

Representation of Three-Dimensional Space in Primate Visual Cortex

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Abstract

Primates can accurately judge the size of objects from a wide range of viewing distances. Size perception depends on both the size of the image projected onto the retina as well as the perceived distance to the object. Size constancy is the ability to compensate for changes in retinal image size as viewing distance changes. This work describes experiments that examine the neural basis of size constancy in the primate visual system.

Viewing distance and gaze angle modulate neural responses in dorsal cortical areas (the “where” pathway, leading to parietal cortex); these areas are known to be involved in visuospatial coding. However, lesions to dorsal areas do not disrupt size constancy judgments in monkeys, suggesting that the visuospatial information utilized for size constancy is encoded in other areas. Area V4 is at an intermediate level in the ventral visual cortical pathway (the “what” pathway, leading to inferotemporal cortex) and contains a large proportion of size-selective neurons. We were thus interested in examining the representation of size and distance in primate area V4.

We found that over half of the neurons recorded from areas V1, V2, and V4 showed significant changes in response with viewing distance and observed that distance interacts with retinal size information by modulating the gain of the neural response. Thus, object distance is represented in ventral cortical visual areas suggesting that spatial processing is not confined to dorsal cortical areas. Another focus was to explore the influence of various cues to distance. We measured size and distance tuning under restricted viewing conditions that removed or reduced cues to distance. Results from these experiments indicate that a combination of retinal and extraretinal cues contribute to distance modulation in V1, V2 and V4.

The encoding of both retinal size and distance information by ventral cortical neurons is consistent with these neurons serving as a basis for size constancy. We speculate that like retinotopic maps, an abstract representation of three-dimensional space is a characteristic feature of all visual cortical areas.

Contents

Acknowledgements	iii
Abstract	iv
1 Introduction	1
1.1 Historical Background	2
1.2 Behavioral Studies	3
1.2.1 Visual Cues for Distance and Size Constancy	4
1.2.2 Non-Visual Cues For Distance	9
1.3 Electrophysiology and Neuroanatomical Background Work	12
1.3.1 Brain Lesion Studies	12
1.3.2 Representation of Object Size in Ventral Visual Cortical Areas	14
1.3.3 Physiology of Dorsal Visual Cortical Areas	15
1.3.4 Representation of Distance in Primary Visual Cortex	16
1.3.5 Parallel Systems for Distance Perception	17
1.4 Neural Representation of the Third Dimension	19
2 Representation of Distance and Size in V1, V2 and V4	20
2.1 Introduction	20
2.2 Methods	23
2.2.1 General Methods	23
2.2.2 Training and Surgery	23
2.2.3 Recording	24
2.2.4 Visual Stimuli	24
2.2.5 Data Analysis	27
2.3 Results	30
2.3.1 Qualitative Results	31

2.3.2	Quantitative Results	33
2.3.3	Distance Effects	34
2.3.4	Population Analysis: Distance Modulation Index	34
2.3.5	Retinal Size Tuning	37
2.3.6	Combination of Effects.	38
2.3.7	Interactions Between Distance and Retinal Size	39
2.3.8	Restricted Viewing Experiments	41
2.4	Discussion	47
2.4.1	Distance Modulation in V1/V2 and V4	47
2.4.2	Restricted View Experiments: Multiple Cues for Distance . .	50
2.4.3	Possible Mechanisms For Size Constancy	55
2.4.4	Conclusions	56
3	Conclusions	62
3.1	Cortical Visual Processing Mechanisms	63
3.2	Development of Size Constancy	69
3.3	Future Studies and Limitations	71
3.4	Specific Contributions	72
A	Cortical Cytochrome Oxidase Topography in Two Lemur Species	73
	Abstract	74
A.1	Introduction	75
A.2	Methods	76
A.2.1	Histology and Flattening	76
A.2.2	Reconstruction of Cytochrome Oxidase Topography	77
A.3	Results	77
A.4	Discussion	79

List of Figures

1.1	Retinal image size depends on the actual size of the object as well as the viewing distance. Size constancy is the perception that apparent size remains constant over a wide range of viewing distances.	4
1.2	Perspective cues for depth. The three cylinders have the same actual dimensions, but they appear to be different sizes.	7
1.3	Ebbinghaus illusion. Central disc is the same absolute size for both.	8
1.4	Ponzo illusion. Upper and lower horizontal lines have the same physical dimensions.	9
1.5	Muller-Lyer illusion.	10
1.6	Relationship between viewing distance and accommodative power. Note that the difference in lens power for shifting fixation from 20 centimeters (the approximate near point for an adult human observer) to one meter is 5 diopters while shifting fixation from 1 meter to 5 meters results in a change of only 0.8 diopters.	11
1.7	The “what” and the “where” pathways, proposed by Ungerleider and Mishkin [1982]. Area V4 lies at an intermediate stage of visual processing in the ventral or “what” pathway that leads to IT cortex. Posterior parietal (PP) cortex and other dorsal areas are thought to be involved with spatial or “where” processing.	18
2.1	General experimental approach. We measured responses to systematic changes in retinal image size at several viewing distances. Stimuli were scaled to keep retinal image size constant with changing viewing distance.	22

2.2	Distance viewing setup. The monkey was trained to fixate a spot on a computer monitor which could be placed at three to five different viewing distances.	24
2.3	Retinal size tuning at five viewing distances.	26
2.4	Trial structure. Responses during fixation only and during stimulus presentation over the receptive field of the neuron were measured each trial, and mean spike rate for both portions of the trial were calculated. The monkey was required to maintain fixation throughout the duration of the entire trial.	27
2.5	Distance modulation in two different V4 neurons. Responses during fixation only are also modulated by viewing distance (squares to the right of each tuning curve). A. Nearness cell. Cell responds in a monotonic fashion to increasing proximity. B. Farness cell.	30
2.6	Peaked V4 cell. Example of a neuron recorded from V4 that exhibited non-monotonic distance modulation. Most non-monotonic cells were peaked, but a few cells with a notched response profile were also observed.	31
2.7	Distance invariant V4 cell. Example of a neuron that does not exhibit significant modulation in mean firing rate with changing distance.	32
2.8	Tuned inhibitory neuron. Stimuli presented within the receptive field suppressed this neuron's firing rate compared to responses to fixation. Horizontal dotted lines indicates mean firing rate during fixation only in the absence of stimuli in the receptive field.	33
2.9	Summary results of ANOVA analysis. Percentage of cells that had significant ($p < .01$) distance, size and interaction effects. Results from V1/V2 and V4 are shown separately. Significant distance modulation for fixation only is shown on the far right.	34

- 2.10 Distance Modulation Index (population analysis). **A.** Distribution of DMI values for cells with monotonic distance response changes recorded from V1/V2. Cells that had significant distance modulation effects (ANOVA $p < .01$) are shown in black. **B.** DMI distribution for V4, with cell that had significant effects shown in gray. **C.** Classification of cells that had significant distance modulation. Nearness cells were the most common type in both V1/V2 and V4. Farness cells were more commonly observed in V4 than in V1. . . . 36
- 2.11 Distance Modulation Index for fixation only response (population analysis). **A.** Distribution of DMI values in V1. Cells with significant ANOVA distance modulation are shown in black. **B.** V4 results. Significant cells are shown in gray. A much larger proportion of V4 cells prefer increasing fixation distance. **C.** Classification of cells with significant distance modulation for fixation only. . . . 37
- 2.12 Combined effects. Proportions of cells significantly (ANOVA, $p < 0.01$) modulated for both distance and size, and both distance and fixation. The arrow indicates expected values for independence of the effects. . . . 39
- 2.13 Distribution of Shift Index values for **A.** V1/V2 and **B.** V4. Shift Index values for cells with significant ANOVA interaction effects are overlaid as filled bars. Negative values indicate shifts in size tuning preference with distance in the direction of size constancy. Mean values for both V1/V2 and V4 are shown by the triangles and do not differ significantly from zero. . . . 41

- 2.14 Sharpness Index for **A.** V1/V2 and **B.** V4. The Sharpness Index did not differ significantly from zero in either case. Positive values indicate that the cell is more sharply tuned to retinal size at the preferred distance compared with the distance that elicited the least responses. Negative values indicate a broadening of size tuning. Sharpness Index values for cells with significant ANOVA interaction effects are overlaid as filled bars. 42
- 2.15 Percentages of cells that maintain significant distance modulation under monocular and binocular restricted viewing conditions. A smaller proportion of cells in V4 maintain distance modulation under restricted viewing conditions, suggesting that cues related to the surrounding visual context have a greater influence in V4 than in V1. 44
- 2.16 Overall results from ANOVA for cells recorded during monocular restricted viewing ($n = 45$). A smaller percentage of the cells in both V1/V2 and V4 were modulated by viewing distance. Size tuning was relatively unaffected. 45
- 2.17 Example neurons recorded from area V1/V2. **A.** Nearness cell. This particular cell had a low overall spike rate, but distance effects were significant. **B.** Farness. **C.** Distance Invariant. 58
- 2.18 Examples of context independent cells. For these cells, restricted viewing conditions are sufficient for significant distance modulation. **A,B.** V1 cell that maintained significant distance modulation under both binocular full and restricted viewing conditions. **C,D.** V4 cell that exhibited distance modulation under both binocular full field and monocular restricted viewing conditions. 59

2.19	Context dependent V4 cell. A. Distance modulation under binocular full field conditions. B. Distance modulation was abolished by binocular restricted viewing. C. Responses at the preferred distance (45 cm) under monocular full field conditions were not attenuated compared to binocular full field, indicating that binocular disparity cues are not necessary for distance modulation. D. Results from frame test. Cell was measured at 45cm with a cardboard frame that matched the retinal dimensions of the monitor frame at 180cm. The frame alone did not suppress the neurons response.	60
2.20	Fraction gain for different viewing conditions. A. Binocular Free. B. Monocular Restricted. C. Binocular Restricted. D. Mean fractional gain for each population. The star indicates significant effects ($p < .01$, t-test).	61
A.1	Photomicrograph of flatmounted section through superficial layers of <i>Eulemur</i> visual cortex. Staining for CO reveals many characteristic features of cortical anatomy including a system of CO blobs in primay visual cortex.	81
A.2	Cebus monkey cytochrome oxidase stained flatmount. Anthropoid visual cortex is characterized by a system of small, punctate CO blobs in V1 and clear alternating stripes in V2. CO blobs in V1 of the Cebus monkey are much smaller than those identified in either Lemur species. The functional significance of blobs size is not well understood.	82
A.3	Lemur V2.	83
A.4	Microcebus CO blobs.	84
A.5	Summary of reconstruction.	85

Chapter 1 Introduction

The natural world for primates is three-dimensional. One of the primary functions of the primate visual system is to efficiently process the two-dimensional images from the retina into three-dimensional perceptions. The goal of this dissertation is to make significant and unique contributions to our understanding of the neural representation of the three-dimensional world in the primate neocortex.

The perception of distance and object size is intimately linked with three-dimensional perception. Objects have physical size, but the dimensions projected onto the retina frequently change as function of distance and viewing position. Size constancy is the ability to compensate for changes in the projected retinal dimensions, so that the apparent size of the object does not change over a wide range of viewing distances. In behavioral experiments, chimpanzees, macaque monkeys and cats have demonstrated visual size constancy [Davis et al., 1964; Freeman, 1968; Gunter, 1951; Kohler, 1915; Locke, 1937]. It is likely that all animals with good distance vision have size constancy, since perception of object size in three-dimensional space is of critical importance to an animal's survival. Size constancy has also been extensively studied in human subjects. These behavioral studies have determined that many cues for distance are utilized in size constancy including linear perspective, pictorial cues, relative proportions and oculomotor cues. Despite extensive behavioral study in animals and humans, relatively little work has been done to examine the underlying neural mechanisms of size constancy.

The study of size constancy provides an excellent framework for approaching the problem three-dimensional perception, especially because the phenomenon is robust and animals have the capacity to make size constancy judgments. Therefore, much of the following work will emphasize the mechanisms of size perception and size constancy as a means of understanding three-dimensional perceptual mechanisms.

1.1 Historical Background

As early as 300 B.C., Euclid discussed the relationship between the perception of the size of objects and the retinal image size they subtended. In his *Optics*, Euclid stated in his fourth postulate (taken from Lindberg [1976]):

“Things seen under a larger angle appear larger, those under a smaller angle appear smaller, and those under equal angles appear equal.”

Euclid did not take into account the role of distance in size perception in his fourth postulate. Later, in the 10th century Ibn al-Haytham (Alhazen) developed the concept of geometrical perspective in which size constancy is an implicit feature. The phenomenon of size constancy has been recognized explicitly since at least the 13th century when John Pecham wrote in his *Perspectiva Communis* (taken from Lindberg [1970]):

“As experience proves, the faculty that apprehends size considers the magnitude of distance from the observer and not only the (visual) angle.”

The geometrical concepts of perspective developed by Ibn al-Haytham and his followers profoundly influenced the representation of size and depth by the great artists of the Renaissance such as Piero della Francesca and Leonardo da Vinci [Kemp, 1990].

In the 17th century Descartes developed a conception of size constancy that accounted for some non-visual contributions to distance perception, including cognitive cues and oculomotor cues. Descartes wrote on the discrimination of the size of objects (taken from Descartes [1985]):

“We judge their size by the knowledge or opinion that we have of their distance, compared with the size of the images they imprint on the back of the eye - and not simply by the size of these images... The

shape of the eye undergoes hardly any perceptible variation when the object is more than four or five feet away... And if one is looking at an object at all far away, there is also hardly any variation in the angles between the lines joining the two eyes and the lines from the eyes to the object.”

Descartes’ “shape of the eye” and the “angles between the lines joining the two eyes” probably refer to binocular vergence and accommodative changes that accompany focusing at different distances. Descartes accurately assessed that these oculomotor cues have a greater magnitude at close viewing distances than at far distance. A prediction from the anatomy and geometry of binocular vision that Descartes observed is that oculomotor cues exert greater influence on distance perception at close viewing distances than at far distances. Behavioral studies, beginning in the 1940’s, began to look explicitly at the influence of distance cues on size constancy and size perception.

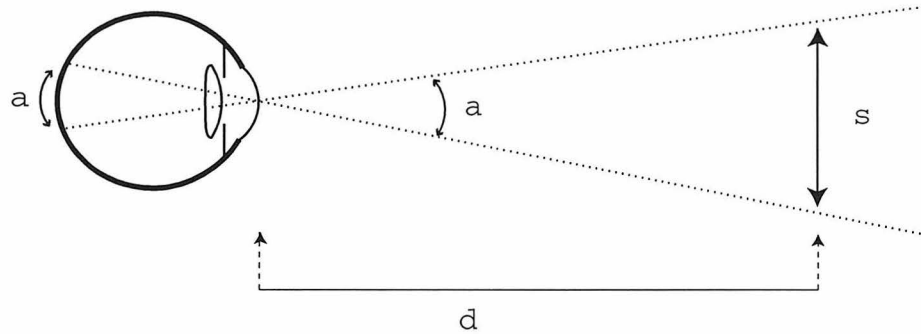
1.2 Behavioral Studies

Extensive psychological and behavioral studies have examined the perception of distance and size in humans and animals. These behavioral studies have shown that the distance cues, both visual and non-visual, are used by the visual system for size constancy. While a behavioral approach alone cannot answer deeper questions about the neural mechanisms that underlie size constancy, behavioral study can explore and compare the relative effects of the various external signals and cues that the brain is utilizing for size perception.

