and food restricted to 85% of their ad-lib weight in order to provide motivation to perform on the behavioral tasks. Gerbils were tested in random order each day between the hours of 9:00am to 7:00pm. All care and use of the animals were in accordance with protocols approved by the Emory University Institutional Animal Care and Use Committee (IACUC).

Behavioral testing

Luminance Levels

Three luminance levels were used during behavioral testing: bright light (akin to low daylight; ~1000 lux), dim light (approximating dawn or dusk; ~100 lux), and low light (approximating moonlight; ~1 lux). A windowless room with uniform walls, adjustable lighting, and no admittance of external light was used in order to manipulate light levels. At the lowest light level (~1 lux), a 20 LED infrared illuminator and sensitive security camera (Sony SSC-M183) were used so as to make video monitoring possible. While we found that our pilot gerbils could see in the red light range (620 – 750 nm) that is typically used in rodent behavioral work, we are fairly certain that they cannot detect light in the IR range. Jacobs and Neitz (1989) report that the gerbil’s vision drops off at around 620nm, which is below the beginning of the IR range: ~700nm.

Jumping stand

The gerbils’ jumping ability and depth perception were tested by training the animals to jump between two platforms in a procedure modified from Ellard (1984) (see Figure 2). Our modified apparatus is pictured in Figure 3. The apparatus consisted of two raised platforms 21 cm high and covered with rubbery shelf liner to aid in traction. The “take-off” platform was 20 x 18 cm. The landing platform was two feet wide, so that it would be perceived by the gerbils as infinitely long. It was previously found that after gerbils have been trained at a particular distance with a landing platform of a standard width, changes in landing platform width resulted in over- or under-estimates of distance; narrower platforms appear further away and vice versa (Carey et al., 1990); we used a wide platform to minimize retinal image size as a depth cue. The depth of the landing platform was 9cm: wide enough to support the animal, but narrow enough for overestimates of gap distance to result in overshoots.

Background surface. A background surface (40 x 40cm) was positioned 14cm behind the landing platform (see Figure 4). A naturalistic image was used to provide the animal with visual cues for depth perception or for perceiving depth through motion parallax. In contrast to the checkerboard patterns used as backgrounds in previous studies (i.e. Ellard et al., 1984), a naturalistic image allows for a range of obliquely oriented edges in addition to those which are vertical and horizontal. It was created through a composition of elements from online photographs of Mongolia (the gerbils’ native habitat), and, to provide visual detail of desert terrain not easily available in sources of images from Mongolia, comparable desert terrain elements from pictures of Arizona (non-succulent shrubbery and rocks). The image was created to satisfy four requirements: (1) to contain only those elements that could be found in the gerbil’s native habitat, (2) to contain a combination of both light and dark areas, (3) to contain a wide range of spatial frequencies, and (4) to be composed of a variety of oriented edges. The presence of both light and dark areas gives the animals the opportunity to see the image at all light levels. A wide range of spatial frequencies ensures that at least part of the image will be below the animals' acuity thresholds at different distances, and makes available visual stimuli that may be differentially processed in the brain (Parker, 2007).

Training. Jumping stand training lasted approximately one week. During this phase, luminance was kept at the intermediate level ("dim light:" ~100lux). The animals were first trained to cross over a small gap (1-2 cm) between the two platforms for a small food reward (shelled sunflower seed). The jumping platform was then moved away in 1cm increments until the gerbil readily jumped a gap of 45cm to obtain the reward. Further training involved getting the animals accustomed to jumping in three-trial increments at a given distance and being placed in a large plastic holding container between trials.

Testing. Testing was carried out under the three luminance levels described above approximating daylight, dim light, and moonlight. On a single day, testing was carried out at a single luminance level chosen randomly. Jumping distance was varied randomly in 5cm increments between 5 and 45cm. The animals were exposed to three consecutive trials at the same distance and luminance level. Light levels and distances were assigned by using a computerized random number generator. A number between 1 and 3 represented the day's light level, in ascending order of luminance. Light levels were assigned pseudorandomly, as each animal was only tested on three occasions at any given luminance. If, for example, an animal was assigned dim light over the first three testing days, this luminance was not used at all over the next 6 days. As each day's testing consisted of 45 trials, in three-trial chunks at any given distance, with a total of 9 distances, each day a list of 15 random numbers between 1 and 9 was generated. The numbers represented distances in ascending order from 5-45cm. These were entered into a table, and each consecutive number was placed in every third column, each column representing latency and accuracy data for one trial. Before each day's test, the animals were allowed to acclimate to the chosen light level for 15 minutes.

Jumping latency was measured by pressing a timer at the moment the gerbil was placed at the very back of the starting platform. The timer was stopped when the gerbil's feet cleared the platform. If the gerbil did not jump within 30 seconds he was removed from the platform and placed into the holding container until the next trial. On such occasions, the latency was recorded as 30 seconds, and marked as "unwilling." Work with pilot animals led to the choosing of this 30s time limit, as very few gerbils that hesitated this long ended up jumping at all during this trial, many times even after being left on the starting platform for over 10 minutes. Jumping accuracy was determined by assessing the percentage of successful jumps vs. over-or undershoots, where the gerbil missed the landing platform completely.

Acuity

Visual acuity was tested using a modified Lashley jumping apparatus, modeled after Baker & Emerson (1983) (Figure 5). Our modified version, custom-built for our purposes by the Emory Physics Department machine shop, is pictured in Figure 6. The setup is similar to a traditional Y-maze, modified so that the gerbil must jump between two platforms to make a discrimination between two stimuli. The starting platform (9 x 9 x 45cm high) can be moved so that the jumping gap varies between 0 and 45 cm. Platforms were covered in rubbery shelf liner to aid in traction, as for the jumping stand. Each of the two landing platforms (9 x 9 x 45cm high) were situated 2.5cm below two circular apertures (10cm diameter) behind which were attached Plexiglas doors with slots to hold stimulus cards. The doors open backward and outward on a hinge and can be locked shut with a latch. The doors are on delicate springs so as to stay closed, but were easily pushed open by the gerbils. A small reward (shelled sunflower seed) was hidden behind the S+ (correct stimulus) door. On correct trials, the gerbil had to jump from the starting platform to the landing platform, push open the door, and receive the reward behind it; the S- (incorrect stimulus) aperture was blocked.

Training. Animals were already tested on the jumping platform prior to acuity testing, therefore they were already comfortable jumping between two platforms. Nonetheless, they still needed to be familiarized with the new setup and learn to make visual discriminations. As with the jumping stand all training was done under dim light. First, the animals were familiarized with the apparatus at small gap distances. They easily learned to push open the doors when they were held open slightly with the reward behind them. Since many animals began with a side bias in their jumping, they were encouraged (with the use of differential reinforcement) to jump to both sides. Once the animals learned to do this, the starting platform was moved 25cm away from the stimulus cards (making the gap distance 16cm). This distance was chosen as it was far enough so that some effort would have to be expended on the part of the gerbil to make the discrimination (discouraging impulsive jumping), while still being close enough that each gerbil was physically able to execute the jumps safely. Spatial frequencies are calculated based on this distance.

Next, the animals underwent discrimination training, beginning with a black/white discrimination. On trials when the gerbil chose the incorrect stimulus, a correction procedure was used: the trial was repeated until the gerbil made the correct choice. After 3 consecutive incorrect trials, the gerbil was placed on the landing platform in front of the S+ and allowed to push open the door to receive the reward. Each gerbil received 40 trials in a daily session until the criterion of 90% correct was met for 3 consecutive days. Throughout training and testing, the position of the S+ was randomly varied between left and right apertures. After reaching criterion on black/white, the gerbil was moved on to discrimination of gratings vs. blanks. During grating/blank training, the gerbil was rewarded for jumping to a low-spatial-frequency grating (0.6 cy/deg), avoiding a uniform grey card of the same luminance as the grating. Once the gerbil reached criterion (described above), testing was begun.

Testing. As in the jumping stand assessments, testing was done at 3 luminance levels: daylight, dim light, and moonlight. Once again, one light level was used each day per gerbil. Each day each gerbil received 40 trials in 5-trial blocks, beginning at a 0.6 cy/deg. If 4 or 5 correct responses were made in one block, the spatial frequency was increased on the next block. If more than one error occurred, the spatial frequency was decreased on the next block, but all 5 trials were given. This procedure produced a frequency-of-seeing curve each day at a given light level. The number of trials on which a correct response was given at a particular spatial frequency is expressed as a percentage of the total trials given at that frequency and plotted as a function of spatial frequency. The acuity cutoff was set at 70% correct. The spatial frequency at which performance fell below 70% correct was considered to be at the gerbils' acuity threshold.

Activity Levels

Continuous measurements of the animals’ activity level at different times of day were not financially and logistically possible for this project. Crude measurements of activity, however, were systematically undertaken so as to see if these could be important in explaining our data and thus a priority for consideration in future research.

The animals were accessed (and weighed) every day at random hours between 9:00am and 6:00pm. The activity level of each gerbil was noted immediately after the doors to their chamber in the animal facility were open. The level of activity was quantified on a scale between 1 and 4, 1 representing the lowest, and 4 the highest level of activity. A score of 1 was assigned when the gerbil was completely hidden, motionless, in its nest. A score of 2 was assigned if the gerbil was in its nest, but alert enough to peer motionlessly out at the experimenter. A score of 3 was assigned when the gerbil was moving about inside the nest, or when it was woken enough to exit the nest at least briefly. A score of 4 was assigned when the animal was clearly alert and moving about outside its nest.

Records were also taken of the animals’ activity levels at various points during the time that they were in the lab for testing. These were separated into categories based on whether the gerbil was waiting to be tested, had just been tested, or had been waiting for a while after being tested. We chose not to use measures in any of these categories, however, as they were inconsistent with one another, and because the level of activity was clearly affected by testing and handling. Activity levels in the animal facility were reasoned to be a better reflection of the animals’ natural tendencies.

Because all activity measurements were taken during the day, all were averaged together. We conceptualized gerbils that were less active overall during the day (less ‘day-active’) as being more nocturnal than gerbils that were on average more active (see Results and Discussion).

Neuroanatomy

Following completion of behavioral testing, animals were euthanized with isoflourane. After removal from the skull, each brain was flattened and postfixed overnight in formalin solution and then in a solution of 30% sucrose. Brains were labeled with numbers unrelated to the gerbils’ identity, so that the measurements could be performed blind. The cortex was then placed flat white-matter-side-up on top of an ice platform and cut in parallel sections measuring 40 microns thick by hand with a standard Microtome. It was then stained for myelin (Gallyas, 1979) and analyzed for the presence of distinctive visual areas and compartments within them. The brainstem was prepared separately for measurements of the relative size and degree of laminar differentiation of subcortical visual structures for later studies. The Gallyas stain reveals myelin-covered axons in neural tissue, staining darkly with heavy myelination. The resulting sections appear dark brown to black in color, with relative contrast between cytoarchitectonic areas (see Figure 9).

After staining was complete, the sections were studied on a light table. Particular attention was paid to ways in which visual structures varied between flatmounts and levels from deep (i.e., close to the white matter) to superficial (i.e., close to the pial or outer surface). These observations also helped in devising a strategy for analysis. Readily noted was the absence of a clear binocular zone in primary visual cortex, as mentioned in our predictions. The pattern of staining was qualitatively quite similar to that seen in rat flatmounts, and the identity of several heavy myelinated areas was reasonably inferred (i.e. primary auditory cortex, the barrel fields of somatosensory cortex) by comparison. In particular, primary visual cortex was clearly demarcated. The presumed area comprising extrastriate cortex appeared as a wedge lateral to V1, as in the rat, and consistently contained a very dark triangle at the far lateral edge. The dark staining and positioning of this area corresponded strikingly to area TP in the ground squirrel. Tentatively, we chose to call this area “proto-TP” in the gerbil. With our original plans and predictions in mind, we decided to take areal measurements of both V1 and proto-TP.

Also as per our plans, we decided to take qualitative measurements of both the compartmentalization of V1 and the distinctiveness of proto-TP. Rating scales were devised based on these preliminary observations. The compartmentalization of V1 was rated on a 1-5 scale, 1 being the most uniform, and 5 being the most compartmentalized. The rating system and examples are shown in Figure 8 and detailed in the figure legend. Visual distinctiveness of proto-TP was rated on a scale of 1-5, 1 being the least distinct, and 5 being the most. The rating system and examples are shown in Figure 7.

For proto-TP, ratings were kept for the three most superficial sections in which it is clearly visible, as this area was consistently more distinct in superficial sections. For V1, ratings were kept for the most ideal section chosen for areal measurements and the two sections flanking it. Two raters (Q. Abid and H. Rodman) performed this analysis independently after some discussion of the rating system. Both were completely blind to the identity of the gerbils, and unaware of any trends in the behavioral data. Inter-rater reliability was highly correlated for both TP (Spearman r (66) = .64, $p<.001$), and V1 (Spearman r(56) = .362, $p<.05$). Therefore, the final rankings were averaged across the three relevant sections, across raters, and between the two hemispheres of any particular brain – resulting in one value per animal.

For areal measurements, scans of individual flatmount sections were imported into Canvas software [Deneba Software, Inc.], For each hemisphere, in order to utilize comparable levels through the cortex across animals, the section selected for areal measurements was chosen to be the most complete section in which the somatosensory barrel fields and primary auditory cortex, as well as areas V1 and proto-TP, were clearly evident. Areas V1 and proto-TP were selected for measurement based on our predictions and initial observations that these areas were distinct and reliably visible (see Figures 9 and 10. – and Results).

Tracings were performed by one of the observers (H. Rodman) blind to the identity of individual flatmounts. Canvas software includes a function for automatically providing output regarding the area of a traced shape. Expressing visual areal measurements as a function of the total cortical area was not possible due to differences in flattening and the frequency of tissue incompleteness or shredding along the anterior boundaries of the flatmounts. It was determined instead that the most reliable standard of comparison was a measure of the total area of cortex lying posterior to a straight line flanking the edges of auditory and somatosensory cortex, which are easily made out in all sections (see Figure 9). Based on previous studies in a variety of rodents, notably squirrels, this area likely consists primarily of visual cortex as well as polysensory areas with visual responses (Sereno et al., 1991; Rodman et al., 1992) (Figure 9). Because the left hemisphere was torn and unusable in 4 our 14 animals, only values for right hemispheres were entered in the analysis.

Results

Behavior

Jumping Stand

There were a total of 9 distances used on the jumping stand between 5 and 45 cm. These were collapsed into three groups: short (5-15cm), medium (20-30cm), and long (35-45cm) distances for greater ease in running the analysis. Preliminary observations of jumping behavior at all 9 distances suggested that latencies increased abruptly for most animals at some medium distance. Because this distance varied between animals, deciding on a cutoff in a two category system (short and long) proved difficult. The three category system works well as it keeps short and long distances separate from one another while allowing the midpoint to fall somewhere in the medium category. There were very few inaccuracies, when the gerbils undershot or overshot the platform. Overshoots occurred at short distances only. All gerbils successfully completed jumps of 45cm at least once throughout testing.

Prediction # 1: Relationship of jumping accuracy to gap distance and illumination level

Accuracy was normally distributed with the mean score across all gerbils being 95.4%, (SD = 2.9). Although there was a ceiling effect overall, accuracy did decrease with increasing distance $\chi^2(2, N = 12) = 19.3$, $p < .001$ (Figure 11), as expected, with mean scores of 99.8% (SD = .32) at short distances, 98.5% (SD = 1.52) at medium distances, and 87.9% (SD = 7.86) at long distances. A nonparametric Friedman test was performed as the data violated the assumption of equal variances.

Although there was no main effect of light level $F(2, 22) = 2.621$, $p = .095$, as tested with a repeated measures ANOVA, within-subjects contrasts revealed a significant linear trend for increased accuracy at brighter luminance levels F(1,11) = 6.849, $p < .05$, partial $\eta^2 = .384$ (Figure 12) with mean scores of 94.1% (SD = 4.4) for low light, 95.5% (SD = 4.12) in medium light, and 96.6% (SD = 2.0) in bright light. Although we predicted accuracy would be highest in dim light, the condition in which training occurred, this was not the case.

Prediction #2: Relationship of jumping latency to gap distance and illumination level

As expected, there was a main effect of increased latency with increasing distance, as determined by a repeated measures ANOVA, F(2, 26) = 35.24, $p<.001$, Partial $\eta^2 = .731$ (Figure 13), with mean latencies of 2.2s (SD = 2.05) at short distances, 8.2s (SD = 8.04) at medium distances, and 15.7s (SD = 8.52) at long distances.

Contrary to our predictions, there was a significant main effect of increased latency with increasing light levels, as determined by a repeated measures ANOVA, F(2, 26) = 3.611, $p<.05$) (Figure 14), with mean latencies of 7.9s (SD = 5.53) in the dark, 8.5s (SD = 6.18) in dim light, and 9.8s (SD = 6.58) in bright light. In other words, the gerbils on average jumped faster in low light than in bright light. We expected the opposite trend, with better performance in brighter light, and perhaps greater performance in dim light, which was not the case.

Acuity Apparatus

Prediction #3: Relationship of acuity threshold to illumination level

Also contrary to our predictions, acuity did not increase with increasing light level, as revealed by a repeated measures ANOVA, with a main effect of F (2, 20) = .372, $p = .694$, and a within-subjects linear contrast value of F(1, 10) = .528, $p = .484$ (Figure 15).

Activity Levels

Activity level were expressed as an average score on a continuum between 1 and 4, but animals were also divided into two groups (corresponding to less, and more day-active) for the purpose of making dichotomous comparisons roughly equivalent to the nocturnal/diurnal distinction, but which we cannot use with confidence until further analysis is performed. Gerbils with average activity levels above 3 (active in nest or alert outside of nest) were categorized as more day-active. Gerbils with average activity levels below 3 (completely hidden in nest or motionless and peering out) were classified as less day-active.

Prediction # 7: Relationship of jumping latency (and acuity) to activity level and illumination

Consistent with our predictions, within-subjects contrasts revealed a significant linear interaction between latency at the different light levels and activity level, $F(1,12) = 3.4$, $p < .1$) (Figure 16) partial $\eta^2 = .221$. The effect of light level on latency appears to be driven by the less day-active group. At the lowest light level, less day-active gerbils had a mean latency of 5.7s (SD = 3.77), and diurnal gerbils had a mean latency of 9.6s (SD = 6.26). At the brightest light level, nocturnal gerbils had a mean latency of 9s (SD = 6.7), and diurnal gerbils had a mean latency of 10.4s (SD = 6.89). A significant positive correlation supporting the interaction between activity level and illumination was found between activity level and latency at the lowest light level, meaning that more active gerbils were faster than less active gerbils in the dark, pearson's r (12) = .544, $p<.05$ (Figure 17).

Although we did not make specific predictions regarding the role of activity pattern in visual acuity, within-subjects contrasts revealed a significant quadratic interaction between acuity at different light levels and activity level, F (1,9) = 6.255, $p < .05$) (Figure 18). At the medium light level, mean acuity thresholds for less and more day-active gerbils were similar (this was the light level at which training took place) (less day-active: 1.29 cy/deg (SD = .19), more day-active: 1.28 cy/deg (SD = .29)). However, at both dark and bright light levels, more day-active gerbils' acuity threshold increased, while less day-active gerbils' decreased (means for less day-active gerbils in low light: 1.09 cy/deg (SD = .47) and bright light: 1.16 cy/deg (SD = .05), means for more day-active gerbils in lowlight: 1.34 cy/deg (SD = .45) and bright light: 1.44 cy/deg (SD = .5)).

Prediction #4: Relationship between jumping latency and acuity threshold

Contrary to both parts a) and b) of prediction #4, no significant correlation was found between jumping latency and acuity thresholds r (12)= .073, p = .804) (Figure 19).

Trials to Criterion

No predictions were made involving trials to criterion. However, trials to criterion on the acuity apparatus was significantly correlated with several jumping stand variables. There was a negative correlation between Trials to Criterion and accuracy at short distances r (12) = -.745, $p < .01$ (Figure 20), a positive correlation between Trials to Criterion and average latency in the dark r (12) = .676, $p < .01$ (Figure 21), as well as with average latency at the medium jumping distances r (12) = .555, $p < .05$ (Figure 22). In other words, gerbils that took longer to reach criterion were less accurate and slower on the jumping stand in certain contexts. However, trials to criterion were not correlated with acuity thresholds (for average acuity: r (12) = .121, p = .68) (Figure 23), suggesting that our measure of acuity was not affected by initial differences in the speed of learning and/or level of motivation.

Neuroanatomy

No distinct binocular zone (as seen in the ground squirrel) was found in gerbil primary visual cortex (V1). V1 did not appear completely uniform, however (see Figures 9 and 10). Typically, the lateral edge was darker in appearance than the tissue found medially, although this was not as distinct in some flatmounts, and a couple of cases did contain dark zones in the medial portion of V1. In some flatmounts, a lighter area appeared at the center of V1. It is assumed that this is a real phenomenon and not simply an artifact of the tissue preparation process, as it appeared in both hemispheres when present and in more than one animal. It is possible that this region represents the optic nerve head of the retina, as the optic nerve head contains no photoreceptors, and hence does not project much information to visual cortex. Such an area is distinctly and reliably seen in the ground squirrel, where it has been identified electrophysiologically (Sereno et al., 1991; Rodman et al., 1992)

A darkly stained “wedge” was located laterally to V1 and is assumed to be extrastriate cortex, as is found in other rodent flatmounts, and identified on the basis of electrophysiology. The most lateral portion of presumed extrastriate cortex in the gerbil was characterized by a dark triangle of cortex in the approximate relative position as area TP of the ground squirrel, known to be involved in motion processing. Therefore, this area is referred to by us as “proto TP.” This area differed across flatmounts in terms of how distinctly it separated from the rest of extrastriate cortex in visual contrast. Also, a smaller distinct dark area sometimes appeared to be distinctly separate from TP anteriorly (see Figure 7).

Brain-Behavior Correlations

General

There were no significant correlations between the distinctiveness of proto – TP or the compartmentalization of V1 and any behavioral variables. The normalized areal measurements of proto-TP and V1 were normally distributed with means of 7% (SD = 1.2) and 35.8% (SD = 3.73) of the total area of posterior cortex, respectively. The size of proto-TP ranged from 5.03% to 8.76%, and of V1 from 26.5% to 41.4% of the total area of posterior cortex across all gerbil flatmounts.

Prediction #5: Relationship between jumping latency and neuroanatomical measures

As mentioned above, no distinct binocular zone was found in gerbil primary visual cortex. However, consistent with our predictions, the normalized relative size of proto-TP was significantly negatively correlated with average latency on the jumping stand, collapsed across light levels and distances $r(12) = -.658$, $p < .05$ (Figure 24). The smaller normalized relative size of proto-TP, the slower the animal. There was also a significant main effect for the interaction between jumping latencies across distances and the normalized relative size of proto-TP, as revealed by a repeated measures ANOVA, $F(2, 24) = 5.29$, $p < .05$, partial $\eta^2 = .306$ (Figure 25). For this analysis, gerbils were divided into two groups based on their relative expanse of proto-TP. Areas below 6% were considered small, and areas of 6% and above were considered large.

Prediction #6: Relationship of acuity threshold to neuroanatomical measures

Also consistent with our predictions, the proportionate area of V1 was close to being significantly correlated with acuity threshold (collapsed across light levels) when only measures of the right hemisphere were used r (12) = .522, p = .055, and reached significance when the left hemisphere was averaged into the measurement r (12) = .54, p < .05 (Figure 26). In other words, animals with a larger relative expanse of V1 had a trend towards better acuity.

Prediction #8: Relationships between activity level and neuroanatomical measures

Contrary to our prediction, neither of the areal measurements correlated significantly with activity level (TP: r (12) = -.295, p = .605; V1: r (12) = .165, p = .572) (Figures 27 and 28, respectively).

Other brain-behavior results

The relative area of proto-TP was not correlated with the relative area of V1 r (12) = -.152, p = .605. Therefore, there does not appear to be a trade-off between the two functions. Some animals had both large V1s and proto-TPs, others had small areas for both regions. The latter individuals may have other dominant functional areas occupying posterior cortex.