Apparent Size and Retinal Image Size

It is important to understand the distinction between the actual physical size of an object, the object’s apparent size, and the retinal dimensions the object projects onto the retina. This relationship is illustrated in Figure 1.1. As an object moves

away from a viewer, the projected retinal dimensions are diminished. It is possible to compute the size of the retinal image if the size of the object and the viewing distance are known (Figure 1.1). Size constancy refers to the perception that the apparent size remains constant as viewing distance and retinal image size changes.



$$\tan a = s / d$$

Figure 1.1: Retinal image size depends on the actual size of the object as well as the viewing distance. Size constancy is the perception that apparent size remains constant over a wide range of viewing distances.

1.2.1 Visual Cues for Distance and Size Constancy

Visual Cues For Size Constancy

Holway and Boring [1941] performed classic experiments that demonstrated that visual cues for distance are involved in size constancy judgments. They examined apparent size perception while systematically removing distance cues. To measure apparent size, subjects viewed two discs in an L-shaped hallway. One disk was movable, and was placed some distance down one branch of the hallway. The other disk was fixed in location and was placed down the other branch of the hallway; the size of the fixed disk was adjustable by the subjects. To view both disks, subjects had to turn their heads 90 degrees to look at one disk or the other. The task was to match the size of the two disks by adjusting the closer to match the farther. The movable disk was kept at a constant retinal size for each of the distances; thus, for

the distances tested (10-120 feet), the absolute size of the movable disk increased linearly with increasing distance. Under normal viewing conditions, subjects were able to make quite accurate judgments of absolute size of the movable disk at different viewing distances. Under restricted viewing conditions, where subjects viewed the distal stimulus through apertures with the room lights off, judgment of apparent size more closely matched the retinal image size. Holway and Boring concluded that visual contextual cues for distance are crucial for size constancy.

Emmert's Law

Holway and Boring's experiments elegantly quantified many of the observations made by psychologists in the late 19th century. Emmert (1881) observed that the apparent size of a retinal after-image is dependent on the apparent distance. An after-image viewed on a far wall looks larger than the same after-image viewed on a sheet of paper at arm's length. Emmert's law states that images of the same retinal size can lead to different apparent size depending on the perceived distance. Emmert's law is closely related to the law of size constancy (which can be phrased as: retinal images of differing sizes can lead to the perception of the same apparent size depending on apparent distance). Holway and Boring kept retinal image size constant by increasing the size of the distant stimuli with increasing distance. Retinal after-images, by definition, remain a constant retinal size when viewed against backgrounds of different distances. Both experiments illustrate size perception is closely linked with the perception of distance.

The Moon Illusion

The moon illusion is probably the most striking illustration of Emmert's law. It has been observed through the ages that the moon looks much larger when it is over the horizon than when it is directly overhead, even though the retinal image size projected by the moon does not change significantly with position above the horizon. Many have speculated that this effect has a physical basis, perhaps in atmospheric magnification. Kaufman and Rock [1962] demonstrated that the moon

illusion is entirely perceptual, and arises as a consequence of distorted distance perception. The horizon is perceived to be a far greater distance than the sky directly above; because the moon seems farther away at the horizon yet retains the same retinal image size, the apparent size is larger. The moon illusion illustrates that perceived distance can have a profound influence on the perception of size. This influence is so strong that it overrides cognitive cues; even when observers know that the moon remains a constant retinal image size, the illusion remains and does not diminish in effectiveness.

Pictorial and Perspective Cues

Psychologists following Holway and Boring continued to examine the effects of the surrounding visual context and the size of the nearby objects in the visual field on the perception of size and distance.

Linear perspective and pictorial cues can be strong cues for distance and size. An example of the effect of perspective cues on apparent size perception is demonstrated by Figure 1.2, adapted from Gibson [1966], in which the three cylinders shown receding into the distance have the same physical size and retinal subtense. Perspective and occlusion cues create a strong distance percept; the cylinders that appear to be more distant appear to be much larger.

Visual illusions illustrate the effects of the surrounding visual context on size perception. A well studied example is the Ebbinghaus illusion (sometimes referred to as the “Tichner illusion” in the literature, Figure 1.3) in which the size of objects in the surround influences the apparent size of a central object. The apparent size of two identical disks can be changed simply by the relative sizes of the surrounding objects. A disk surrounded by larger disks appears smaller and the same disk surrounded by small disks appears larger.

Coren and colleagues [Coren, 1971; Coren and Miller, 1974; Coren and Enns, 1993; Enns and Coren, 1995] showed that the magnitude of the Ebbinghaus illusion was dependent on the similarity in the shape of the objects in the center and the surround. When the inducing objects in the surround were less similar to the center

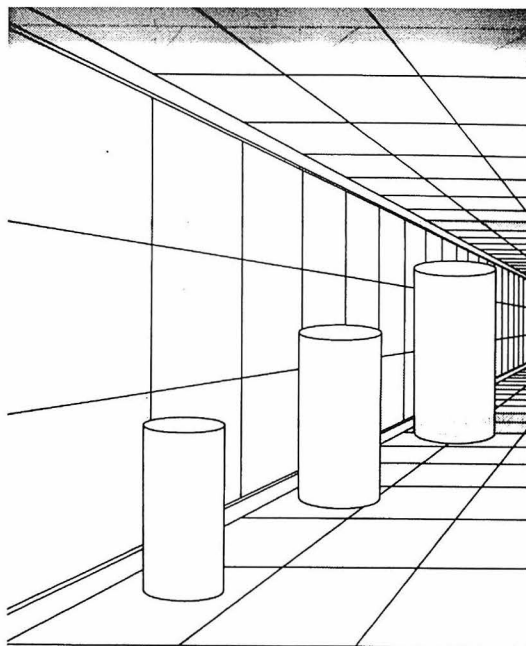


Figure 1.2: Perspective cues for depth. The three cylinders have the same actual dimensions, but they appear to be different sizes.

object, the magnitude of the effect was proportionally reduced.

Additionally, Coren [1971] showed that changes in the perceived size of the central figure in the Ebbinghaus illusion could be induced by presentation of the surrounding objects in stereoscopic depth. Changes in binocular disparity make the surrounding objects appear larger or smaller than the central figure, even though the retinal dimensions are the same. These results showed that size perception is not only dependent on proportional size and involves comparisons of like objects, but also that perceived depth can influence the effects of the surrounding visual context.

Gregory [1963] suggested many visual illusions of apparent size distortion arise as a consequence of inappropriate size constancy scaling. Gregory suggested that two-dimensional line drawings or simple figures are interpreted as three-dimensional scenes that depict depth through perspective cues. The Ponzo illusion, shown in Figure 1.4, is an example of inappropriate size constancy scaling. Most viewers report that the upper horizontal line appears longer, even though the two lines are

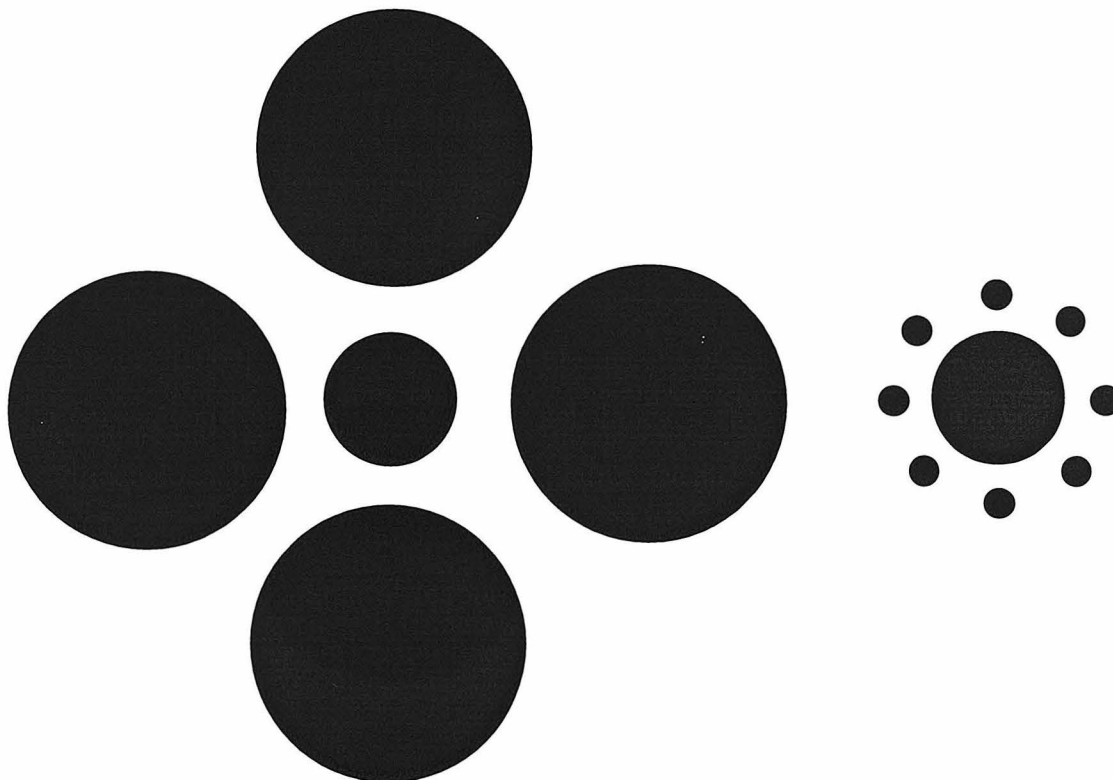


Figure 1.3: Ebbinghaus illusion. Central disc is the same absolute size for both.

equal in physical size. Gregory's theory suggests that our visual system interprets the converging lines as perspective cues for distance and the upper horizontal line has greater apparent size because it is interpreted as having greater apparent depth. To illustrate this point, the magnitude of the Ponzo illusion is greatly diminished if the figure is rotated 90 degrees, because the suggestion of depth from the converging lines is diminished.

Another example of inappropriate size constancy scaling is illustrated by the Muller-Lyer illusion (Figure 1.5). The arrow with the outgoing fins (Figure 1.5A) could represent an inside corner, while the opposite arrangement (Figure 1.5B) could represent an outside corner. The inside corner is interpreted as having greater apparent distance, and hence, greater apparent size. Again, the two retinal images sizes projected by the two vertical lines are equivalent.

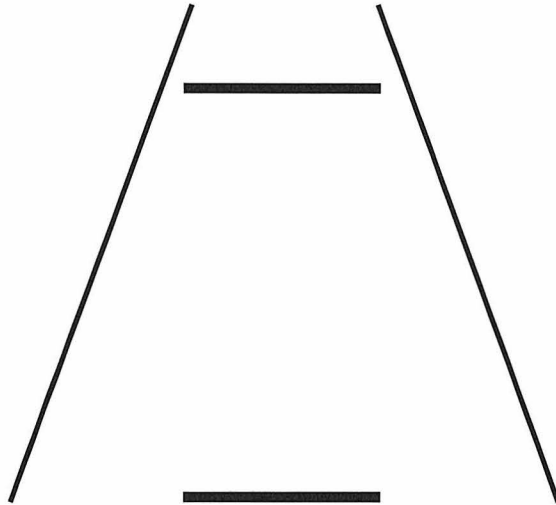


Figure 1.4: Ponzo illusion. Upper and lower horizontal lines have the same physical dimensions.

1.2.2 Non-Visual Cues For Distance

Oculomotor Cues

Oculomotor cues, such as accommodation and vergence, can be quite effective signals for determining distance at close ranges, and are used for size constancy judgments for distances up to about one meter.

The closest distance tested by Holway and Boring [1941] was ten feet away from the subject. Later experiments examined the perception of apparent size and distance operational at closer ranges. Leibowitz and Moore [1966] showed that subjects are able to make good judgments of object size for close distances (up to about one meter) even when stimuli are viewed through binocular apertures that mask the surrounding visual context. For distances greater than one meter under the same viewing conditions, size judgments are based on retinal image size. This result suggests the mechanisms for judging distances of less than one meter (approximately arm's length in humans) are different than the mechanisms operating at farther distances. Thus, when the visual cues for depth are greatly reduced, size constancy is preserved at near distances but fails at greater distances.

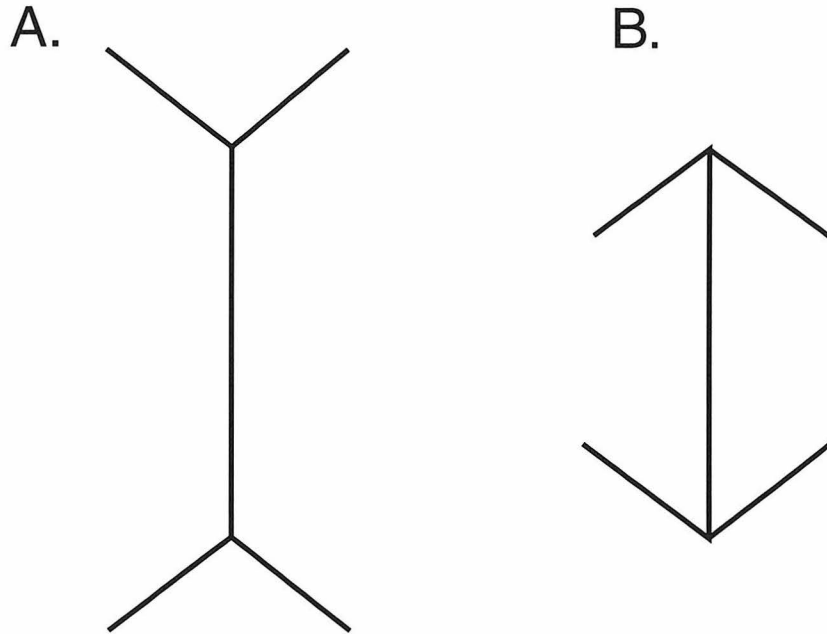


Figure 1.5: Muller-Lyer illusion.

As was briefly discussed earlier, Descartes predicted these results to some degree, when he noted that the magnitude of vergence angles and accommodative power are much greater for close objects than for far. The geometry of binocular vision and the optics of the eye are physically constrained. For example, the difference in lens power for shifting fixation from 20 centimeters (the approximate near point for an adult human observer) to one meter is 5 diopters. On the other hand shifting fixation from 1 meter to 5 meters results in a change of only 0.8 diopters (Figure 1.6).

The primate oculomotor system undergoes three principle changes as fixation distance decreases. 1) The two eyes converge on the fixation point to minimize binocular disparity. 2) The lens of the eye accommodates to minimize blur on the retina. 3) The pupils constrict and depth of field increases ([Fincham, 1957; Semmlow and Heerema, 1979; Mays and Gamlin, 1996]). It has been known for over a century that accommodation and vergence are not independent processes [Maddox, 1893]. Changes in magnitude of either the accommodative power or binocular con-

vergence are accompanied by corresponding changes in the other system. Thus, the two major components of the oculomotor system, vergence and accommodation, must interact and together form a strong cue for distance judgments and size constancy at close distances.