Neither of the areal measurements correlated significantly with accuracy on the jumping stand (TP: r (12)= -.488, p = .107; V1: r (12) = -.221, p = .489), or trials to criterion on the acuity apparatus (TP: r (12)= -.46, p = .098; V1: r (12)= .37, p = .193).

Neither areal measurement was significantly correlated with its respective measure of distinctiveness or compartmentalization (TP area and TP distinctiveness: r (12) = .11, p = .708; V1 area and V1 compartmentalization: r (12)= -.368, p = .196).

Other Observations

The animals also differed in terms of temperament, as observed by those who handled them. Some gerbils were extremely active when waiting in their cage before testing began. This was evidenced by their climbing on the bars of the food-hopper above them, and chewing on those bars to the point of rubbing some fur from the bridge of their nose. Although it was not analyzed systematically, these animals seemed to be more highly motivated to perform the jumping task. At times, however, over-exuberance on the acuity apparatus translated into poor performance, as the jumping was impulsive and indiscriminate toward one or the other side.

Some animals became so adept at jumping that they eventually learned to jump out of the plastic bin they were held in between testing trials. The sides of the bin were approximately 2 feet high. Often, in these cases, the animals would not jump out of the bin, but would jump onto the ledge, crawling easily into the hand of the experimenter for the next trial. These animals seemed enthusiastic either about the jumping itself or the reward associated with it.

The animals arrived at our facility in batches of 4. It was observed that temperament seemed to differ somewhat between batches. Animals in the second batch, for example, were difficult to handle, and had a tendency to bite. One of these animals had to be excluded from the study. We attempted to determine from the supplier (Charles River) whether batches of animals were likely to be more related to one another, but this information was not available.

Finally, two out of the 14 gerbils included in the analysis developed a tendency to abort trials on the jumping stand by crawling down from the starting platform rather than jumping over the gap or waiting 30 seconds until the next trial. This occurred more frequently at long distances. As a negative consequence, these animals were made to wait longer between trials. This, however, did not discourage the behavior altogether.

Discussion

This project resulted in several important findings. First, myelin-stained flatmounts of gerbil cortex will add to the sparse literature on the organization of the visual system in this species. In addition, they will help to define specific cortical regions across species. There were both purely behavioral findings, as well as significant brain-behavior correlations. Our systematic manipulation of light level, in particular, was shown to have important effects on behavior. Preliminary evidence suggests a role for activity pattern as a mediator of these effects. Areal extents of both V1 and proto-TP were significantly correlated with predicted behavioral measures of interest. This knowledge of brain-behavior correlations may help to understand mechanisms of cortical evolution.

Behavior

The Jumping Stand. The gerbils were clearly quite skilled and motivated jumpers. Training on the jumping stand took approximately one week after the animals were first food deprived, and all gerbils successfully cleared gaps of 45cm at least once during testing. As expected, accuracy decreased with gap distance, while jumping latency increased. There are at least two possible reasons for this decrease in performance with increasing distances. First, jumps were more physically demanding at the longest distances. Accuracy could have decreased because the animals may not have pushed off the starting platform with sufficient energy. Also, latency could have increased as the animals prepared themselves physically for the jump and/or weighed the costs and benefits of expending such energy for the expected reward. As the gap distance was subject to change every three trials, an easier reward could be obtained with a little patience. The second reason, supported by our data, is that wider gaps put increasing constraints on vision. In this case, inaccuracies are the result of incorrect depth estimation, and higher latencies are due to a lack of confidence in the judgment of visual distance.

Our neuroanatomical data suggest that visual ability actually did play a strong role in performance on the jumping task. Gerbils with larger normalized relative proto-TP areas jumped faster than gerbils with smaller proto-TP areas. Because proto-TP is likely a visual structure based on its location in comparison to data from other rodent species, it is parsimonious to assume that the behavioral advantage associated with it is based in visual ability. In turn, the relationship between latency on a visuomotor task and relative size of proto-TP lends weight to the idea that this cortical region is in fact equivalent, or perhaps even homologous, to the specific area TP defined in sciurid rodents and in tree shrews (Sereno et al., 1991; Rodman et al., 1992). Further, if such an equivalence can be supported by additional data (e.g., patterns of connections or electrophysiology), it would add weight to the case for an evolutionarily conserved, lateral motion processing/ visuomotor region similar to area MT of primates (discussed in more detail below under Anatomical Findings.

The finding that the gerbils jumped faster on average in lower light levels was unexpected, particularly because bright light provides more contrast information and better stimulates photoreceptors in the retina, particularly cones. While previous studies have found evidence for a small functional cone system in the gerbil retina (Jacobs &

Neitz , 1989), perhaps this system is not as relevant to gerbils in certain situations (such as during visuomotor activity) as the rod system. Because there was an interaction with activity level (discussed in further detail below), it seems there is yet another factor affecting latency - motivation. As was predicted, less day-active gerbils appear to have a preference for jumping in low light. This finding could have implications for strategies of behavioral testing in other nocturnal (or partially nocturnal) species.

The fact that activity level was positively correlated with latency only at the short distances, coupled with the interaction of proto-TP area with latency at the different distances suggests that behavior should be analyzed separately at the different distances. During testing, we did suspect that the latency measure on the jumping stand did not purely reflect differences in visual ability, but also motivation. This data suggest that both suspicions are true. Jumping latencies do appear to reflect motivation at short distances, as evidenced by the correlation with activity level, which was not shown to be correlated with neuroanatomical measures. At longer distances, differences in jumping latency do appear to reflect visual ability, as evidenced by the correlation with areal measurements of proto-TP.

The above findings are consistent with correlations involving the trials to criterion measure. When animals took longer to reach criterion, they were slow learners, which may be related to the level of motivation. These animals were also less accurate and slower on the jumping stand at short distances, when vision was not being taxed, just as was found with less day-active animals. Because trials to criterion was not correlated with activity level, it was not the case that less day-active animals were less motivated in general. The results simply suggest that motivation – either general or specific to light preference – has an impact on jumping latency when vision is not being taxed. Highly motivated gerbils, whether hungry, eager, or especially alert, seemed to jump and learn with particular vigor when given an easy opportunity.

Comparison to previous gerbil studies. A few previous studies utilizing the jumping task have looked at brain-behavior correlations, primarily by means of lesion experiments. Surprisingly, the use of retinal image size as a distance cue was intact even in gerbils with bilateral lesions of striate cortex (Carey et al., 1990), suggesting that the neural mechanisms for using retinal image size as an indicator of distance lies somewhere other than primary visual cortex. This makes sense in light of our finding that the relative expanse of V1 does not correlate with jumping measures. This study did not measure head movements, however, which could have aided depth perception by producing motion parallax cues.

Ellard et al. (1986) showed that cortical lesions did have an effect on jumping task behavior, in terms of both decreased accuracy and a great increase in latency to jump. While these gerbils performed more head bobs than sham-operated gerbils, the resulting motion parallax information apparently could not be utilized by the animals to estimate distance. The motor program for generating the head movements, the authors reasoned, must be located elsewhere. This area was later identified to be the anteromedial cortex (AMC) (Ellard & Ilkov-Moor, 1995). Gerbils with AMC lesions carried out fewer head movements in a jumping task than both sham and frontal-cortex operated gerbils. They were also less accurate at distance estimation, particularly at longer distances, showing that these movements are used to heighten jumping precision.

It is somewhat unclear from the two lesion studies mentioned above, however, the extent to which extrastriate regions were affected by the treatment. Too little was known about the gerbil brain at the time, and too little is still known about the gerbil visual cortex to be sure. As there was no anatomical map of gerbil neocortex, crude estimates were made on the basis of anatomical data on rats. Complete retrograde degeneration of the dorsal lateral geniculate nucleus (dLGN) suggested that V1 was destroyed in all cases. Damage to extrastriate cortex was described as variable and probably minimal (Ellard, 1986). In addition, as with all lesion studies, a question that cannot be answered is the degree to which secondary impairments (not directly related to the lesion site) might be responsible for the impairments in performance of the task.

The current study explores cortical involvement using a different approach than lesion studies. First, it is correlational rather than experimental, so any differences that exist have not been manipulated, eliminating the possibility of secondary impairments. Second, the anatomical analysis is more subtle, exploring striate as well as extrastriate areas. These areas are intact, so differences in size and differentiation are the focus of attention instead of the effects of complete damage.

Another difference between the current study and previous studies is that our version of the jumping stand was designed to eliminate monocular cues such as retinal image size. The leading edge of the platform is 2 feet wide, so that it will cover most of the field of view at any distance. Other monocular cues, such as texture gradient and linear perspective were eliminated by placing a uniform, non-textured shelf-liner on all visible surfaces. Theoretically, then, the gerbils would only be able to determine depth by means of binocular disparity and/or motion parallax. Previous studies did not explore the possible use of binocular disparity as a depth cue in gerbils.

Acuity. There was no main effect of light level on acuity, which was surprising, because more contrast information should be available to the eye in brighter light, improving vision. Consistent with the jumping stand data, lack of an increase in acuity with light level reflects a less-than-optimal cone system in the gerbil eye, in contrast to what has been suggested by previous studies (e.g. Baker & Emmerson, 1983). The jumping distance used in the Baker & Emmerson study, however, was much larger (29cm) than that used in the current study (15cm). It is possible that the different findings are the result of an elimination of motivational factors involved in performance with the use of this shorter distance. The Mongolian gerbil retina is composed of 13-14% cones (vs. rods). As a point of comparison, the rat retina is composed of 1% cones, while in the ground squirrel, cones comprise approximately 95% of the total photoreceptor population (Szel et al., 1996). The function of the cone system, however, also relies on its distribution. Primates are known to have a rod-free zone at the center of their visual field called the fovea. Many animals living in open terrain have an elongated retinal zone with higher cone densities termed the “visual streak” (Szel et al., 1996). These facts, coupled with behavioral evidence, need to be taken as a whole in order to gain a better understanding of the differential functioning of the cone system across species.

The interaction of acuity at different illuminations with activity level reveals a difference between acuity thresholds in gerbils classified as either more or less day-active. All animals were trained in dim light, and so it was expected that performance at this light level might differ in some way from that at other light levels. It appears as though both less- and more- day-active gerbils had similar acuity thresholds in the dim condition. In both the dark and bright conditions, however, the acuity of more day-active gerbils was higher than that of less day-active gerbils.

In contrast with behavioral differences across activity pattern on the jumping stand, this difference in acuity thresholds cannot be explained by motivational factors. All gerbils were highly motivated, as evidenced by consistent criterion-level (90%) performance at low spatial frequencies. In addition, no correlations were found between activity level and neuroanatomical measures. This tentatively points to a difference in peripheral aspects of the visual system between more or less day-active gerbils. As mentioned above, it may be worthwhile to study differences in the rod/cone ratio and density between animals with differing activity patterns. In addition, there are other characteristics of the eye that could affect acuity, which could also be compared across individuals. One is size. Nocturnal animals tend to have larger eyes which let in more light. A larger eye increases sensitivity to light with a relative decrease in resolving power (Kiltie, 2001).

The relative size of V1 was also correlated with acuity, as expected, if both hemispheres were averaged (and the relationship approached significance if the right hemisphere alone was used. It was surprising, however, that this effect appears unrelated to activity level. Perhaps there exists a dissociation between peripheral and central contributions to spatial resolution in the visual system.

Neuroanatomical Findings

At this point, there is not sufficient information to speculate with much conviction about the functional role of a highly distinct binocular zone in V1 of squirrel species, as none was found in the gerbil flatmounts. We did, however, consistently find that the lateral edge of V1 appeared dark in the myelin stain. Future studies may examine whether this more subtle compartmentalization reflects the segregation of the binocular zone in V1 of the gerbil. We began by speculating that this zone may play a role in binocular depth perception. As the gerbils were shown to be highly skilled jumpers, they must also have good depth perception. However, better performance was correlated with the size of proto-TP, and not with the compartmentalization of V1. Until head-bobs are analyzed, it cannot be said whether proto-TP aided in depth perception by means of stereopsis or motion parallax. It is possible that once animals are segregated on the basis of head-bob behavior, some relationship may emerge between compartmentalization within V1 and jumping stand performance.