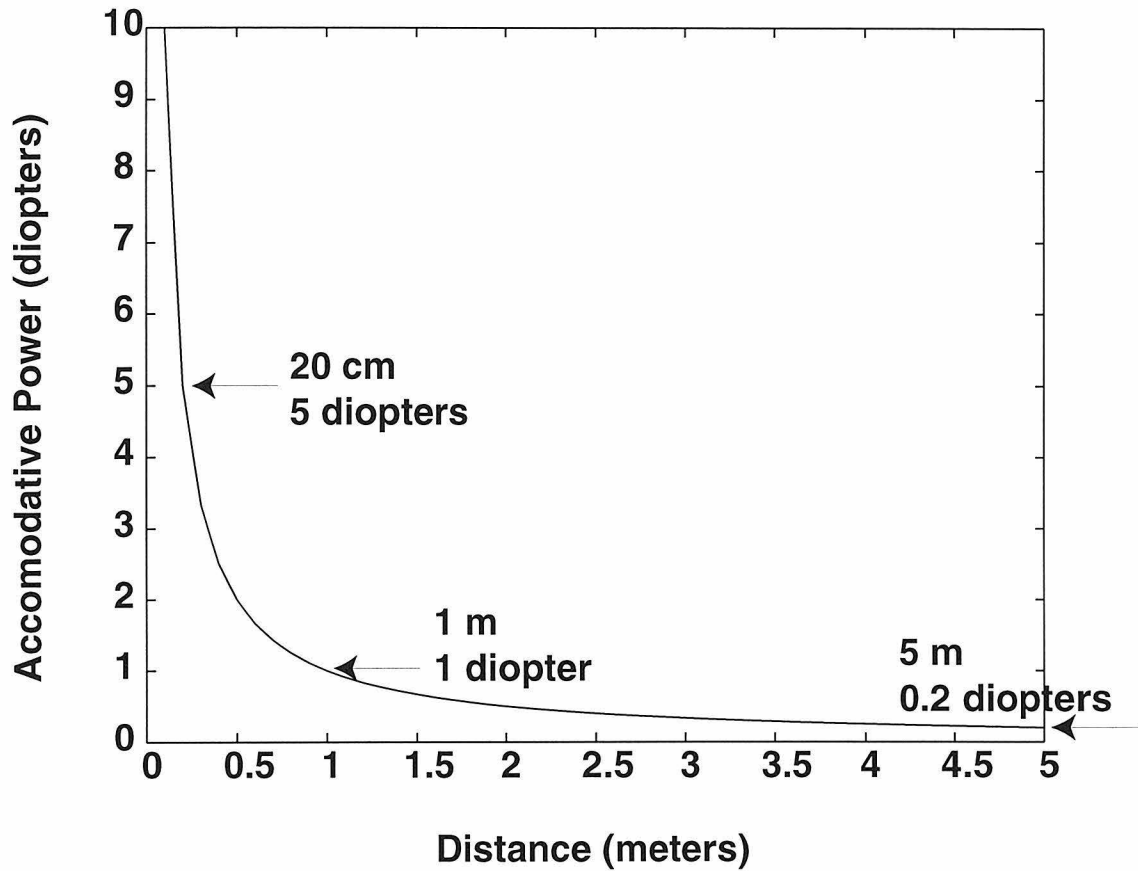


Figure 1.6: Relationship between viewing distance and accommodative power. Note that the difference in lens power for shifting fixation from 20 centimeters (the approximate near point for an adult human observer) to one meter is 5 diopters while shifting fixation from 1 meter to 5 meters results in a change of only 0.8 diopters.

1.3 Electrophysiology and Neuroanatomical Background Work

Although much is now known about the psychophysics of size perception and size constancy, relatively little is known about the underlying neural mechanisms of size perception. Previous work relevant to the study of size constancy includes a number of brain lesion and electrophysiological studies.

Brain lesion experiments and clinical studies have localized the general areas of the cortex that are necessary for size constancy; interpretation of these results suggest potential areas where size and distance information might converge.

While a large number of neurophysiological studies have examined either spatial coding or size tuning separately, there are very few studies that explicitly examine the representation of both size and distance in the visual cortex. However, previous work on that examined either the representation of size or distance can give us insight into potential mechanisms that size constancy might employ. Results from lesion studies will be reviewed first, followed by a review of relevant electrophysiological studies.

1.3.1 Brain Lesion Studies

Parietal and Inferotemporal Cortex Lesions

Humphrey and Weiskrantz [1969] made large lesions in either inferotemporal (IT) cortex or parietal cortex, in monkeys that were trained to make size discriminations of stimuli presented at different distances. They found that IT lesions severely impaired size constancy judgments in all four monkeys tested; three out of four of the monkeys tested did not recover the capacity to make size judgments at different distances. Monkeys with large parietal lesions did not show any deficits in size constancy. Humphrey and Weiskrantz also reported that the monkeys alternated between two incorrect strategies: discrimination was based on either size or distance judgments. They suggested that monkeys with IT lesions were unable to use

both size and distance information together.

Extrastriate Lesions in V2 and V4

Ungerleider et al. [1977] made lesions in pulvinar, IT and in a large area of extrastriate cortex that included large portions of V2 and V4. Their results confirmed that IT lesions severely impaired size constancy; in contrast, they found that pulvinar lesions did not impair size constancy. Lesions in IT did not cause any systematic errors in distance or retinal size judgments. However, their large “prestriate” (extrastriate) lesions disrupted size constancy, resulting in a misjudgment of the distance of test objects. All monkeys in Ungerleider’s study recovered the capacity to make size constancy judgments, suggesting that multiple mechanisms are involved in the perception of size constancy.

Lesions made by Humphrey and Weiskrantz [1969] and Ungerleider et al. [1977] were very extensive and involved large areas of cortical gray matter. The areal extent of the lesions are very difficult to interpret, and the exact cortical visual areas that were impacted by these large lesions are not precisely known.

Focal Lesions to V4

Schiller [1993] made small lesions in V4 that could be localized to specific retinotopic locations in the visual field. This approach allowed Schiller to compare results from stimuli presented in the unaffected versus the visual field locations corresponding to the lesioned cortex. Schiller found severe deficits in the monkey’s capacity to discriminate the size of objects in the affected part of the visual field. He emphasized that the deficit was most pronounced when the monkey’s task was to detect the smaller object from an array of larger objects, but there were also marked deficits when the monkey had to detect a larger object from an array of smaller ones, except when the size difference between the target and the array was very large. These experiments were only conducted with stimuli at one viewing distance. However, the reported deficits in the discrimination of the size of objects were so severe that it is likely that the same lesions would also have disrupted size constancy

and the capacity to judge size independent of distance. Finally, he observed milder deficits in color, brightness and form discrimination and no deficits in stereopsis following V4 lesions.

Human Clinical Studies

Cohen et al. [1994] studied two patients with circumscribed unilateral lesions in extrastriate cortex probably involving the central visual field representations in V2 and V4 (see Sereno et al. [1995]). The locations of the lesions were confirmed by autopsy in one case and MRI in the other. The subject had a homonymous hemianopsia; after resolution, the lesions produced hemimicropsia, a reduction in the perceived size of objects in the visual hemifield contralateral to the lesion. No deficits in color or motion perception were reported.

1.3.2 Representation of Object Size in Ventral Visual Cortical Areas

Neurons in ventral visual cortical areas leading up to and including inferotemporal cortex are known to carry information about the retinal dimensions of the stimuli.

Hubel and Wiesel [1965] described a class of neurons in area 19 of cats that preferred bars of a particular length, shorter than the spatial extent of the receptive field; they termed these cells “higher order hypercomplex cells.” These cells are not simply endstopped; they respond to the preferred length at multiple spatial positions within the receptive field.

Petersen et al. [1980] described a class of dimensionally selective neurons in area DL of the owl monkey (DL is homologous to V4 in macaque monkeys). These neurons were selective for a particular length and width of stimuli, presented at any location within the larger receptive field. They reported that the majority of neurons in area DL are dimensionally selective. Neurons in three other visual areas, MT, DM and M, were much less dimensionally selective than DL. Desimone and Schein [1987] confirmed these results for V4 in macaques.

Higher in the pathway to inferotemporal cortex, many neurons are reported to be size-invariant [Gross et al., 1972; Gross and Mishkin, 1977; Lueschow et al., 1994]. For the specialized population of IT neurons that are selectively responsive to the images of faces, most cells were invariant with respect to the physical size of the stimulus [Rolls and Bayliss, 1986]. Rolls and Baylis did test a subset of the face cells recorded at different viewing distances and found that only a very small percentage showed tuning characteristics that resembled size constancy.

It is notable that size-invariance and size-constancy have quite different requirements with regard to distance information. To achieve size invariance, the system must discount distance information; on the other hand, for size constancy, distance must be accurately estimated. Psychophysical experiments support the idea that object recognition mechanisms are size-invariant [Fiser and Biederman, 1995; Biederman and Cooper, 1992]; thus an object’s size can be perceived independent of distance (size constancy), while an object’s identity can be recognized independent of image size (size invariance). One hypothesis, consistent with a separation of visual processing into two anatomically separate (dorsal vs. ventral visual cortex) processing streams (the “what” vs. “where” streams, [Ungerleider and Mishkin, 1982]), is that the spatial aspects of object perception are subserved by dorsal visual cortical areas. Spatial information necessary for size constancy could possibly be derived from connections from dorsal to ventral cortex.

To explore this idea, relevant electrophysiological studies in dorsal cortical visual areas will be briefly reviewed in the next section followed by a discussion of dorsal versus ventral cortical processing streams.

1.3.3 Physiology of Dorsal Visual Cortical Areas

Physiological experiments in dorsal cortical areas have examined in great detail the neural representation of visuospatial relationships, including distance and angle of gaze. These studies can give us insight into possible neural mechanisms for encoding distance necessary for size constancy. Extensive work in parietal areas has

shown that gaze angle and object depth modulates the gain of responses in parietal areas [Sakata et al., 1980; Andersen and Mountcastle, 1983; Galletti and Battaglini, 1989; Colby et al., 1993; Gnadt and Mays, 1995]. The primary mechanism for gaze modulation is reported to be linear gain modulation of the neural response (for reviews see Andersen et al. [1993] and Andersen [1997]).

Sakata et al. [1980] recorded from area 7a of posterior parietal cortex in macaque monkeys that were trained to fixate on a movable screen that varied in distance from the monkey. They found that the neurons fired when the monkey fixated on the target and that for visually responsive neurons in area 7a, the magnitude of the response was related to fixation distance. Sixty-five percent of the depth sensitive neurons preferred closer fixation distances and 29% preferred farther distances.

Neurons in the ventral intraparietal area (VIP) are sensitive to the absolute distance of stimuli when the fixation distance is constant [Colby et al., 1993]. Some of these neurons responded best to extremely close stimuli that were only 5 cm from the monkey. These distance related effects in VIP neurons could be obtained with monocular stimulation.

1.3.4 Representation of Distance in Primary Visual Cortex

Distance information is represented as early as primary visual cortex and also in parietal cortex. Trotter et al. [1992, 1996] recorded from V1 in awake monkeys trained to fixate on a spot on a movable monitor that was varied in distance from the monkey. They tested responses to binocular disparity at 2-3 viewing distances. The stimuli were scaled so that retinal dimensions were kept constant. The primary result was that the magnitude of these responses was modulated by viewing distance for about 80% of the neurons studied. Angle of gaze is also represented as early as primary visual cortex [Weyand and Malpeli, 1993]. Although this study was performed in cats, it is likely that direction of gaze is represented in V1 of primates.

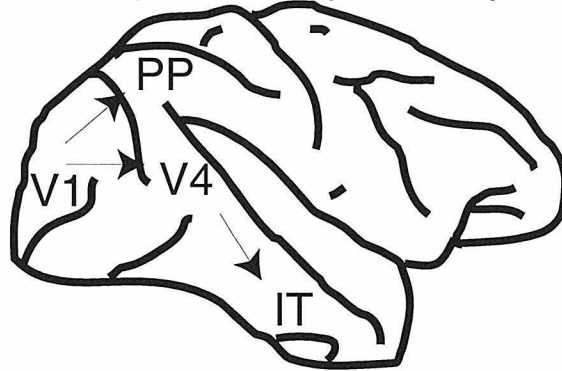
1.3.5 Parallel Systems for Distance Perception

“What” vs. “Where” Pathways

Ungerleider and Mishkin [1982] first proposed that anatomically and functionally distinct parallel processing streams exist within the visual cortex, based on contrasting effects of lesions to either posterior parietal or inferotemporal (IT) cortex. Figure 1.7. Monkeys with posterior parietal lesions were severely impaired on a spatial landmark task but could perform an object discrimination task at normal levels. Monkeys with IT lesions could not learn to discriminate two objects based on their features, but could perform the spatial landmark task. Based largely on these results, the streams have often been labeled as the “what” and the “where” pathways, leading to dorsal and ventral cortex respectively. This idea has achieved widespread appeal and extensive electrophysiological, anatomical and lesion studies have supported the notion that there are distinct dorsal and ventral processing streams in the visual cortex.

A number of other studies have cast doubt on the validity of a two-stream visual system, and the labels of “what” versus “where” [Goodale and Milner, 1992; Ferrera et al., 1992, 1994; Milner and Goodale, 1993; Schiller, 1993]. This debate is especially relevant to the study of size perception and size constancy. Size is a fundamental attribute of objects and is encoded in ventral stream neurons. However, for size constancy, spatial information about viewing distance must be combined with retinal size information. An important, and as yet unanswered, question is where in the visual cortex are distance and size information combined? A strict interpretation of the two stream theory would suggest that distance is encoded by neurons in dorsal areas and that object size is encoded in ventral stream areas. However, lesion studies, reviewed above, suggest that ventral areas (including V2, V4 and IT) are necessary for size constancy and that parietal areas are unnecessary [Humphrey and Weiskrantz, 1969; Ungerleider et al., 1977; Schiller, 1993].

"where" (dorsal or parietal pathway)



"what" (ventral or
inferotemporal pathway)

Figure 1.7: The “what” and the “where” pathways, proposed by Ungerleider and Mishkin [1982]. Area V4 lies at an intermediate stage of visual processing in the ventral or “what” pathway that leads to IT cortex. Posterior parietal (PP) cortex and other dorsal areas are thought to be involved with spatial or “where” processing.

Behavioral Experiments

Goodale et al. [1991] and later Aglioti et al. [1995] performed behavioral experiments that compared two different behavioral measures of size perception: reports of apparent size, and grasping accuracy. Subjects were asked to report the size of the central disk in the Ebbinghaus illusion (see Figure 1.3); size was also measured by asking the subjects to grasp the central figure and the grasping angle was measured. They found that the motor system is not fooled by the Ebbinghaus illusion. Subject’s grasp angles closely matched the actual size of the central object rather than the apparent visual size. This dissociation might be related to the distinction between the dorsal and the ventral processing streams.

These results comparing grasping and perceiving suggest that the information about the surrounding objects in the visual field, used for size constancy and visual size perception, is not used during grasping actions. These experiments also sup-

port the possibility that size and distance are represented independently in both visual streams.

1.4 Neural Representation of the Third Dimension

The study of size constancy provides an excellent framework for approaching the problem three dimensional perception, especially because the phenomenon of size constancy is robust and animals have the capacity to make size constancy judgments.

Lesion studies have localized the general regions of the brain that are necessary for normal size perception in monkeys. Extensive electrophysiological work has examined the representation of distance and object size in the primate visual cortex; however, these studies examined either distance or object size separately, in different areas of the primate brain.

Despite this extensive background work, relatively few studies have examined size and distance perception together, at the single neuron level. The next chapter of this thesis reports new electrophysiological findings that advance our understanding of three-dimensional spatial coding in the primate brain. This study examines the representation of object size and distance at a neural level. Our experiments have primarily sought to examine the effects of viewing distance on neural responses in ventral cortical areas, where object size information is known to be encoded. We also examined the relative contributions of distance cues on neural response in V1 and V4, and examined possible size constancy effects in the neural population response.

Chapter 2 Representation of Distance and Size in V1, V2 and V4

2.1 Introduction

Size perception depends on the dimensions of the image projected onto the retina as well as the viewing distance. Size constancy is the ability to compensate for changes in retinal dimensions as viewing distance changes, so that the perception of object size remains constant over a wide range of distances. Humans and monkeys have been shown to have size constancy and can make good judgments of object size over a wide range of viewing distances [Locke, 1937; Holway and Boring, 1941; Gilinsky, 1955; Davis et al., 1964; Humphrey and Weiskrantz, 1969; Ungerleider et al., 1977].

Lesion studies have localized the general regions of the brain necessary for size constancy. Ventral visual areas leading up to and including inferotemporal cortex are necessary for accurate size discrimination in monkeys [Humphrey and Weiskrantz, 1969; Ungerleider et al., 1977; Schiller, 1993] and accurate size perception in humans [Cohen et al., 1994; Milner and Harvey, 1995]. A large percentage of neurons in ventral visual areas are known to carry information about object size; neurons in area V4 of macaques and DL of owl monkeys are selective for object dimensions [Petersen et al., 1980; Desimone and Schein, 1987]. Additionally, Hubel and Wiesel [1965] described a class of neurons in area V3 that was sensitive to bars smaller than the overall size of the receptive field (higher-order hypercomplex cells).

Viewing distance and angle of gaze are known to modulate the responses of neurons in parietal cortex [Sakata et al., 1980; Andersen and Mountcastle, 1983]. While it has been firmly established that parietal cortex is involved in visuospatial coding (for reviews see Wise and Desimone [1988], Andersen et al. [1993] and

Andersen [1997]), lesions to parietal cortex do not disrupt size constancy judgments in monkeys [Humphrey and Weiskrantz, 1969; Ungerleider et al., 1977], suggesting that the spatial information utilized for size constancy is encoded in non-parietal areas. The primary focus of this work was to further localize the anatomical regions of the visual cortex where distance information is being combined with retinal size information. We were especially interested in whether or not distance information is encoded in area V4, an intermediate stage of visual processing in the ventral visual cortex.

Distance and angle of gaze exert influence on neural responsiveness as early as V1 [Trotter et al., 1992; Weyand and Malpeli, 1993; Trotter et al., 1996] by modulating the gain of the neural response. The second goal of this study was to describe the representation of distance and size information and how these factors are being combined and incorporated by the visual system. Rolls and Bayliss [1986] reported that a small number of neurons in inferotemporal cortex shift their retinal size tuning preference with changing distance in a manner consistent with size constancy. We sought to address the question of how size and distance information interact at early and intermediate stages of processing in the ventral visual cortex. We were especially interested in knowing if any neurons in these areas respond as a function of an object's apparent size.

Extensive psychological and behavioral research suggests that both visual and non-visual cues for distance are involved in size perception [Holway and Boring, 1941; Leibowitz and Moore, 1966; Freeman, 1968; Bayne and Davis, 1983; Coren, 1971; Erkelens and Regan, 1986; Bradshaw et al., 1996]. Our third goal was to describe the relative influence and representation of different types of distance cues that are behaviorally relevant for size constancy.

To approach these problems, we sought to examine the effects of changing distance on constant retinal image size in awake monkeys trained to fixate at different distances. Our experimental paradigm was designed to vary retinal size systematically at several viewing distances; stimulus size was scaled with distance so that the same retinal size range was studied at each viewing distance (Figure 2.1). Ex-

periments were repeated under restricted viewing conditions in a subset of the total population studied.

Our results indicate that neurons in these areas are sensitive to viewing distance, and that distance interacts with retinal size information by modulating the gain of the neural response. Distance modulation begins as early as V1, but also exerts a significant effect in area V4. This finding suggests that visuospatial coding is not unique to dorsal stream neurons.

Preliminary versions of this work have been previously reported [Dobbins et al., 1996].

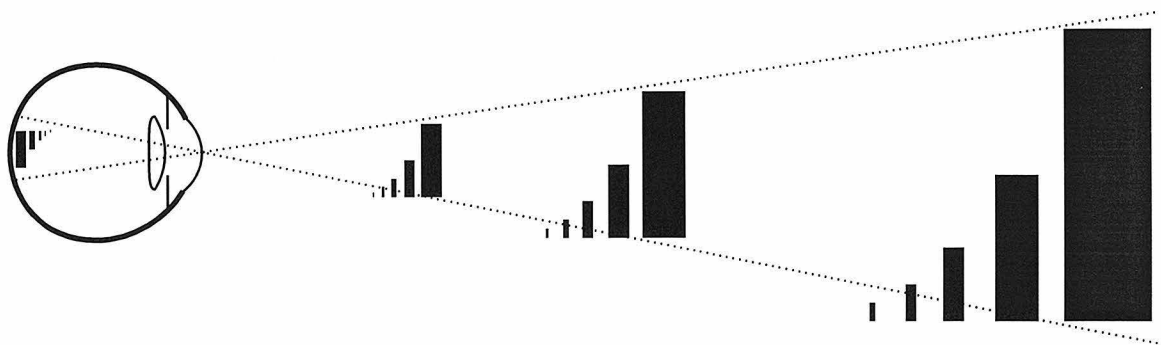


Figure 2.1: General experimental approach. We measured responses to systematic changes in retinal image size at several viewing distances. Stimuli were scaled to keep retinal image size constant with changing viewing distance.

2.2 Methods

2.2.1 General Methods

All surgical, training and neurophysiological recording procedures conformed to the National Institutes of Health and USDA guidelines for animal research, and were carried out under a protocol approved by the Caltech Institutional Animal Care and Use Committee (IACUC).

2.2.2 Training and Surgery

Two adult male macaque monkeys (one *M. mullata* and one *M. fascicularis*) were used in this study. The monkeys were trained to sit in a standard monkey chair and fixate a small square on the computer monitor for a juice or water reward. Prior to training, a stainless steel headpost was implanted to permit head restraint for fixation training and recording. The headpost was fixed to the skull using orthopedic straps and bone screws (Synthes, USA) under sterile conditions and general anesthesia (xylazine 0.5 mg/kg, ketamine 10 mg/kg). Post operative analgesic drugs (buprenorphine, codeine, acetaminophen) and were administered for several days following the surgery. Fixation was monitored with a non-invasive infrared video-based eye tracker [Barbur et al., 1987]. Following fixation training the second aseptic surgery was performed to implant a recording chamber (Caltech Central Engineering) over a craniotomy to allow controlled and sterile insertion of microelectrodes. The chamber was placed over perifoveal V1, V2 and V4, using skull and sulcal landmarks. The chamber and implant margins were carefully monitored for infection, and were cleaned daily with saline and dilute chlorhexidine diacetate (0.05%). The chamber was filled with inert sterile oil (either heavy silicon or mineral oil) during and between recording sessions. Sterile ophthalmic antibiotic ointment (Bactracin-Neomycin-Polymixin, Gentacin or Chloramphenicol) was used as necessary (for 10-14 day periods), to inhibit bacterial growth in the recording chamber.

2.2.3 Recording

To record the activity of single neurons, the intact dura was penetrated with sterile glass insulated platinum-iridium microelectrodes, using a stepping motor micro-drive (Herb Adams, Caltech Central Engineering). Single neurons were isolated with a window discriminator (Mike Walsh, Caltech Biology Electronics Shop), and spike times recorded to 1 ms resolution with a PC running the software package “Cortex” (data acquisition program developed by Robert Desimone, Tom White and colleagues at the NIH).

2.2.4 Visual Stimuli

Setup and Receptive Field Mapping

The computer monitor was placed on a movable platform on a set of tracks about 4 meters in length (Caltech Central Engineering). This arrangement allowed the monitor to be placed at different distances from the monkey. The viewing distances were set at 22.5 cm, 45 cm, 90 cm, 180 cm or 360 cm.

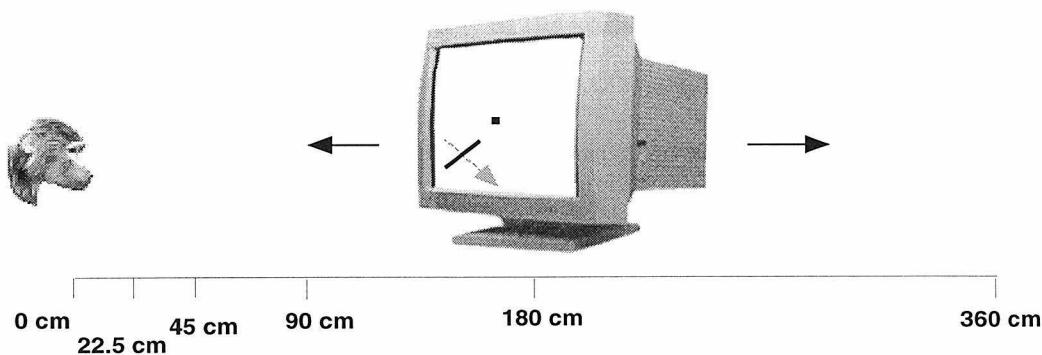


Figure 2.2: Distance viewing setup. The monkey was trained to fixate a spot on a computer monitor which could be placed at three to five different viewing distances.

When a single neuron was isolated, the optimal receptive field characteristics (spatial extent, preferred direction, orientation, aspect ratio and color) were esti-

mated by hand at one or two viewing distances (usually 45cm and/or 90cm). The optimized parameters were used when possible. If the cell was broadly orientation tuned, either vertical or horizontal bars were used to eliminate pixellation effects.

Size Tuning Curves

We then tested the isolated cell for retinal image size tuning as a function of viewing distance. The stimuli were scaled with distance such that the range of retinal image size was constant with changing distance. At each distance, 6-10 trials of each retinal image size (0.2, 0.4, 0.8, 1.6, or 3.2 degrees) were presented over the receptive field during fixation. Multiple, randomly interleaved, blocks of data were collected at three to five viewing distances..

Speed and length of excursion of the stimuli were also scaled proportionally with distance to keep retinal speed and retinal excursion constant. At 22.5cm the smallest bar (0.2 degrees) was omitted and at 360cm the largest bar (3.2 degrees) was omitted due to physical limitations of the monitor and pixel size. Stimulus intensity was $160.96 \pm 3.4 \text{ cd} \cdot \text{m}^{-2}$ at the three farthest distances.

Note that in order to keep retinal image size constant, it was necessary to scale the actual size (both length and width) of the stimuli with distance. The experiment measured a 16-fold range of distances (22.5 - 360 cm) and a 16-fold range of retinal image size (0.2 - 3.2 degrees visual angle). Both distance and size were tested in octave steps, so that there was overlap in the actual size of the stimuli at each distance (for example, a bar that subtends 0.4 DVA viewed at 45 cm subtends 0.2 DVA at viewing distance of 90 cm).

To calculate retinal size tuning curves at each distance, mean firing rate was calculated for each stimulus condition. Each spike that occurred during the stimulus period was time stamped to 1 ms resolution. Mean spike rate was calculated by dividing the spike count by the stimulus duration. Mean spike rate was also measured each trial for fixation only Figure 2.4.

A two-way (size and distance) analysis of variance (ANOVA) was used to quantify the statistical significance of size and viewing distance modulation. Response

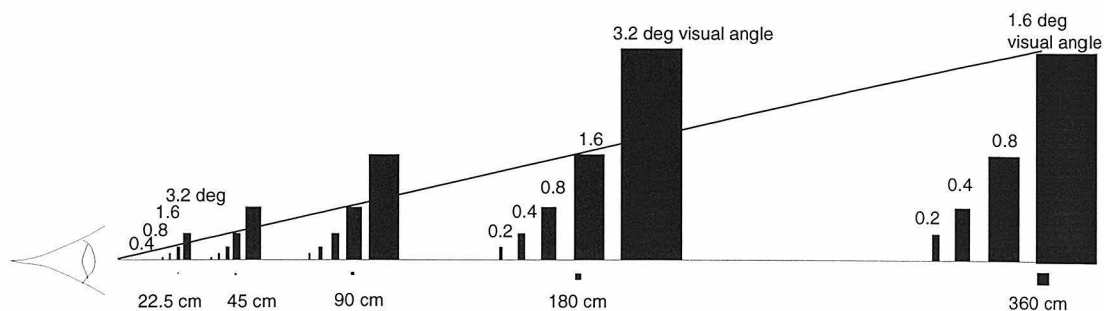


Figure 2.3: Retinal size tuning at five viewing distances.

to the fixation stimulus was also analyzed using a one-way ANOVA.

Restricted Viewing Conditions

Multiple, randomly interleaved blocks were first obtained at three to five of the viewing distances. In a subset of the cells, measurements were repeated under either binocular or monocular restricted viewing conditions. Testing under restricted viewing conditions depended on the stability and our ability to hold each isolated cell. Because of this limitation, few cells were tested under both restricted viewing conditions.

During restricted viewing, the monkey viewed the stimuli through either monocular or binocular apertures (6.5 degrees diameter). The remainder of the scene was masked such that only the monitor screen was visible to the monkey. Following this series, the experiment was again repeated under binocular full field conditions.

Note that under binocular full field viewing, horizontal binocular disparity is near constant with changes in monitor position; horizontal disparity was always near zero, because all receptive fields were in or close to the fovea (< 2.5 degrees eccentric in all cases). Additionally, motion parallax cues were not available as a distance cue because the monkey's head was fixed during recording.