The similarity in the staining pattern and location of what we are calling proto-TP in the gerbil to TP in the ground squirrel, coupled with the fact that ground squirrel TP has direction-selective properties (Sereno et al., 1991; Rodman et al., 1992) , leads us to suggest that gerbil proto-TP is involved in motion processing. Supporting this view is proto-TP’s - apparent role in visuomotor ability as evidenced by jumping stand performance, and depth perception that is possibly mediated by body movements. However, a more basic argument could be made for the role of proto-TP in mediating proper hand-eye coordination. This simpler hypothesis could be tested with behavioral measures that require hand-eye coordination with the exclusion of bodily motion and depth processing.

At the same time, we must also consider the possibility that proto-TP is involved in binocular depth perception. In the primate visual system, area MT, well-known to be involved in processing the direction of motion, has also been found to be selectively responsive to differing degrees of binocular disparity (DeAngelis et al., 1998). An interesting question for future studies to address is whether areas that process motion are also involved in the processing of binocular disparity.

The fact that gerbil visual cortex was found to contain an extrastriate area which appeared more similar to the ground squirrel pattern than the rat or hamster pattern begs the question as to what behavioral characteristics gerbils and ground squirrels share to the exclusion of hamsters. Activity level is one possibility, and will be discussed below. Another salient possibility is visuomotor behavior, specifically jumping. Gerbils differ from both rats and hamsters in that they have long hind limbs which allow them to jump with great efficiency. Squirrel species are highly adept climbers in general. We believe that future studies of other jumping/climbing rodents would be useful in better understanding this relationship.

Contrary to our predictions, we did not see any significant correlation (either positive or negative) between jumping latencies and acuity thresholds, or between the size of proto-TP and the size of V1. Therefore, there does not appear to be a trade-off between visuomotor and acuity functions, or a clear separation of animals into more- or less- visually adept categories. Correspondingly, this reflects some flexibility in the layout of the visual system. Posterior cortex in some animals was occupied sometimes by a large V1 and proto-TP, or a small expanse of both areas, and anything in-between. Gerbils representing the two extremes on this continuum, however, could be compared in future studies for adeptness in the processing of other kinds of information that is represented in posterior cortex. Audition is one possibility.

Activity Levels.

Our decision to study individual differences in Mongolian Gerbils was partially sparked by the finding that striking variability exists in the activity patterns of these animals (Refinetti, 2006). This finding is interesting because activity pattern, in particular, is a characteristic that is usually applied to a species as a whole. While our original proposal for this project included sophisticated mechanisms for circadian monitoring, the focus narrowed into specifically analyzing individual differences on the other two behavioral measures. While this alone resulted in strong claims for brain-behavior interactions, we still believe that activity levels are a relevant variable of interest related to our results.

This belief is tentatively supported by the sample of activity level measurements we were able to obtain. While crude, this measure of activity emerged in our analysis as a variable which interacted significantly with both of our other behavioral measures. Specifically, less day-active gerbils were shown to drive the trend toward faster jumping latencies at lower light levels, and more day-active gerbils had better acuity than less day-active gerbils with the exclusion of the dim light level used in training. There was no evidence, however, for any correlations between activity levels and neuroanatomical variable. Further analysis should be performed to properly explore this relationship

Development and Evolution

It was interesting to find such striking individual differences in brain and behavior in a species with very little genetic variability (Rizzoli et al., 2003). At the same time, the gerbils in our study had very similar experiences throughout development, as all were put through the same handling, training, and testing procedures. The only possibly relevant difference in experience between individuals is activity pattern, as it would result in differential exposure to high and low levels of illumination throughout development. However, our measure of activity levels did not correlate significantly with neuroanatomical measures. Because the visual system has an early critical period, and its organization does not appear to be affected developmentally by activity pattern, some heritable differences must exist in regard to the organization of visual cortex, despite little genetic variability in the species. These differences, in turn, appear to have an effect on behavior.

The presence of individual differences is exactly what is required for the evolutionary changes that result in adaptation and speciation. Currently, Mongolian gerbils are a common pet and laboratory animal, and are specifically bred for these purposes. It is interesting to hypothesize, however, about how the individual differences that exist in this species would play out over time if the animals were left alone in the wild. First, animals with differing visual abilities may be able to better exploit differential resources. This can be due to differences in landscapes traversed, foodstuffs that can be seen and/or reached, and escape movements or other behaviors that can be performed. Animals with differing activity patterns may also exploit different resources, and may be faced with differential predatory threat. Furthermore, animals that find themselves in similar environments are more likely to mate with one another, preserving the very characteristics that led them there in the first place.

Conclusion

Because many significant findings were derived from our study of within-species individual differences, the general approach appears to be justified. Instead of collapsing across these differences and placing all animals of one species into the same category, it has proven worthwhile to exploit individual differences to study brain-behavior relationships. While not “comparative” in the sense of focusing on cross-species differences, this study does get at the comparative organization of the brain with differences in behavior – which addresses similar issues to that of cross-species studies. An added advantage of this approach is that members of one species are very similar to one another on many characteristics, a fact that allows greater specificity in identifying what differs. This is not to say that cross-species comparisons are not necessary. To the contrary, we also hope to compare the findings to this study, particularly the neuroanatomical measures, to patterns found in other rodent species.

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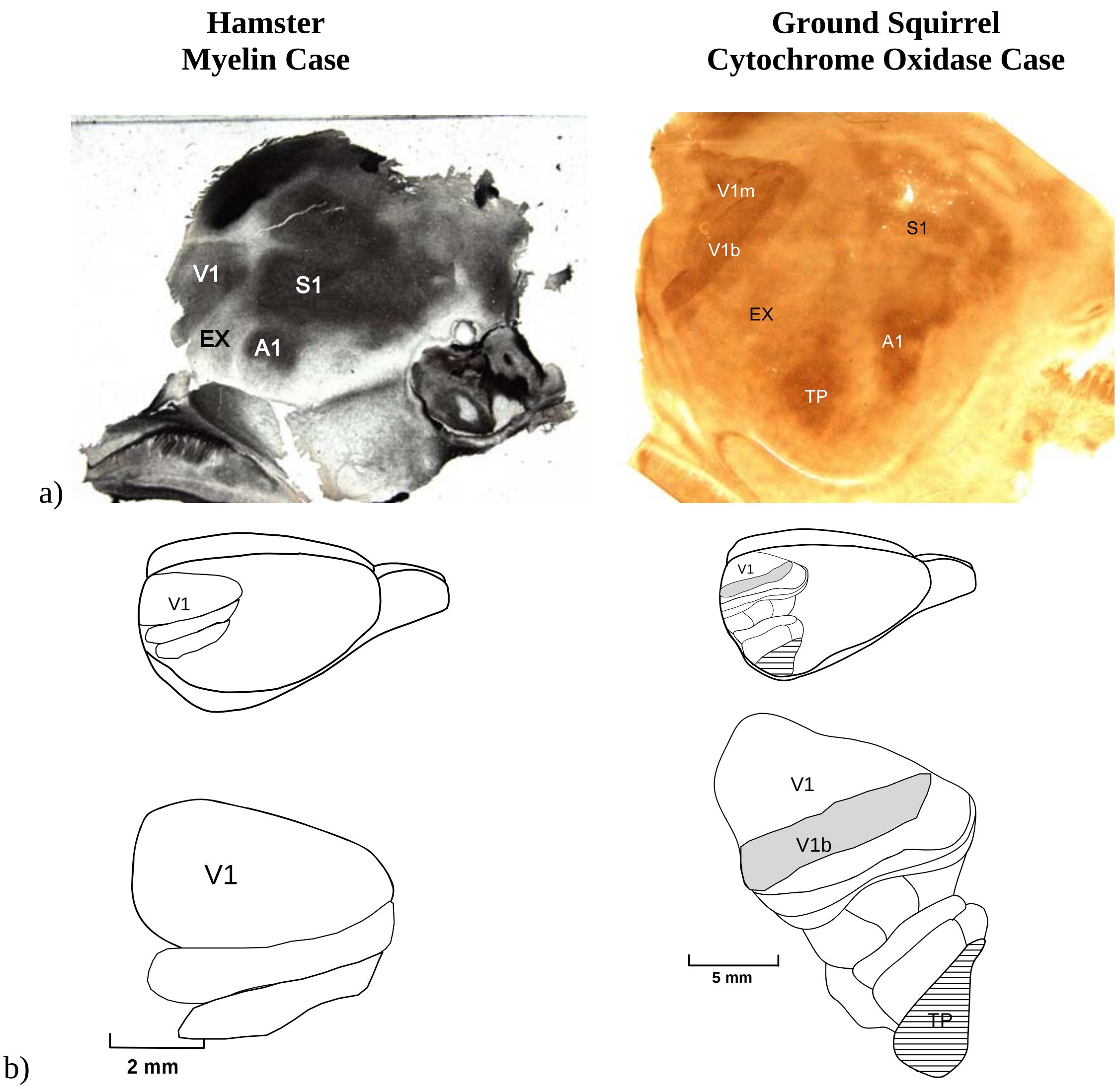

Figure 1. Examples of visual cortex organization in hamsters (left) and ground squirrels (right). A) Flatmount sections treated with either myelin (hamster) or Cytochrome Oxidase (CO) (ground squirrel). CO shows similar patterns of staining as Myelin. It was not used in this study, as it was better to have two myelin stained hemispheres per animal, rather than risking one to possible damage. B) Drawings representing the outlines of distinctive visual areas in the cortex of both species. The entire cortex is pictured above, and a flattened version of just visual cortex is pictured below. Abbreviations: V1 – primary visual cortex, V1m – V1 monocular, V1b – V1 binocular, EX – extrastriate cortex, S1 – primary somatosensory cortex, A1 – primary auditory cortex, TP – temporal posterior area.

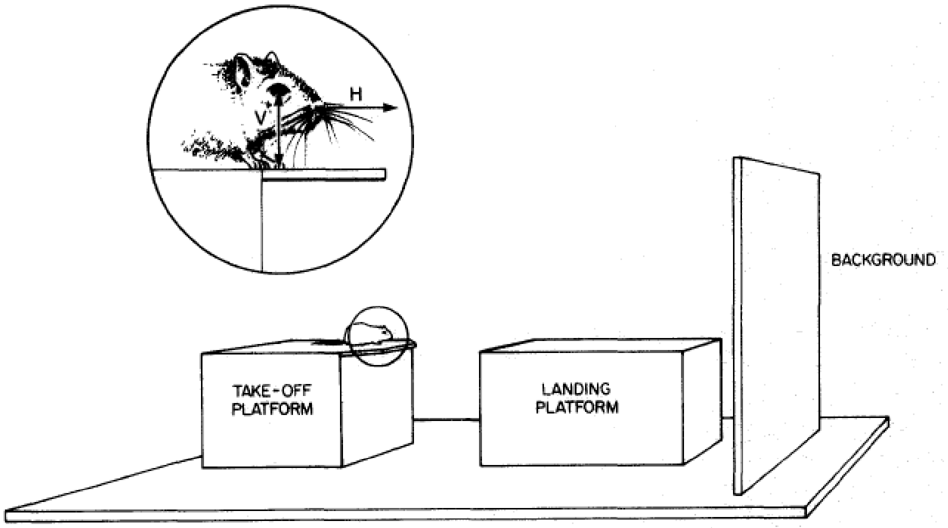

Figure 2. A schematic diagram of the jumping stand, as taken from Ellard (1984). Measures of head movement are also detailed above and left. These were not analyzed in the current study.