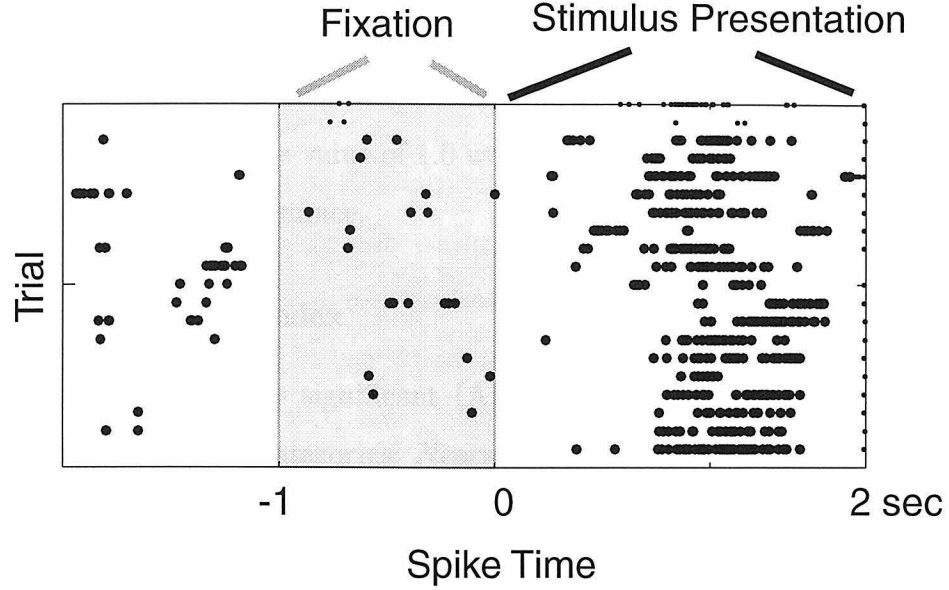


Figure 2.4: Trial structure. Responses during fixation only and during stimulus presentation over the receptive field of the neuron were measured each trial, and mean spike rate for both portions of the trial were calculated. The monkey was required to maintain fixation throughout the duration of the entire trial.

2.2.5 Data Analysis

Area Classification

Cells were assigned to a visual cortical area based on receptive field position, size, and properties, and position relative to the lunate sulcus. In the absence of histological classification, uncertainty about whether certain cells were in V1 or V2 led us to combine V1 and V2 for quantitative analysis.

Fractional Gain

The modulation of the mean response at each distance (MDR) was quantified by calculating the fraction gain between the highest and the lowest mean response values:

$$\text{Fractional gain} = \frac{MDR_{max} - MDR_{min}}{MDR_{max}} \quad (2.1)$$

were MDR_{max} is the highest mean response associated with a viewing distance and MDR_{min} is the lowest. The lowest possible fractional gain value of 0.0 would indicate that mean response strength was completely unaffected by viewing distance. The highest possible value of 1.0 would indicate that responses were absent for at least one viewing distance.

Distance Modulation Index

Cells that had statistically significant (ANOVA, $p < 0.01$) distance modulation were classified into three categories: *Nearness* (monotonically increasing responses with proximity), *Farness* (monotonically decreasing response with proximity), and non-monotonic. Non-monotonic cells with significant distance modulation were analyzed separately. For monotonic cells, a distance modulation index (DMI) was calculated as follows:

$$DMI = (\text{fractional gain}) \times (\text{classification}) \quad (2.2)$$

where classification = 1 for Far and classification = -1 for Near.

Shifts in the Preferred Retinal Image Size

A possible change in response characteristics as a function of distance would be a systematic change in preferred retinal image size. A very small percentage of cells in inferotemporal cortex have been reported to be sensitive to apparent size rather than retinal size [Rolls and Bayliss, 1986], but little is known about the interaction of retinal size and distance information in early and intermediate cortical areas.

If a hypothetical cell is tuned for apparent size rather than retinal size, the preferred retinal image size should decrease with increasing distance. In order to quantify systematic shifts in retinal size tuning preference with changing viewing distance, we calculated a shift index. The preferred retinal size was calculated at each distance, and was plotted against viewing distance on a log-log scale. Preferred retinal size was calculated by weighting each retinal size by its corresponding

response and computing the weighted mean:

$$\text{Preferred retinal size} = \frac{\sum_{i=1}^N (\text{Response}_i)(\text{Retinal size}_i)}{\sum_{i=1}^N \text{Response}_i} \quad (2.3)$$

Preferred retinal size for each distance was fitted with a least squares regression line, and the slope of the line was calculated as the shift index. A shift index of 0.0 would indicate no change in preferred retinal size tuning. A positive shift index indicates that the preferred retinal size is increasing with distance (anti-size constancy) and a negative shift index indicates that preferred retinal image size is decreasing with distance (size constancy). The same analysis was done using the retinal size that elicited the maximal response at each viewing distance.

Changes in Size Tuning Sharpness

Another possible interaction between size and distance information would be to increase or decrease size tuning sharpness with changing distance. To explore this possibility, we calculated a sharpness index as follows:

$$\text{Sharpness Index} = \left(\frac{R_{max} - R_{min}}{R_{max}} \right)_{MDR_{max}} - \left(\frac{R_{max} - R_{min}}{R_{max}} \right)_{MDR_{min}} \quad (2.4)$$

Where R_{max} and R_{min} are the responses to the retinal size that elicited either the highest mean spike rate or lowest mean spike rates at either the preferred distance (MDR_{max}) or the distance that elicited the least response (MDR_{min}).

Positive sharpness index values indicate that the size tuning response is more peaked at the distance in which the cell responds maximally (MDR_{max}) compared to the distance the elicits the least response (MDR_{min} .) Negative sharpness index values indicate that the retinal size tuning response is broadening.

2.3 Results

Our experiments were designed to examine how neural responses (measured by mean firing rate of the neuron during stimulus presentation) depend on viewing distance in the ventral pathway at both early and intermediate stages of visual processing. We studied a total of 178 cells (85 in V1 and 93 in V4), collected from two monkeys, while they performed a fixation task (see Methods section).

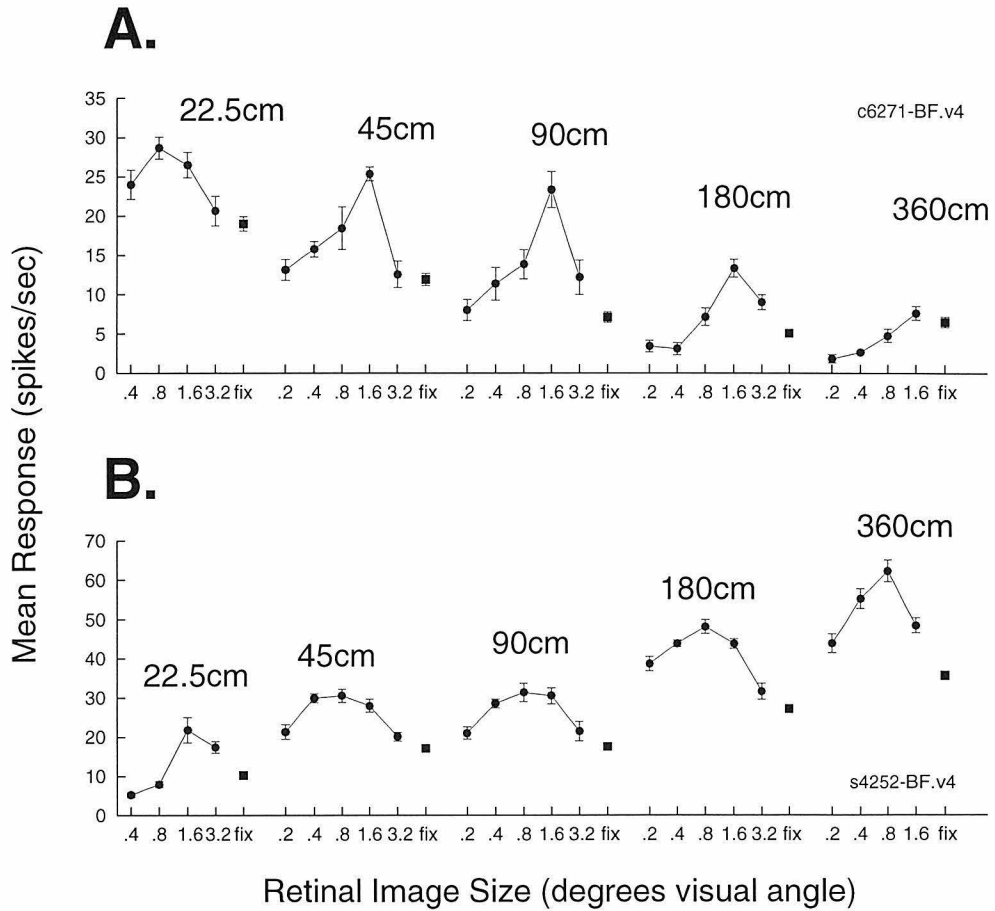


Figure 2.5: Distance modulation in two different V4 neurons. Responses during fixation only are also modulated by viewing distance (squares to the right of each tuning curve). **A.** Nearness cell. Cell responds in a monotonic fashion to increasing proximity. **B.** Farness cell.

Binocular full field experiments were designed to determine if and how viewing distance changes retinal size tuning properties. We found that retinal size tuning

generally does not change as a function of viewing distance, but for the majority of neurons in all areas studied (V1/V2 and V4), the gain of the response is strongly distance dependent.

All cells were first tested under binocular full field conditions. Responses under restricted viewing conditions were measured for a subset of the population of neurons, in order to compare the effects of different types of distance cues. Results from these restricted view experiments suggest that both retinal and extraretinal cues for distance exert an influence in V1/V2 and in V4.

Results will first be described qualitatively and then followed by quantitative population analysis.

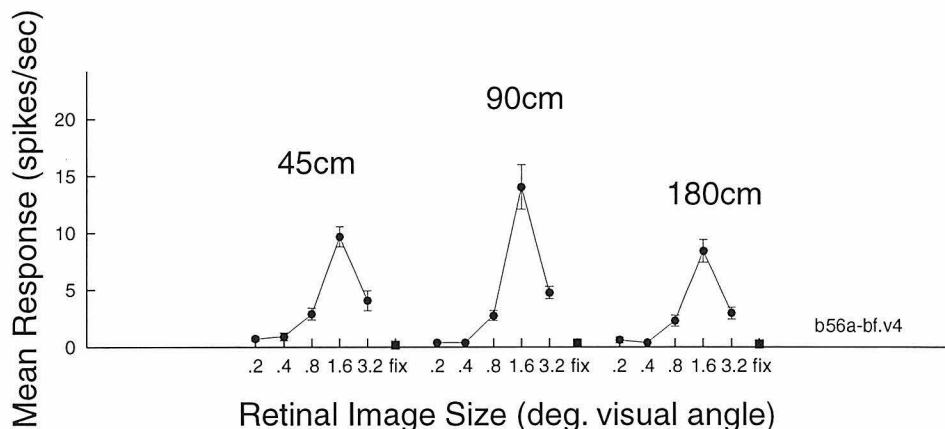


Figure 2.6: Peaked V4 cell. Example of a neuron recorded from V4 that exhibited non-monotonic distance modulation. Most non-monotonic cells were peaked, but a few cells with a notched response profile were also observed.

2.3.1 Qualitative Results

Distance Response Characteristics

The most common type of cell exhibited a monotonic increase in mean firing rate with increasing proximity to the animal (*Nearness* cells, Figure 2.5A). The opposite type (*Farness* cells, Figure 2.5B) were also observed, as were cells that

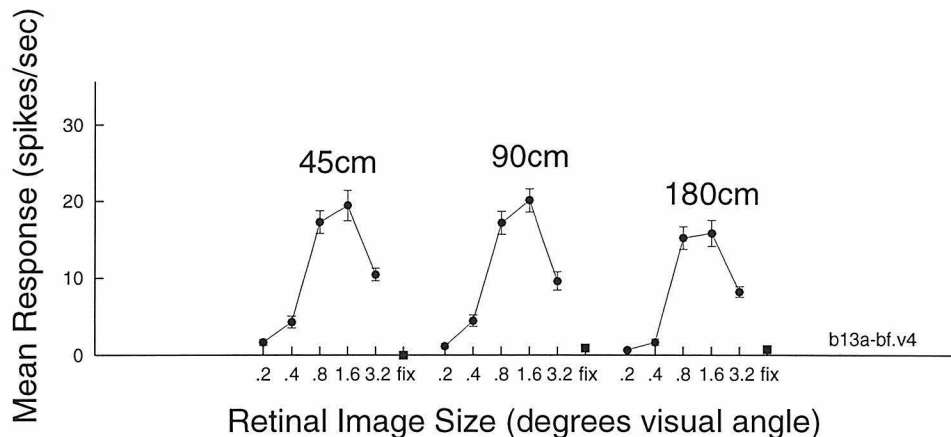


Figure 2.7: Distance invariant V4 cell. Example of a neuron that does not exhibit significant modulation in mean firing rate with changing distance.

exhibited non-monotonic responses with distance (*Peaked* or *Notched* cells, Figure 2.6). We also recorded cells that did not show any modulation in firing rate with distance (*Distance Invariant* cells, Figure 2.7). Example cells illustrated in Figure 2.5 - Figure 2.7 were recorded from area V4. The results from V1/V2 and V4 were qualitatively similar and all cell types found in area V4 (*Nearness*, *Farness*, *Peaked*, *Notched*, *Distance Invariant*) were also present in area V1/V2. Figure 2.17 illustrates retinal size tuning curves of three example cells recorded from area V1/V2.

Fixation Only Results

For each trial, the monkey was required to maintain fixation for one second prior to stimulus presentation. Mean firing rate at each distance was calculated for this “fixation only” period (Figure 2.4). We observed that mean firing rate during fixation only often changed as a function of viewing distance (Figure 2.5, squares). In fact, the background activity level (the “hash,” monitored by ear) was often observed to increase remarkably at the preferred viewing distance of the isolated cell being studied. This suggests that there is a topographic representation of distance in V1/V2 and V4, with neighboring cells responsive to similar viewing

distances.

While most of the neurons studied had excitatory receptive fields, we found that a small number of neurons had inhibitory receptive fields yet were still tuned for distance and retinal size (*Tuned inhibitory cells*, Figure 2.8). These cells dramatically illustrate distance modulation even in the absence of visual stimuli. Tuned inhibitory cells responded maximally during the fixation only period and one or more distances.

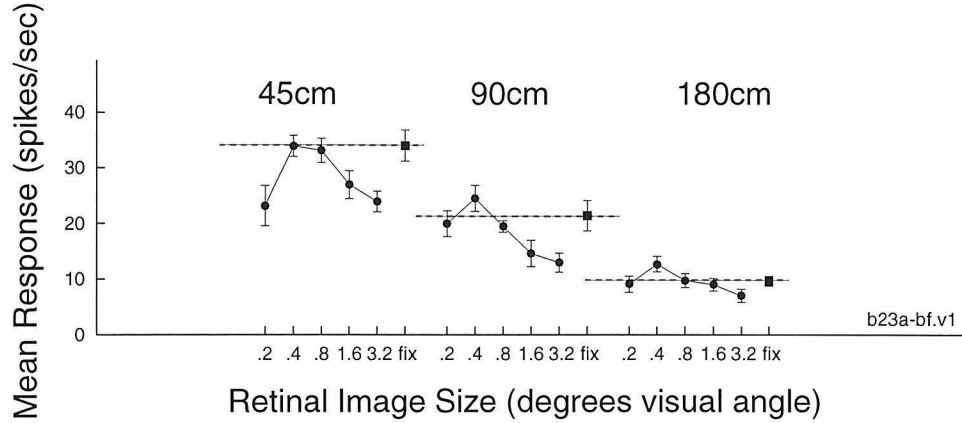


Figure 2.8: Tuned inhibitory neuron. Stimuli presented within the receptive field suppressed this neuron’s firing rate compared to responses to fixation. Horizontal dotted lines indicates mean firing rate during fixation only in the absence of stimuli in the receptive field.