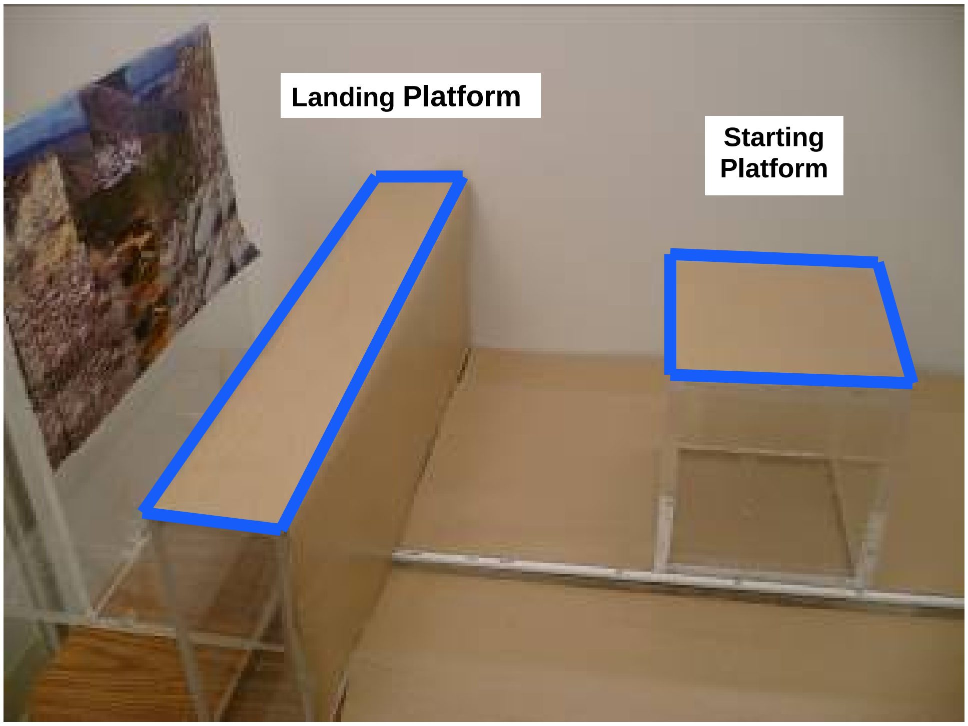

Figure 3. Picture of the jumping stand in the current study. In the current experiment, the landing platform is modified to be 2 feet wide and 9cm in depth, so that the leading edge appears infinitely wide, and so that overshoots would result in inaccuracies. Distances (varying between 5 and 45cm) are measured with a permanent ruler which also keeps the starting platform centered. A naturalistic background image is used. All surfaces are covered in rubbery shelf-liner with a uniform texture. In this picture, the gap distance is approximately 25cm.

Figure 4. Picture of the background image used for the jumping stand. A variety of features naturally occurring in the Mongolian Gerbils' natural habitat were fused in order to provide ecologically relevant visual cues.

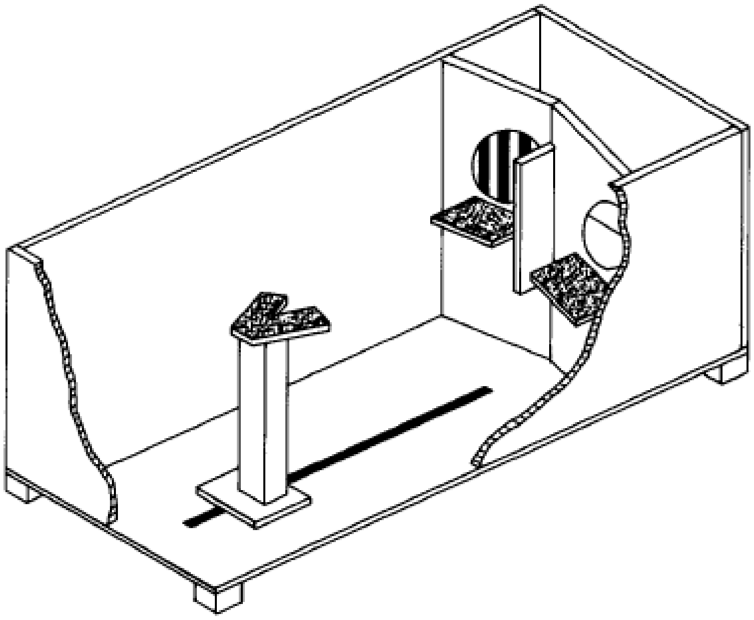

Figure 5. A cut-away schematic of the acuity apparatus, as taken from Baker and Emerson (1983). If the gerbil jumps to the grating (vs. a uniform gray card), he can push down the door containing the grating and retrieve a food pellet on the floor behind.

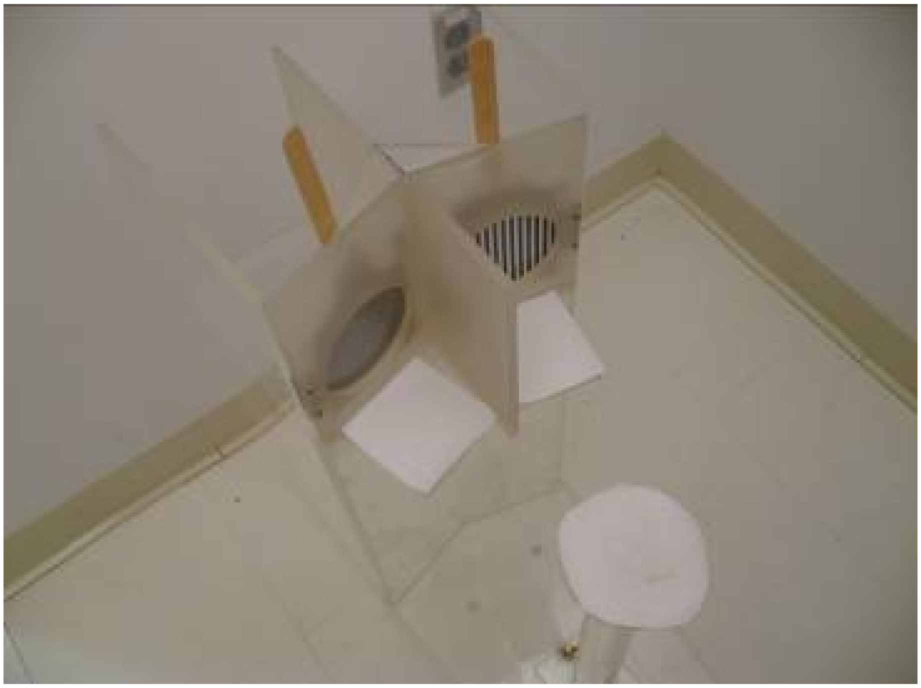

Figure 6. Picture of the acuity apparatus built for the current study. There are no walls, for ease of handling the gerbils. The starting platform is pictured at the correct jumping distance (a gap distance of 15cm). Plexiglass doors containing stimulus cards open outward on hinges, and could be closed shut with a latch in back. The spatial frequency pictured is .6cy/deg from the relevant viewing distance. Shelf liner covered the surfaces to aid in traction.

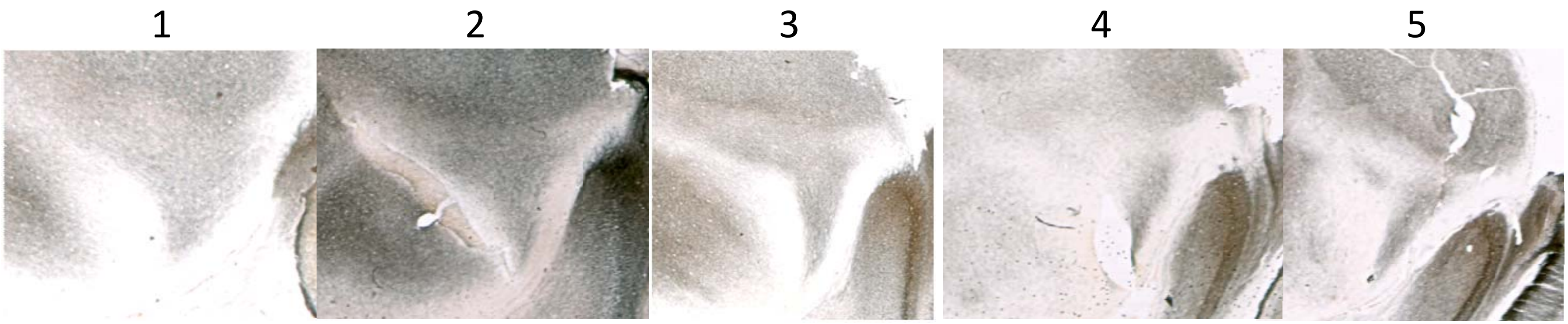

Figure 7. Example sections illustrating the scale used to evaluate the distinctiveness of area proto-TP from V1 and the area in-between. Scale: 1- uniform; 2 – hint of distinctness of proto-TP; 3 – TP is well-defined, but the area in-between it and V1 is still visibly stained; 4 – proto-TP is well defined, and the adjacent area does not show much staining, 5 – proto-TP appears distinct with the addition of a small area located anterior to it.

Figure 8. Example sections illustrating the scale used to evaluate the compartmentalization of area V1. No completely uniform section was found. Scale: 1 – V1 completely uniform, 2 – V1 with a hint of compartmentalization, 3 – V1 with a clear dark lateral edge, 4 – V1 with a dark lateral edge and a lighter area in the center of V1, 5 – V1 with abnormal compartmentalization such as dark staining on the medial edge.

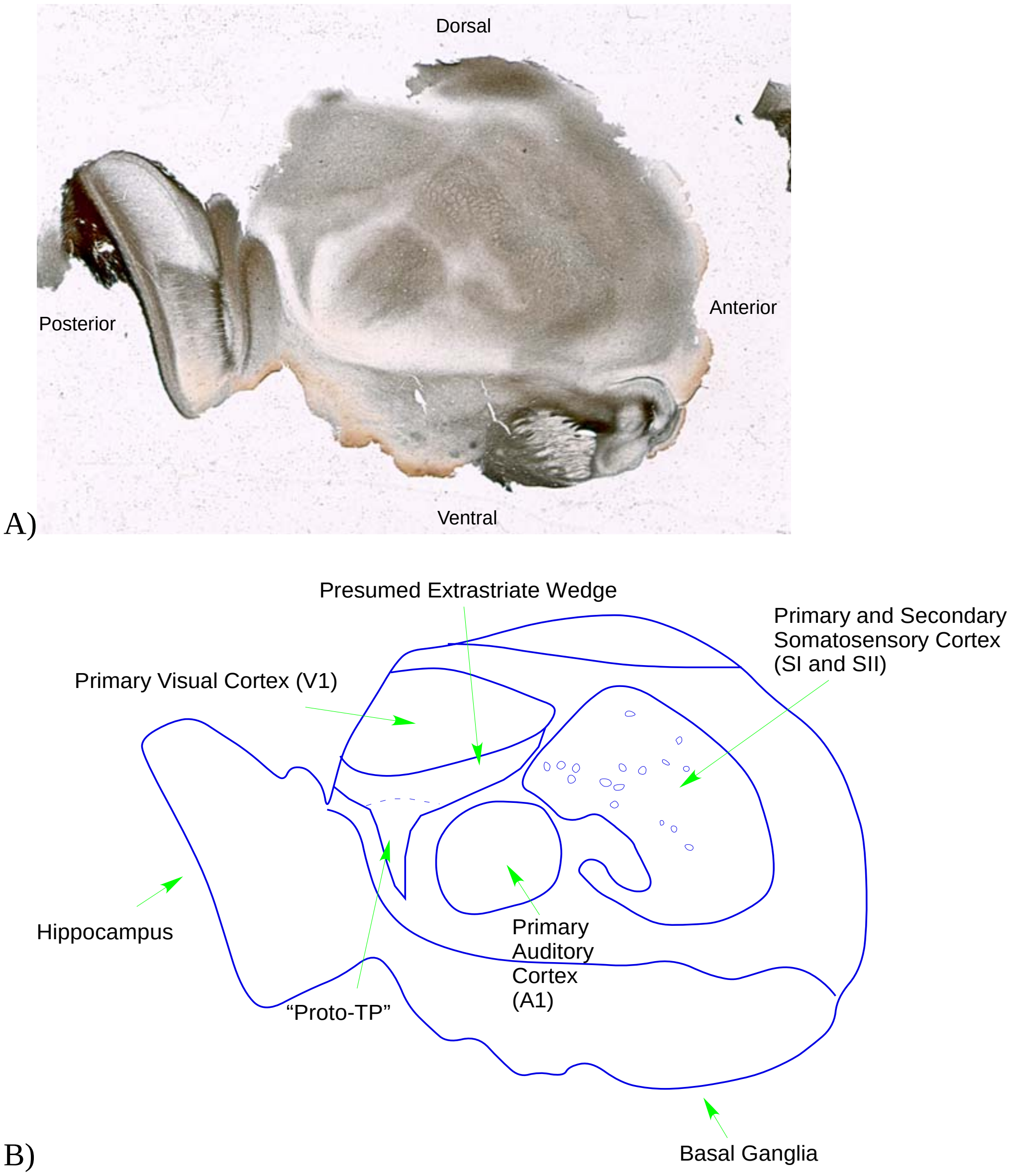

Figure 9. A representative flatmount section of gerbil cortex. Right hemisphere. A) Scan of the myelin-stained flatmount. This example is relatively complete, with slight tearing along the edges of cortex. It is shown because it illustrates the location of all relevant areas. B) An outline of the same section, with specific areas identified.

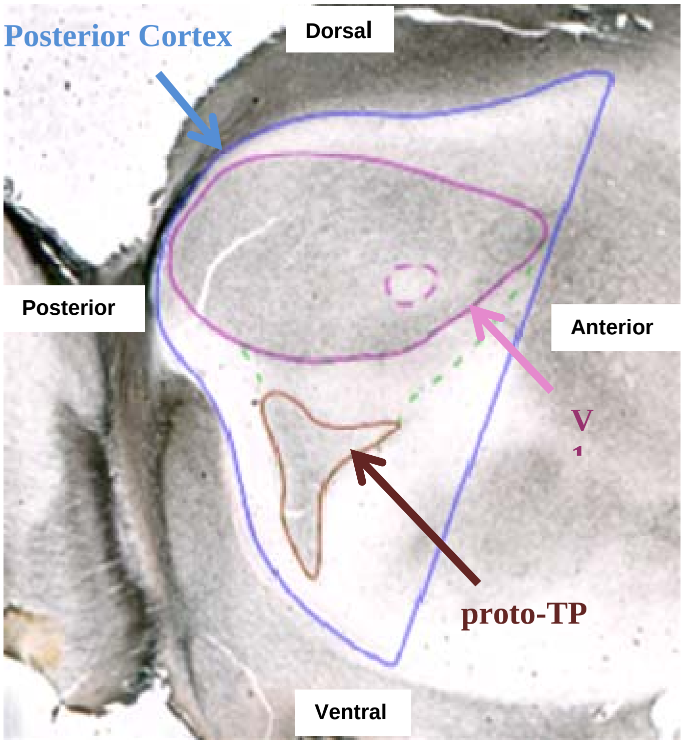

Figure 10. An example section with outlines used to quantify the areal extent of visual areas. Areal measurements of V1 and TP were expressed as a percentage of the total area of posterior cortex, which is thought to include visual cortex as well as polysensory areas. A light zone at the center of V1, thought to represent the optic-nerve head, is tentatively outlined, as well as the potential edge of extrastriate cortex.

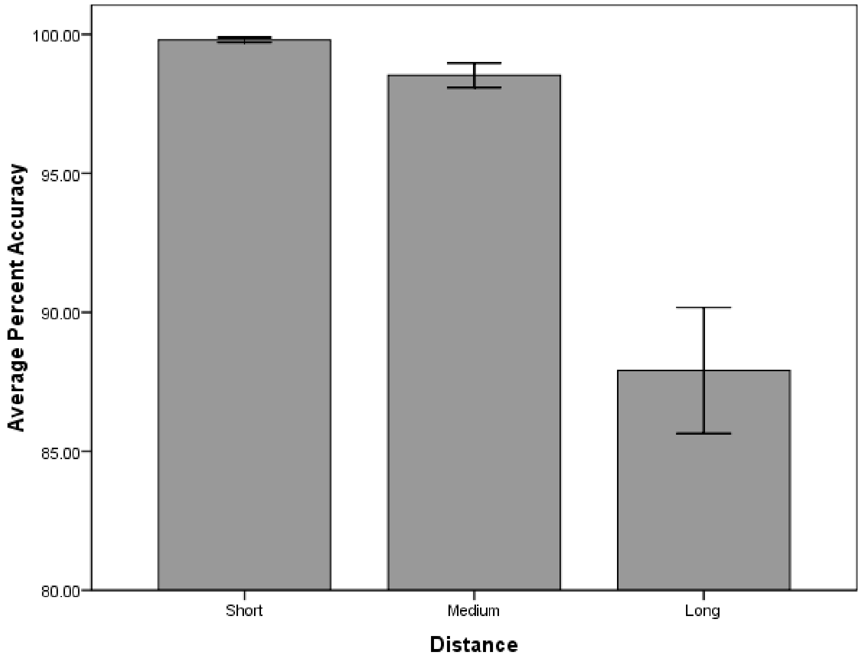

Figure 11: Jumping stand accuracy as a function of distance. Average percent accuracy (collapsed across light level) decreases with increasing distance $\chi^2(2, N = 12) = 19.3$, $p < .001$. A nonparametric Friedman test was performed as the data violated the assumption of equal variances. Note: From here on, error bars represent 1 standard error of the mean.

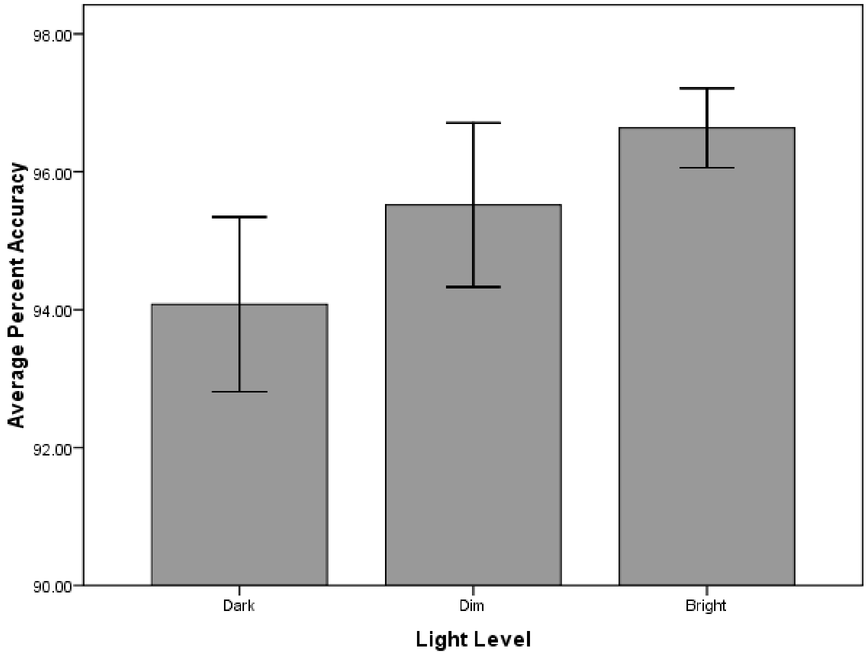

Figure 12. Jumping stand accuracy across light levels. There is a within-subjects linear trend for average percent accuracy (collapsed across distance) to increase with increasing light level, $F(1,11) = 6.849$, $p < .05$, as revealed by a repeated measures ANOVA.

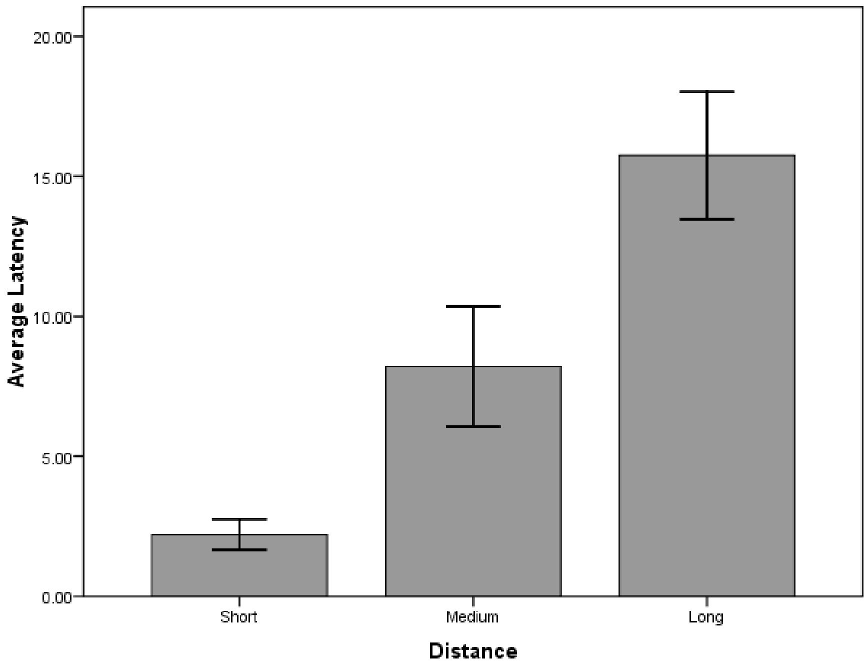

Figure 13. Jumping stand latency as a function of distance. There was a main effect of increased latency with increasing distance, F(2, 26) = 35.24, p<.001, as determined by a repeated measures ANOVA.

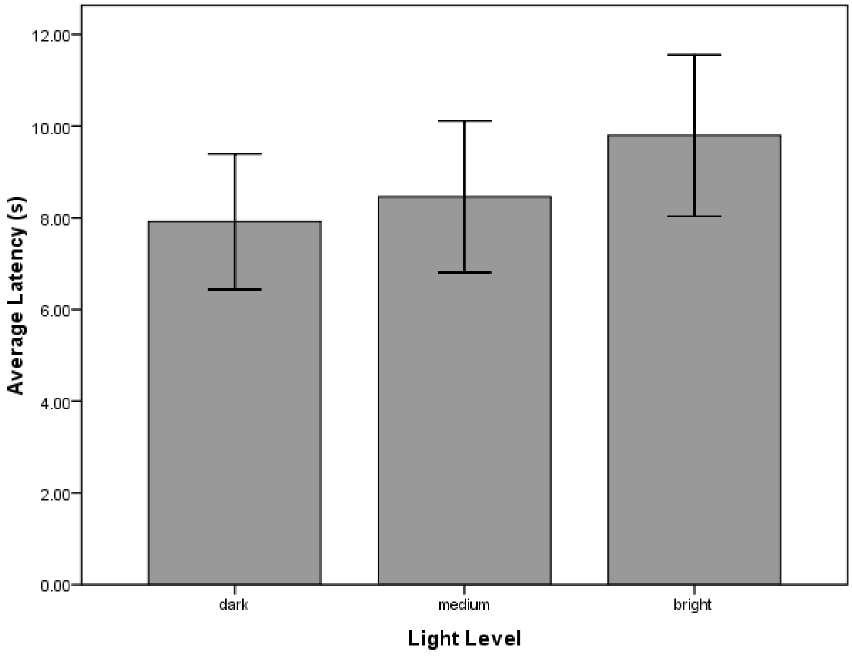

Figure 14. Jumping stand latency across light level. There was a significant main effect of increased latency with increasing light level, F(2, 26) = 3.611, p<.05, as determined by a repeated measures ANOVA.

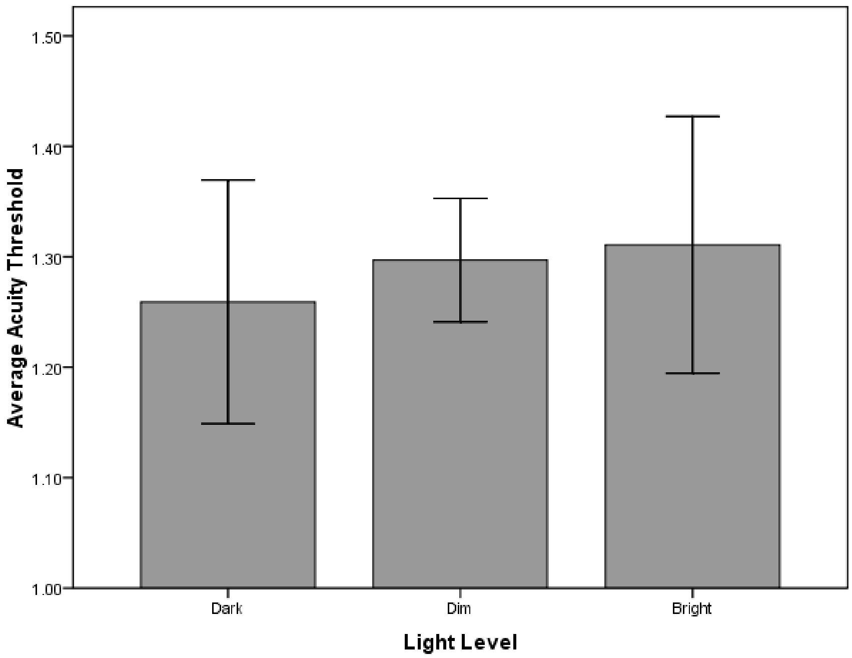

Figure 15. Acuity across light level. There was no significant difference in acuity across light level.