2.3.2 Quantitative Results

In order to quantify the relative effects of changing stimulus size and viewing distance on the mean firing rate for each neuron, we performed a two-way analysis of variance (ANOVA). To further examine and visualize the population responses we developed several indices (see Methods). Viewing distance effects were analyzed using a Distance Modulation Index (DMI), and interactions between distance and retinal size were analyzed with two indices: Shift Index and Sharpness Index.

2.3.3 Distance Effects

ANOVA: Viewing Distance

We qualitatively noted that most cells responded as a function of viewing distance; results from ANOVA were consistent with the suggestion that viewing distance determined the response of the majority of neurons sampled. Sixty-five percent (55/85) of the V1/V2 cells showed statistically significant ($p < .01$) changes in mean firing rate with distance as did 63% (59/93) of the cells in V4 (Figure 2.9).

ANOVA: Fixation Only

A surprising number of cells showed significant modulation of response rate during fixation only. Fifty-one percent of V4 cells (48/93) and 47% of V1 cells had significant ($p < .01$) distance modulation measured by one-way ANOVA (Figure 2.9).

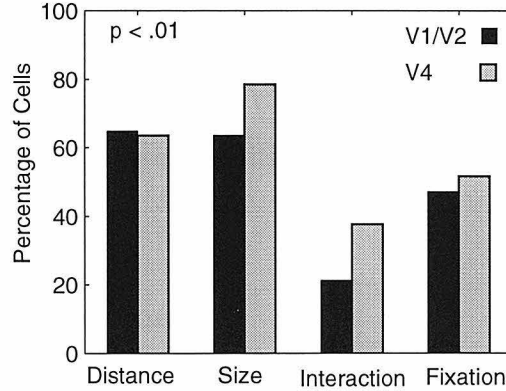


Figure 2.9: Summary results of ANOVA analysis. Percentage of cells that had significant ($p < .01$) distance, size and interaction effects. Results from V1/V2 and V4 are shown separately. Significant distance modulation for fixation only is shown on the far right.

2.3.4 Population Analysis: Distance Modulation Index

In order to quantify the distribution and magnitude of distance modulation effects we calculated a distance modulation index (DMI, see Equation 2.2). Non-

monotonic cells that had significant distance effects (e.g., Figure 2.6) were excluded from this analysis (7/85 cells in V1 and 8/93 cells in V4). A DMI was calculated for each cell and the distribution of DMI's was plotted for V1/V2 and V4 (Figure 2.10A,B). Cells that had statistically significant effects (ANOVA, $p < 0.01$) are shown as filled bars, in black for V1/V2 cells (Figure 2.10A) or in grey for V4 cells (Figure 2.10B). Negative DMI values indicate that the greatest mean response occurred at the closest monitor position; positive values indicate that the farthest viewing distance elicited the greatest mean response. In V1/V2, most cells had negative and very few cells had positive DMI values.

DMI: Fixation Only

A DMI was also calculated for each cell for spikes that occurred during fixation only (Figure 2.11A,B). Histograms of cells with significant distance modulation during fixation only (filled bars on the histogram) are overlaid against the entire population results. Results were very similar to those obtained with visual stimuli, with a large proportion of cells in V1/V2 having negative DMI values, while in V4, the distribution is more balanced with a bimodal distribution of negative and positive DMI values.

DMI: Cell Type Classification

The relative proportions of the different types of distance modulation are plotted in Figure 2.10C and Figure 2.11C. Cells were classified into three categories: Nearness (negative DMI values), Farness (positive DMI values) and other (non-monotonic responses with distance). Only cells that had significant distance effects (ANOVA, $p < 0.01$) were included in this analysis.

A majority of the cells in V1/V2 (72%, 41/55 cells) and V4 (56%, 33/59 cells) responded best at the closest tested distance. Farness cells were relatively rare in early visual areas and only made up about 13% of the sample of V1/V2 neurons (7/55 cells). In V4, Farness cells were more common and accounted for 31% of the cells (18/59 cells).

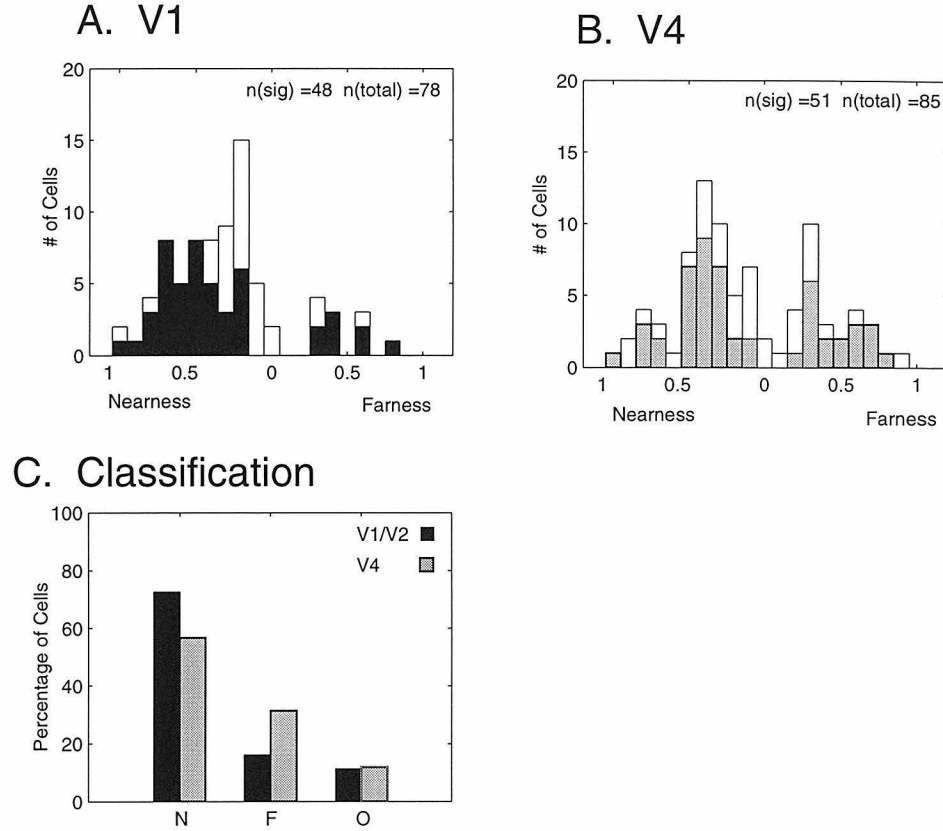


Figure 2.10: Distance Modulation Index (population analysis). **A.** Distribution of DMI values for cells with monotonic distance response changes recorded from V1/V2. Cells that had significant distance modulation effects (ANOVA $p < .01$) are shown in black. **B.** DMI distribution for V4, with cell that had significant effects shown in gray. **C.** Classification of cells that had significant distance modulation. Nearness cells were the most common type in both V1/V2 and V4. Farness cells were more commonly observed in V4 than in V1.

Similar classification results were found for fixation only responses as a function of distance. About 70% (28/40) of cells in V1/V2 and 56% (27/48) of cells in V4 were Nearness cells. Only 12.5% of cells in V1/V2 were Farness cells compared with 38% of cells in V4 (5/40 cells in V1/V2 and 18/48 cells in V4).

The overall results and proportion of cell types were similar for both fixation only and response to retinal stimuli (Figure 2.10, Figure 2.11). The distribution of DMI's is heavily weighted towards negative values for cells recorded from V1/V2. In V4, positive DMI values were more frequently observed, suggesting that far

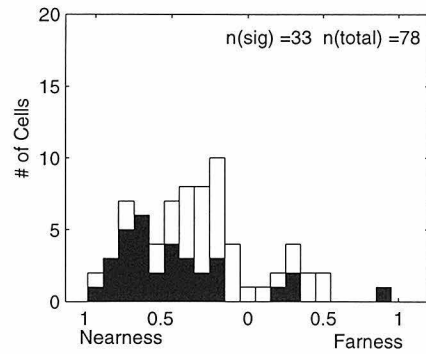
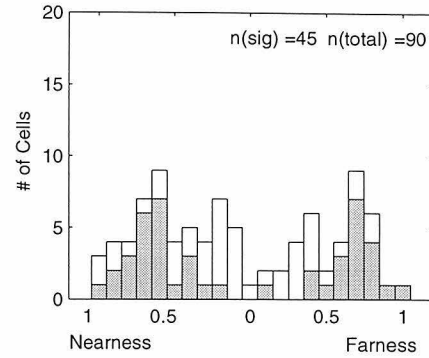
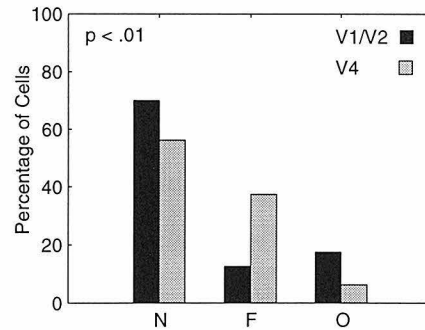
A. Fixation only DMI: V1**B. Fixation only DMI: V4****C. Classification**

Figure 2.11: Distance Modulation Index for fixation only response (population analysis). **A.** Distribution of DMI values in V1. Cells with significant ANOVA distance modulation are shown in black. **B.** V4 results. Significant cells are shown in gray. A much larger proportion of V4 cells prefer increasing fixation distance. **C.** Classification of cells with significant distance modulation for fixation only.

distances have a greater representation in V4 than in V1/V2. This result suggests that the representation of more distant space reflects a higher level of cortical processing.

2.3.5 Retinal Size Tuning

ANOVA: Size Effects in V4

Retinal image size was also a significant factor for most V4 neurons in our sample population, replicating reports that ventral neurons encode object and retinal size information. A large proportion of the cells in area V4 (73/93, 79%, Figure 2.9)

showed significant modulation to retinal size of the stimuli, consistent with earlier electrophysiological studies in area V4 of anesthetized monkeys [Petersen et al., 1980; Desimone and Schein, 1987].

ANOVA: Size Effects in V1

Sixty-three percent of V1/V2 cells (54/85, Figure 2.9) exhibited significant size modulation. However, the observed proportion of V1/V2 cells that showed significant distance modulation probably does not reflect actual proportions of size tuned or “higher order hypercomplex cells” because the ANOVA does not distinguish between size tuned cells, endstopped cells, sidestopped cells and length summation cells; all of the previously mentioned effects might result in significant ANOVA effects for size. Additionally, we purposely searched for size tuned cells in V1/V2 during receptive field mapping, and may have biased our sample to include more V1/V2 size tuned neurons. Nevertheless, our data indicates that retinal size is encoded by neurons at both early as well as intermediate stages of processing in ventral visual cortex.

2.3.6 Combination of Effects.

Figure 2.12 summarizes percentages of cells that showed at least two significant effects, either a combination of significant distance and size modulation or distance and fixation only response modulation.

ANOVA: Distance and Size

Forty percent (34/85) of the neurons in V1/V2 and 53% (50/93) of the cells in V4 had significant modulation for both size and distance (Figure 2.12, left bars labeled “D & S”). The black arrow on the graph indicates expected values, if the variables are acting independently (the expected value is calculated as the product of the two proportions). The observed values of the combinations of size and distance are very close to those expected for independence of effects.

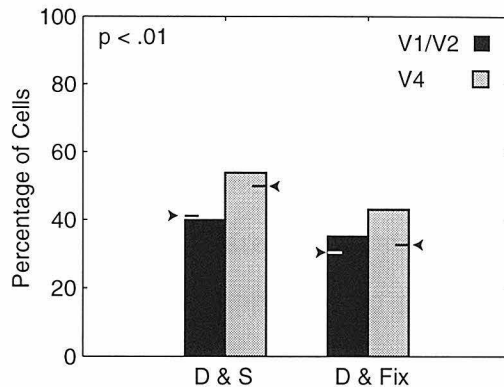


Figure 2.12: Combined effects. Proportions of cells significantly (ANOVA, $p < 0.01$) modulated for both distance and size, and both distance and fixation. The arrow indicates expected values for independence of the effects.

ANOVA: Distance and Fixation

Figure 2.12 also shows cells that had both distance and fixation modulation (right bars labeled “D & Fix”). Thirty-five percent (30/85) of cells in V1/V2 and 43% (40/93) had both distance and fixation effects. These effects are somewhat larger than those expected for independence, suggesting that changes in fixation modulation are associated with changes in response to retinal stimulation.

2.3.7 Interactions Between Distance and Retinal Size

ANOVA: Interaction

Interaction between size tuning and distance modulation was observed in 21% (18/85) of the cells in V1 and in 38% (35/93) of V4 cells (Figure 2.9). Interaction effects were often complex, with partial shifts in retinal image size preference. In order to better understand the interaction between viewing distance and retinal size tuning we examined two likely interaction effects between retinal image size tuning and viewing distance — changes in the preferred retinal image size and changes in size tuning sharpness.

Shift Index

A hypothetical size constancy cell would respond as a function of apparent size and would therefore shift in retinal size tuning preference at different viewing distances. A very small percentage of cells in inferotemporal cortex have been reported to exhibit such shifts consistent with apparent size rather than retinal size [Rolls and Bayliss, 1986]. Although most cells appeared to prefer approximately the same retinal image size at all viewing distances, a few cells exhibited partial shifts in size tuning at one or more distances. We were especially interested in examining shifts in retinal size tuning for cells that had significant interactions between size and distance measured by ANOVA.

While we did not find any neurons that had shifts in size tuning consistent with perfect size constancy in either V1/V2 or V4, we examined the population for overall shifts in retinal size tuning as a function of distance (see Methods, Shift Index). Distribution of Shift Index values is shown in Figure 2.13. The preferred retinal size of the population did not show any significant shifts in tuning with changing distance Figure 2.13. The mean of the distribution of shift indices for V1 and V4 did not significantly differ from zero. The preferred retinal size at each distance, used in Figure 2.13, was calculated using a weighted mean (Equation 2.3). Similar results were obtained using the retinal size that elicited the best response at each distance as the preferred size.