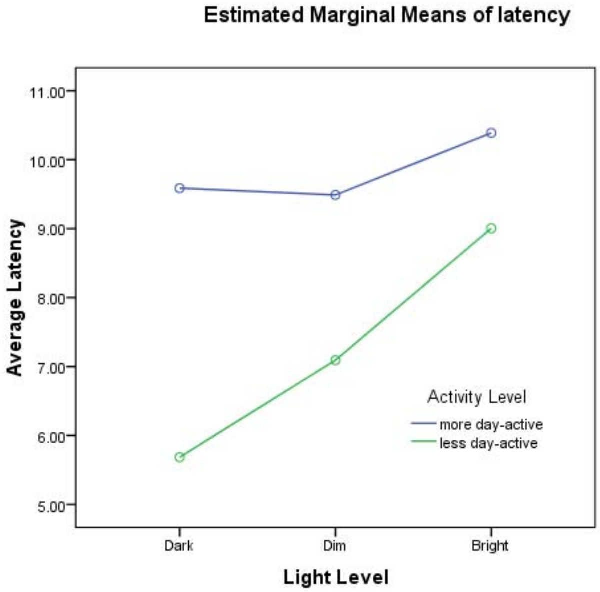

Figure 16: Interaction of latencies across light levels and activity level. A significant linear interaction between latency at the different light levels and activity level, F(1,12) = 3.4, p < .1.

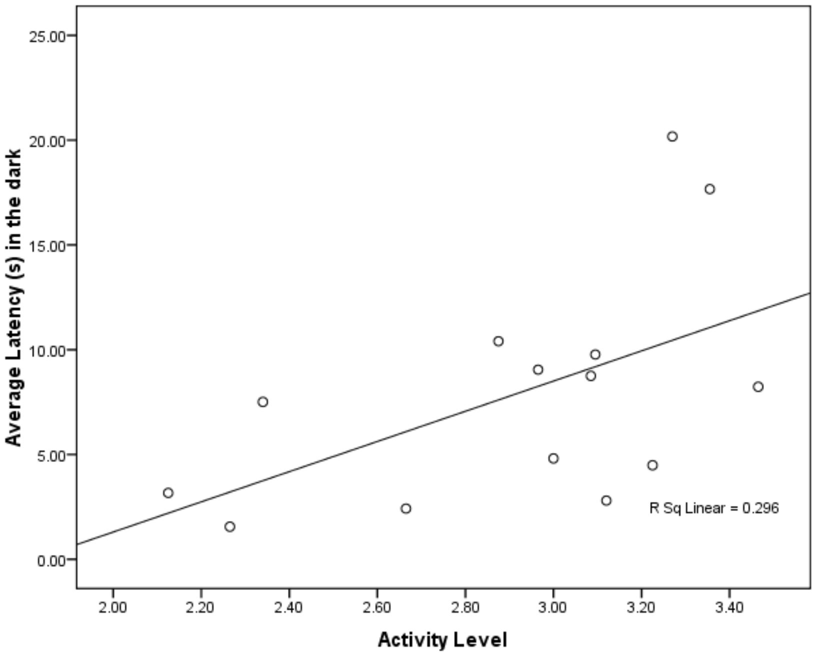

Figure 17. Correlation between activity level and latency in the dark. Average latency in the dark is higher for more active gerbils. Pearson's r (12) = .544, p<.05.

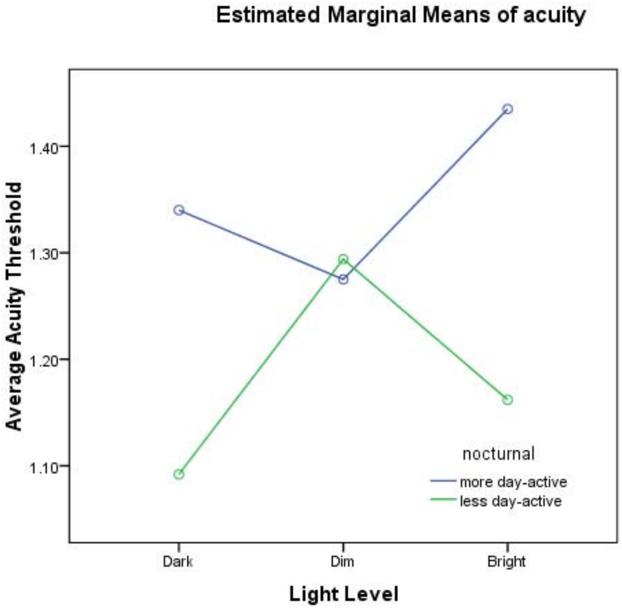

Figure 18: There is a quadratic interaction between acuity at different light levels and activity level. within-subjects contrasts revealed a significant quadratic interaction between acuity at different light levels and activity level, F (1,9) = 6.255, p < .05.

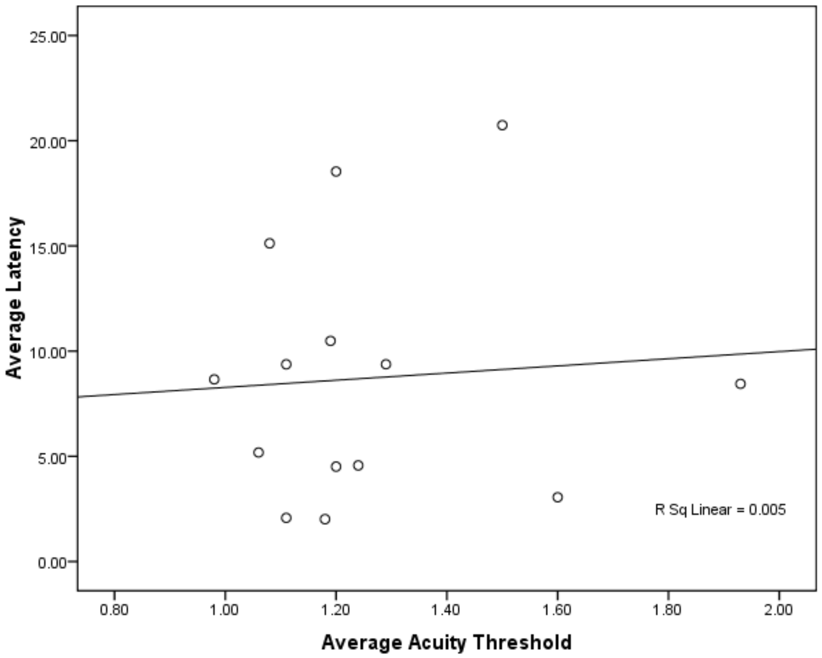

Figure 19. Correlation between average acuity threshold and average latency. Average acuity thresholds were not correlated with latency.

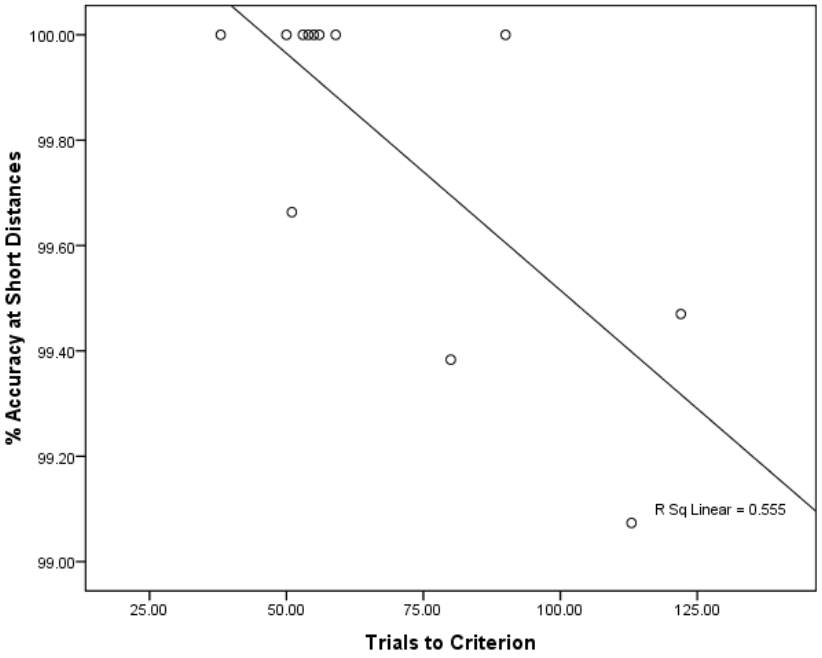

Figure 20: Correlation between trials to criterion and percent accuracy at short distances. There was a negative correlation between Trials to Criterion and accuracy at short distances r (12)= -.745, p < .01.

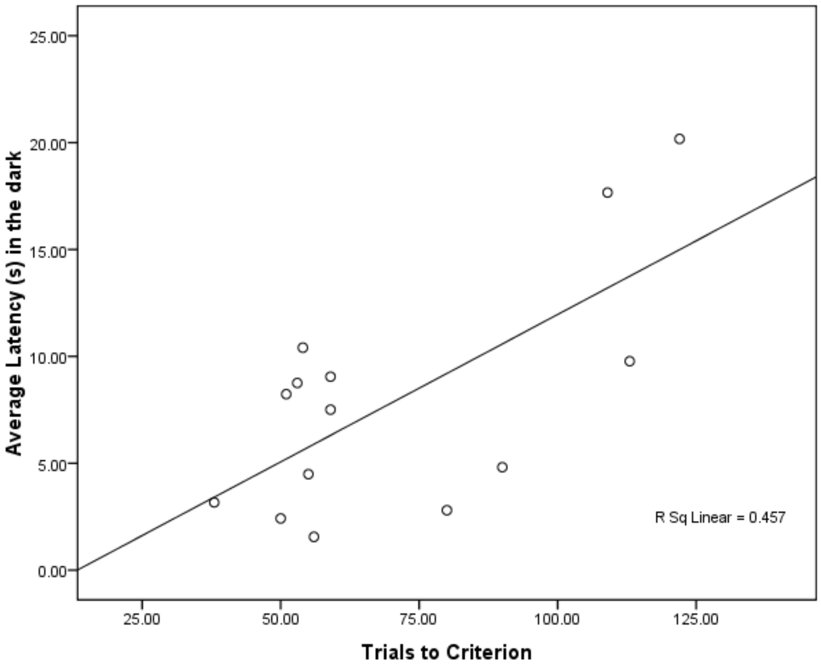

Figure 21: Correlation between trials to criterion and average latency in the dark. There was a positive correlation between Trials to Criterion and average latency in the dark r (12) = .676, p < .01.

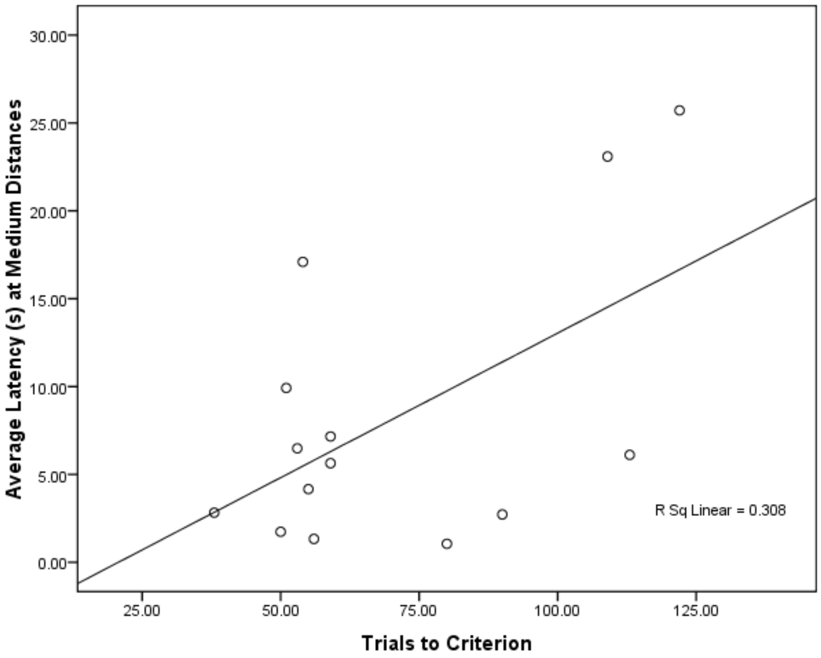

Figure 22: Correlation between trials to criterion and average latency at medium distances. There was a positive correlation between trials to criterion and average latency at the medium jumping distances r (12) = .555, p < .05

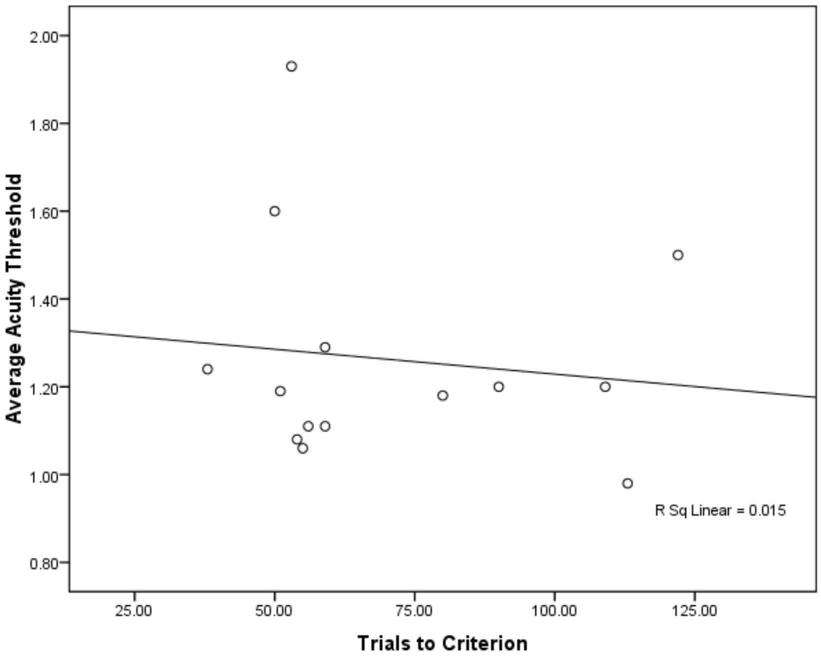

Figure 23: Correlation between trials to criterion and average acuity thresholds. Trials to criterion were not correlated with average acuity thresholds.

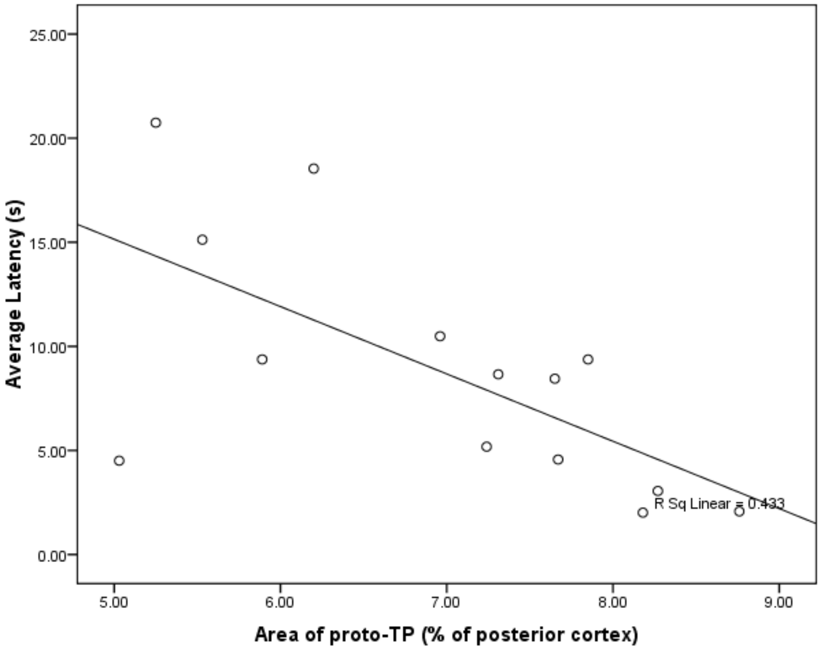

Figure 24: Correlation between normalized area of proto-TP and average latency. the normalized relative size of proto-TP was significantly negatively correlated with average latency on the jumping stand, collapsed across light levels and distances r (12) = -.658, p < .05.

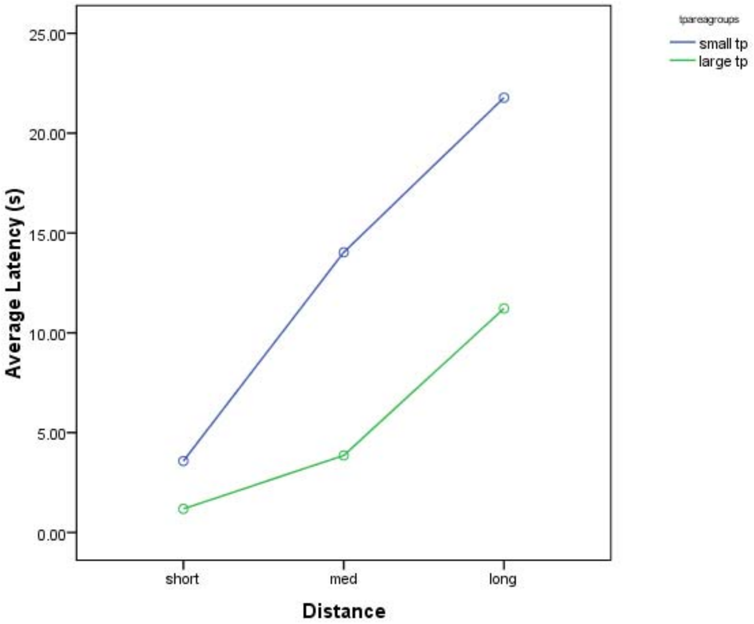

Figure 25: Interaction between latency across distance and the size of proto-TP. There was also a significant main effect for the interaction between jumping latencies across distances and the normalized relative size of proto-TP, as revealed by a repeated measures ANOVA, F(2, 24) = 5.29, p < .05.

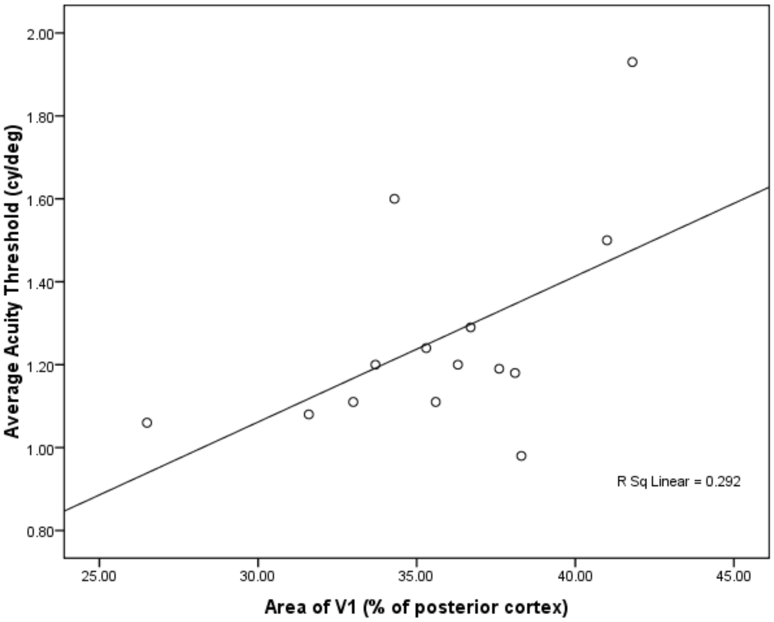

Figure 26: Correlation between the normalized area of V1 and average acuity thresholds. the proportionate area of V1 was close to being significantly correlated with acuity threshold (collapsed across light levels) when only measures of the right hemisphere were used r (12) = .522, p = .055, and reached significance when the left hemisphere was averaged into the measurement r (12) = .54, p < .05.

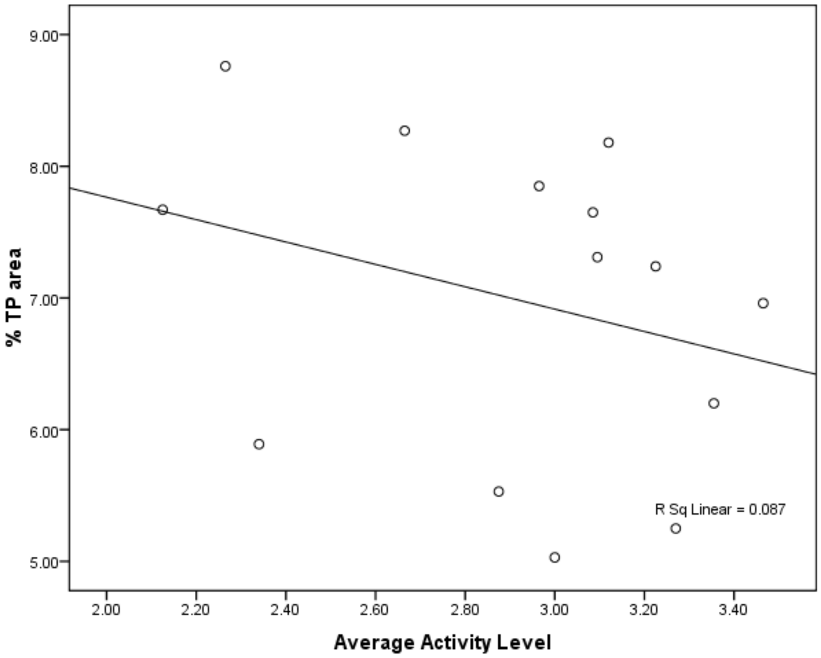

Figure 27. Correlation between average activity level and normalized size of proto-TP. Average activity level was not correlated with the area of proto-TP.

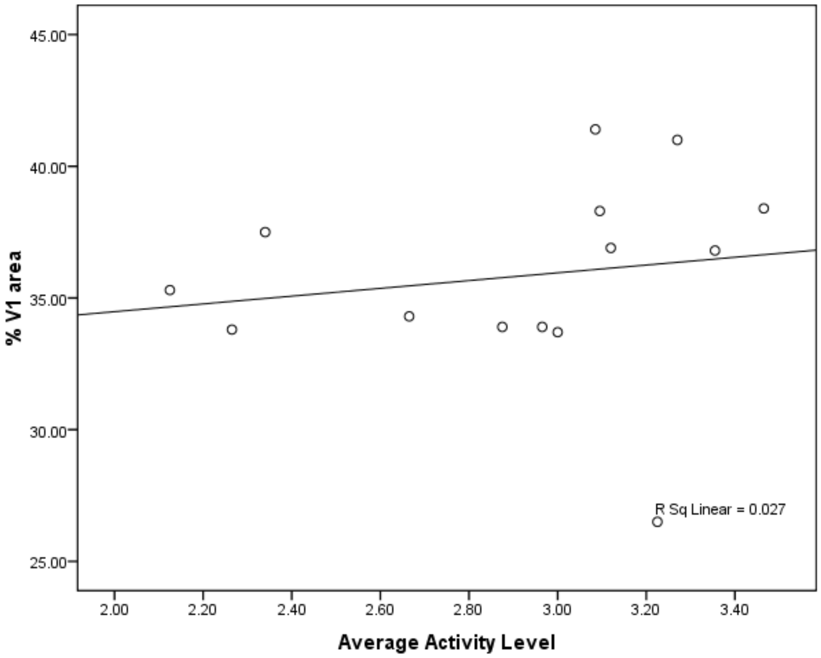

Figure 28. Correlation between average activity level and normalized size of V1. Average activity level was not correlated with V1 area.