Sharpness Index

Interaction between size and distance effects might include sharpening or broadening of size tuning at the preferred distance of the cell. If size tuning were to sharpen, the preferred retinal size would be responsible for a greater proportion of the overall response at the preferred distance. We qualitatively observed that a few cells did indeed sharpen their size tuning at the preferred distance. To quantify this effect and to see if our sample of neurons show this effect as a population, we calculated a Sharpness Index for each cell. The Sharpness Index simply com-

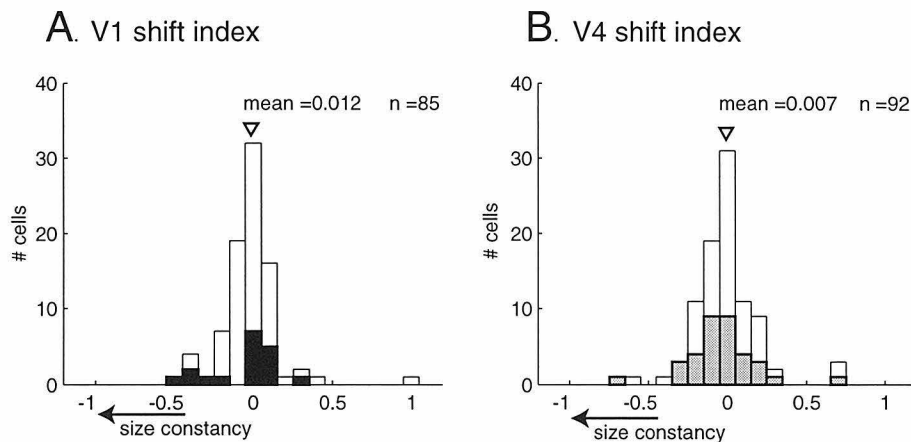


Figure 2.13: Distribution of Shift Index values for **A.** V1/V2 and **B.** V4. Shift Index values for cells with significant ANOVA interaction effects are overlaid as filled bars. Negative values indicate shifts in size tuning preference with distance in the direction of size constancy. Mean values for both V1/V2 and V4 are shown by the triangles and do not differ significantly from zero.

pared retinal size tuning at the distances that elicited the most and the least mean responses (Equation 2.4). Results are summarized in Figure 2.14. Although our sample included cells that both broadened and sharpened their tuning with distance, the mean of the overall effect was statistically indistinguishable from zero. V1 cells tended to slightly broaden their tuning, as the mean of the distribution in V1 was slightly negative (but not statistically significant). V4 neurons did not show any evidence for changing retinal size tuning characteristics.

2.3.8 Restricted Viewing Experiments

In an effort to distinguish between the potential cues for distance modulation, we tested distance modulation under two restricted viewing conditions. For these experiments, the monkey viewed the stimuli through either binocular or monocular apertures that masked off the room and the monitor frame, so that only the monitor

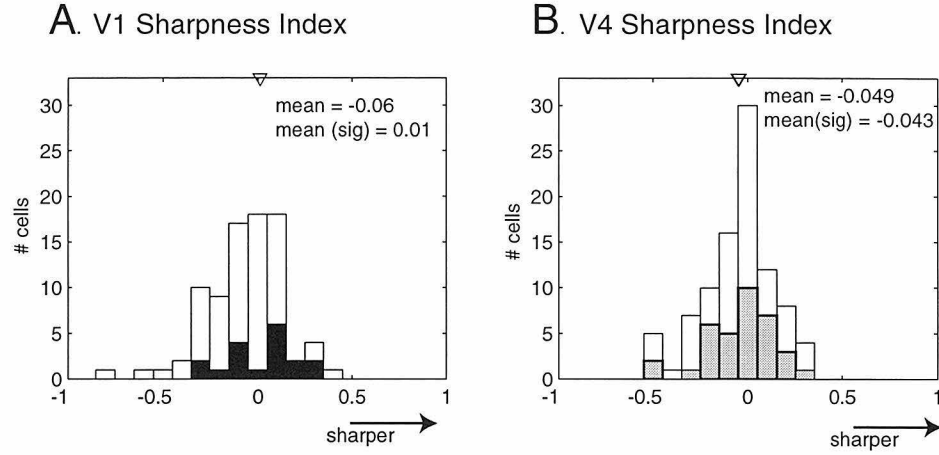


Figure 2.14: Sharpness Index for **A.** V1/V2 and **B.** V4. The Sharpness Index did not differ significantly from zero in either case. Positive values indicate that the cell is more sharply tuned to retinal size at the preferred distance compared with the distance that elicited the least responses. Negative values indicate a broadening of size tuning. Sharpness Index values for cells with significant ANOVA interaction effects are overlaid as filled bars.

screen was visible at the tested viewing distances.

Restricted view experiments were designed to systematically reduce or eliminate cues for distance. Binocular restricted field viewing eliminated visual cues, while leaving most non-visual cues intact, including vergence and accommodation. Monocular restricted viewing further reduced the binocular distance cues available to the animal. However, because vergence and accommodation are linked, some oculomotor cues continue to operate even under monocular restricted viewing.

Overall, combining both binocular and monocular restricted viewing conditions, 53% (28 / 53) of the cells maintained distance modulation under restricted viewing conditions (these cells also had significant distance modulation under binocular full field conditions). A larger proportion of cells maintained distance modulation under binocular restricted viewing than under monocular restricted viewing

conditions (Figure 2.15). Under binocular restricted viewing, most cells (68%) retained significant distance modulation (13/19 cells). A smaller proportion (15/34 cells) retain significant distance modulation under monocular restricted viewing conditions.

Context Independent Cells

A number of cells in both V1/V2 and V4 exhibited distance modulation under restricted view conditions without distance cues provided by the surrounding visual context. We refer to these cells as context independent. Figure 2.18 shows two examples of context independent cells. For these cells, extraretinal cues related to oculomotor signals are sufficient to mediate distance modulation.

Figure 2.18A,B illustrates an example cells recorded from V1 that had nearly identical response characteristics under either binocular restricted viewing and binocular full field viewing conditions. Figure 2.18C,D shows a cell that maintains significant distance modulation under monocular restricted viewing.

Context Dependent Cells

Context dependent cells required the surrounding visual context to maintain distance modulation. For these cells, distance modulation was abolished under restricted viewing conditions. Figure 2.19A shows a cell that had distance modulation under binocular restricted viewing. Figure 2.19B shows the response of the cell under binocular restricted viewing. Significant distance modulation was lost under restricted viewing, indicating that the surrounding visual context was contributing the the cells distance dependent responses. Neither stereopsis nor the monitor frame size could account for the reduction in distance modulation under restricted viewing (Figure 2.19C,D).

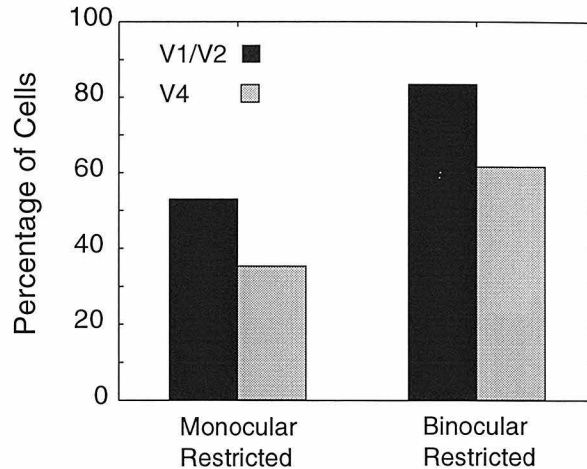


Figure 2.15: Percentages of cells that maintain significant distance modulation under monocular and binocular restricted viewing conditions. A smaller proportion of cells in V4 maintain distance modulation under restricted viewing conditions, suggesting that cues related to the surrounding visual context have a greater influence in V4 than in V1.

Visual Area Comparison

Although a combination of visual and non-visual cues to distance probably determines distance modulation effects, the relative contributions of visual and non-visual cues were different in V1/V2 and V4 Figure 2.15. The majority of cells in V1/V2 were context independent (61% or 14/23 cells); this proportion of context independent cells in V1/V2 was larger than in V4 (47% or 14/30 cells showed context independent distance modulation in V4). These experiments suggest that non-visual cues exert a relatively greater influence on distance modulated cells in early visual areas and that visual effects have a greater influence in higher areas.

Figure 2.15 plots the percentage of cells that maintained distance modulation under restricted viewing conditions and separates the results from monocular and binocular restricted view experiments. A larger proportion of cells in V1/V2 were context independent than in V4. For binocular restricted experiments, over 80% of cells in V1/V2 (5/6) compared with 62% (8/13) in V4 maintained significant distance modulation. Under monocular restricted viewing conditions, a larger pro-

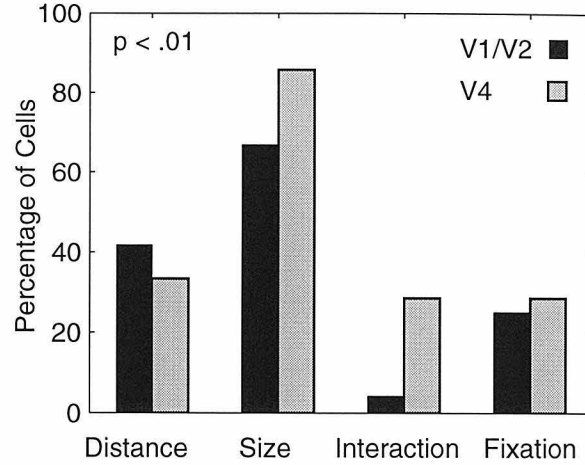


Figure 2.16: Overall results from ANOVA for cells recorded during monocular restricted viewing ($n = 45$). A smaller percentage of the cells in both V1/V2 and V4 were modulated by viewing distance. Size tuning was relatively unaffected.

portion of cells in V1/V2 than in V4 maintained significant distance modulation (53% or 9/17 in V1/V2 compared with 35% or 6/17 in V4, Figure 2.15).

Restricted Viewing and Distance Modulation

The overall results from ANOVA for monocular restricted experiments are shown in Figure 2.16. A much smaller proportion of cells showed distance modulation, while overall size tuning effects were unaffected. This suggests that removing the cues from the surrounding visual context affects distance modulation but not size tuning. See Figure 2.9 for comparison.

To compare average effects of restricted viewing on the gain of the neural response as a function of distance, we calculated the overall fraction gain of the population for each viewing condition (Equation 2.1).

The results are shown in Figure 2.20. Data from both V1 and V4 was combined for this analysis. Cells with significant distance effects are shown as filled bars. Binocular full field viewing experiments showed a higher fractional gain response than either monocular restricted and binocular restricted experiments. The difference between binocular free and monocular restricted was statistically signif-

icant (t-test, $p < .01$), suggesting that removing cues to distance affects the overall gain of the neural response.

2.4 Discussion

The experiments presented here address a relatively unexplored issue in the neurophysiological literature: the interaction between spatial coding and object recognition. Our results indicate that there is an interplay between representation of object size and spatial location at both early and intermediate stages of ventral visual cortical processing. A general discussion of the experimental results from both V1/V2 and V4 are presented in the first section below; issues relating to potential mechanisms of distance modulation, size constancy and theoretical implications are then considered.

2.4.1 Distance Modulation in V1/V2 and V4

Results from V1/V2

Our results from V1/V2 are consistent with the earlier reports of distance modulation in primary visual cortex. Trotter et al. [1992] measured disparity-tuning at multiple distances with random dot stereograms (RDS) in V1 and reported distance modulation in about 80% of cells. Selection of a RDS responsive (and hence disparity-selective) subpopulation of V1 neurons rather than a broader sample is probably the major factor accounting for the slightly higher fraction of distance modulation reported by Trotter and colleagues. Additionally, while we report that 65% of the neurons studied in V1/V2 had statistically significant distance modulation, most of the neurons that we studied in V1/V2 had some differential response as a function of viewing distance (Figure 2.10 and Figure 2.11). Differences between our sample and that of Trotter et al. [1992] might simply reflect different criteria for labeling a neuron as distance modulated. Trotter et al. [1992] also reported that disparity and distance acted independently, and distance modulated the gain of disparity-dependent response.

Our results confirm and extend these findings. First, by using simple shapes rather than RDS, we report here that size and distance information converge in

single neurons in area V1. Second, by comparing full field and restricted field viewing, we found that both visual and extraretinal factors contribute to distance modulation at the earliest stages of cortical visual processing. This finding is supported by reports that V1 neurons depend on angle of gaze dependence [Weyand and Malpeli, 1993], and are influenced by stimuli beyond the classical receptive field [Allman et al., 1990; Knierim and Van Essen, 1992].

Results from V4

The principle finding of this study was obtained from neurons in area V4: object distance modulates neural responses in ventral pathway neurons at intermediate stages of processing. This relatively straightforward result has important consequences for understanding visual processing mechanism and implies that spatial information is encoded in the ventral visual pathway since distance is represented in area V4.

“Where” in the “What” Pathway

Ungerleider and Mishkin [1982] first proposed that anatomically and functionally distinct parallel processing streams exist within the visual cortex, based on contrasting effects of lesions to either posterior parietal or inferotemporal (IT) cortex. Monkeys with posterior parietal lesions were severely impaired on a spatial landmark task but could perform an object discrimination task at normal levels. Monkeys with IT lesions could not learn to discriminate two objects based on their features, but could perform the spatial landmark task. Based largely on these lesion studies, the streams have often been labeled as the “what” and the “where” pathways, leading to dorsal and ventral cortex respectively. This idea has achieved widespread appeal, and further electrophysiological, anatomical and lesion studies have supported the notion that there are distinct dorsal and ventral processing streams in the visual cortex.

However, a number of other studies have cast doubt on the validity of a two-stream visual system, and the labels of “what” vs. “where” [Goodale and Milner,

1992; Milner and Goodale, 1993; Schiller, 1993; Aglioti et al., 1995]. This debate is especially relevant to the study of size constancy. Size is a fundamental attribute of objects and is encoded in ventral stream neurons [Hubel and Wiesel, 1965; Petersen et al., 1980; Desimone and Schein, 1987]. A strict interpretation of the two stream hypothesis suggests that distance is encoded by neurons in dorsal areas and that object size is encoded in ventral stream areas. However, lesion studies that have shown parietal areas are unnecessary for size constancy [Humphrey and Weiskrantz, 1969] support our suggestion that distance information is encoded in ventral stream neurons. Additionally, Ungerleider et al. [1977] showed that monkeys with large V2/V4 extrastriate lesions lose the capacity for size constancy, and make systematic errors related to incorrect distance judgments. We suggest that distance information necessary for size constancy is explicitly represented in ventral cortical areas, and that this representation is independent of dorsal stream influence.

Comparison of Results from V1 and V4

Results from V1/V2 and V4 were surprisingly similar; around 60% of cells in both areas showed significant distance modulation. There were two notable difference between the areas studied: 1) a greater proportion of cells in V4 preferred far stimuli (Figure 2.5B, Figure 2.10B) and 2) visual cues to distance exert a greater influence in V4 than in V1/V2.

Most cells in V1/V2 preferred the closest viewing distance; cells that preferred the farthest viewing distance were relatively rare in V1/V2 (less than 15% of the sample, Figure 2.10A). In V4 Farness cells made up a larger proportion of the sample (about 30%). The emergence of a greater representation of distant space in V4 suggests that Farness cells require a higher level of cortical processing.

Another difference was that visual cues have a greater influence in V4 than in V1/V2. We found that while both retinal and extraretinal cues contribute to distance modulation in both V1/V2 and V4, restricted view experiment results suggest that V4 neurons are more dependent on the surrounding visual context

for distance modulation (Figure 2.15). This suggests that in early visual areas, the representation of distance is based largely on non-visual cues. In intermediate visual areas such as V4, a representation of more distant space emerges; it is likely that visual cues play a major role in the representation of far space in higher cortical visual areas. This finding is consistent with the physical constraints on the oculomotor system — the resolving power of accommodation and vergence is relatively low at far distances. For example, the difference in lens power for shifting fixation from 20 centimeters (the approximate near point for an adult human observer) to one meter is 5 diopters. On the other hand shifting fixation from 1 meter to 5 meters results in a change of only 0.8 diopters.

The suggestion that far space is more dependent on visual cues and is encoded in higher cortical areas is also supported by developmental psychology studies. The development of near and far mechanisms for size constancy seems to progress at different rates and size constancy for far objects is probably learned. Size constancy for near objects is established early in life and is based primarily on vergence and accommodation cues for distance [Frank, 1926; Klimpfner, 1933; Cruikshank, 1941; Leibowitz, 1974; Granrud, 1986]. However, even at close distances, children were much more dependent than adults on binocular disparity and motion parallax for accurate size constancy [Yonas and Hagen, 1973].

2.4.2 Restricted View Experiments: Multiple Cues for Distance

The initial experiment provided the monkey with an unobstructed binocular view of the monitor and room, providing a variety of cues to distance. Under similar viewing conditions humans can exploit oculomotor as well as visual cues to distance such as linear perspective and occlusion [Wallach and Zuckerman, 1963; Leibowitz and Moore, 1966; Collett et al., 1991].

To distinguish the contribution of visual and extraretinal cues, we performed the experiment under two additional viewing conditions. Measurements were repeated

through either binocular or monocular apertures which restricted the animal's view to the monitor screen excluding the monitor frame.

Restricted viewing experiments suggest that multiple cues for distance, originating from both retinal and extraretinal sources, are responsible for the observed changes in neural responsiveness in both V1/V2 and V4. Additionally, restricted view experiments also provide valuable controls for the basic phenomenon of distance modulation, observed under binocular full field viewing. Control experiments will be discussed first followed by a discussion of the relative influence of different types of distance cues.

Control Experiments

Although we attempted to scale all of the stimulus characteristics in proportion with viewing distance, artifacts not related to distance perception could potentially be the source of the distance modulation that we have reported in V1/V2 and V4.

Restricted view experiments were designed to tease apart the relative contributions of different cues for distance; these experiments also serve as controls for the our primary result (i.e. viewing distance modulates the gain of the neural response). Any local visual variations with viewing distance, such as changes in pixellation, brightness or contrast, are common to the restricted viewing conditions and cannot account for observed differences between full field and restricted field responses.

A specific criticism that has commonly been raised regarding the design of these experiments is that the retinal dimensions of the monitor frame change at different distances. Knierim and Van Essen [1992] reported that a large proportion of neurons in area V1 of awake monkeys are suppressed by non-classical surrounds. The monitor frame might be impinging on the non-classical surround of V1 neurons at far distances. Several factors suggest that this is not the primary source of the observed distance modulation in our study sample. 1) A majority of neurons tested under binocular restricted viewing conditions retained significant distance modulation (Figure 2.15). 2) Some neurons retain significant modulation even under

monocular restricted viewing conditions (Figure 2.15). These two factors strongly argue against the frame size as the sole source of modulation in mean response of a neuron, since the frame is absent from view during restricted viewing. 3) A few cells have been tested for sensitivity to monitor frame size. Some context dependent cells, that required the visibility of the surrounding visual context (Figure 2.19), were also tested with an artificial monitor frame at close distances. This frame was designed to match the retinal dimensions of the monitor at far distances. We have not observed any neurons that significantly modulate their responses solely as a function of frame size ($n = 8$).

However, it should be emphasized that we do not wish to rule out the changing retinal dimensions of the monitor frame as a potentially useful distance cue, especially for context dependent neurons. We suggest that the changing angular subtense of the monitor (along with differential occlusion effects) is a legitimate visual cue for distance rather than a simple artifact, and might be encoded as an effect from beyond the classical receptive field. Other non-classical receptive field effects will be discussed further in the following section.

Visual Cues and Non-Classical Influences on Response

Pictorial and perspective cues for distance could have modulatory effect on neural responses that is manifested as an effect from beyond the classical receptive field. Inputs from beyond the classical receptive field could be either excitatory or inhibitory. Allman et al. [1985b,a] predicted that non-classical receptive field inputs could serve as a mechanism underlying perceptual constancy. Desimone and Schein [1987] also noted that the mechanisms underlying size tuning in V4 of Macaques probably involve “silent suppressive mechanisms from beyond the classical receptive field”. In general, the effects of visual context on distance modulation can be broadly defined as effects from beyond the classical receptive field.

However, pictorial and perspective cues change little at different monitor positions. Visual cues under binocular full viewing conditions that change as a consequence of moving the monitor include 1) changes in differential occlusion. The

background regions flanking the monitor are differentially occluded at different distances, both binocularly and monocularly [Bradshaw et al., 1995; Shimojo and Nakayama, 1990; Nakayama and Shimojo, 1990]. Unmasking and masking of these flanking regions could suppress or enhance the response of distance sensitive neurons. 2) Vertical disparity also changes at different monitor positions [Mayhew and Longuet-Higgins, 1982; Rogers and Bradshaw, 1993]. 3) Pupillary size and depth of field and 4) binocular disparity both change slightly at different monitor positions. Although the horizontal disparity was always near zero for the fixation point and the stimuli (RF's were always within 2.5 degrees of the center of gaze), the binocular disparity of the surrounding visual context changes with changing distance and vergence angles.

Each of these effects would be manifested as beyond-the-classical-receptive-field contextual influences on the foveal and perifoveal units in our sample, and each would be eliminated under restricted field viewing, leaving only extraretinal cues. Results from restricted viewing experiments indicate that these visual cues contribute to distance dependent responses; however, visual cues are possibly more influential in area V4 than in V1/V2 (Figure 2.15), and non-visual cues are more influential in early areas.

Oculomotor Cues

Although size constancy has been shown to be independent of image blur [Leibowitz et al., 1978], oculomotor cues are effective distance cues operating at short distances [Leibowitz and Moore, 1966].

As the animal fixates at different distances, the oculomotor system undergoes several changes. The two eyes converge on the fixation point (minimizing binocular horizontal disparity) and the lens accommodates (minimizing blur on the retina). Additionally, the pupils constrict at closer distances (increasing depth of field) [Fincham, 1957; Semmlow and Heerema, 1979; Mays and Gamlin, 1996]. Extraretinal signals from these sources may include both feedback from the eye muscles and/or copies of motor commands to converge or accommodate.

It has been known for over a century that the accommodation and vergence are not independent processes [Maddox, 1893]. Changes in either the accommodative power or binocular convergence are accompanied by corresponding changes in the other system. The link between accommodation and vergence explains, in part, the results observed under monocular restricted conditions. Under monocular restricted viewing, the accommodative signal is still operational. While we did not measure binocular eye position, it is likely that systematic changes in convergence angles accompanied changes in accommodation under monocular restricted viewing. We tested a subset of neurons under both restricted and binocular full view conditions; for those neurons that had significant distance modulation under full view conditions, 61% of V1/V2 neurons and 47% of V4 neurons retained significant distance effects. This result suggests for these cells, reduced signals were sufficient to elicit distance modulation. The difference between the two numbers suggests that oculomotor cues have a relatively larger contribution to distance modulation in V1 than in V4.

Studies in dorsal visual areas have established that eye position strongly modulates the gain of neurons [Sakata et al., 1980; Andersen and Mountcastle, 1983]. It was surprising to find that oculomotor cues also exert a strong influence in ventral visual areas. During our experiments, the monkey often made saccadic eye movements and often looked at particular locations in the lab in between experimental trials. We frequently observed dramatic, albeit qualitative, changes in spontaneous rates that depended on where the monkey was looking. However, we cannot rule out the possibility that visual cues were responsible for these qualitative changes in responses. But in combination with results from our restricted view experiments that suggest the oculomotor cues are influential in V4, it is likely that gaze angle may also be represented in ventral visual cortical areas.

2.4.3 Possible Mechanisms For Size Constancy

Gain modulation was characteristic of neurons that modulated their response as a function of distance. In some cells, we qualitatively observed changes in preferred retinal image size and also changes in size tuning sharpness at both the preferred and the non-preferred distances. However, population analysis indicated that neither shifts in preferred retinal size with distance nor sharpening of retinal size tuning were present in the population of neurons in our sample. These results suggest that most neurons simply modulate the gain of response with distance.

Representation of Distance: Gain Modulation

Monotonic gain modulation, measured by a monotonic increase or decrease in mean firing rate was the most commonly observed type of distance modulation. The results illustrated in Figure 2.10 suggest that distance is encoded in a large proportion of cells in V1/V2 as well as V4. Most cells in V1/V2 and V4 modulate their response as a function of distance.

Gain modulation may be a general coding strategy implemented by the mammalian neocortex. Neurons in dorsal visual cortex modulate the gain of response as a function of angle of gaze [Sakata et al., 1980; Andersen and Mountcastle, 1983; Galletti and Battaglini, 1989; Andersen et al., 1993; Colby et al., 1993; Gnadt and Mays, 1995].

Neural response as a function of attention has been an active area of investigation. One of the primary mechanisms for attentional modulation appears to involve changes in the gain of the neural response [Connor et al., 1996, 1997; Luck et al., 1997]. However, other mechanisms, such as gating within the receptive field, might also be at work during attentional modulation [Moran and Desimone, 1985; Olshausen et al., 1995].

Distributed vs. Explicit Representation of Size Constancy

Our results indicate that both size and distance are represented by neurons at early as well as intermediate stages of processing in the visual cortex, consistent with the hypothesis that these neurons could serve as a basis for size constancy. Network models [Zipser and Andersen, 1988; Pouget and Sejnowski, 1994] based on the properties of parietal cortex neurons, in which gaze direction or gaze distance modulate retinal position or disparity signals can achieve coordinate transformations and egocentric distance computation. Our results, and those of Trotter et al. [1992, 1996], imply that such computations can occur as early as primary visual cortex, and that neurons in downstream areas may simply inherit these properties from V1 neurons.

While a small number of neurons in both V1/V2 and V4 exhibit significant interactions between size and distance, we did not observe any systematic shifts or changes in tuning sharpness with distance (Figure 2.13). When combined with data from Rolls and Bayliss [1986], reporting that only a small percentage of neurons in IT cortex have size constancy (respond to apparent size), we suggest that size constancy is represented as a population code in ventral cortical areas.

2.4.4 Conclusions

The experiments presented here confirm that distance modulates the gain of the neural response as early as V1. We also found distance continues to have a significant influence on neural responses in area V4. This finding suggests that visuospatial coding is present in ventral pathway neurons and is not unique to dorsal stream neurons. Multiple mechanisms, including both visual and non-visual sources, contribute to distance modulation in V1/V2 and V4.

We observed that both distance and retinal size information are encoded on a subset of the neurons in V1/V2 and V4. This is consistent with these neurons underlying size constancy. Significant interactions between distance and retinal size was observed in a small number of neurons, but neither systematic shifts in retinal

size preference nor systematic sharpening of the selectivity of the neural response to size was observed in the population of neurons.

When our results are combined with results of earlier studies showing that size constancy is abolished by ventral but not dorsal cortical lesions [Humphrey and Weiskrantz, 1969], a stronger conclusion is warranted: three-dimensional spatial representation is common to the two visual cortical processing streams. We believe this has implications for understanding the functional organization of the visual cortex, in particular, the binding of attributes estimated in different cortical areas.

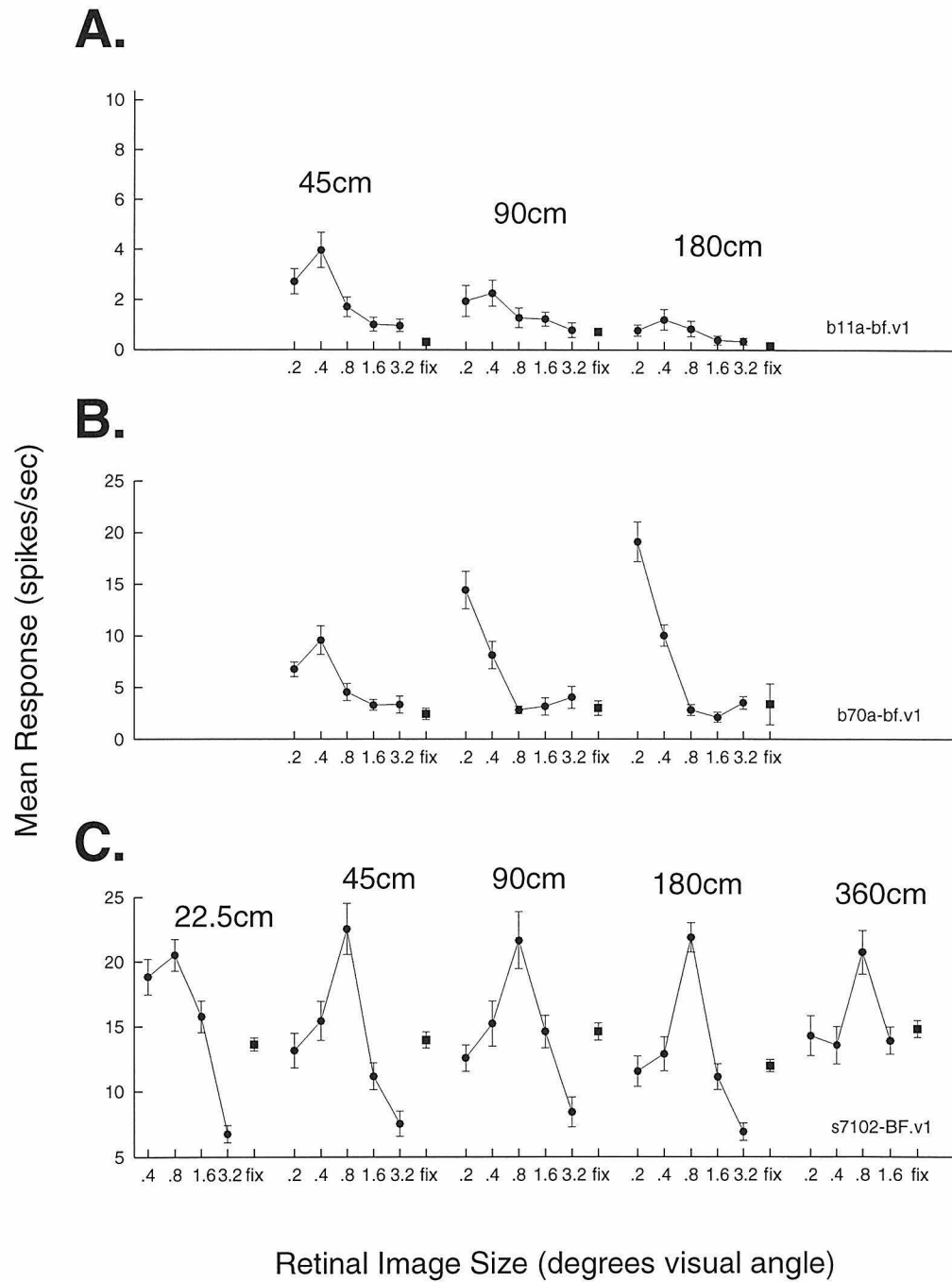


Figure 2.17: Example neurons recorded from area V1/V2. **A.** Nearness cell. This particular cell had a low overall spike rate, but distance effects were significant. **B.** Farness. **C.** Distance Invariant.

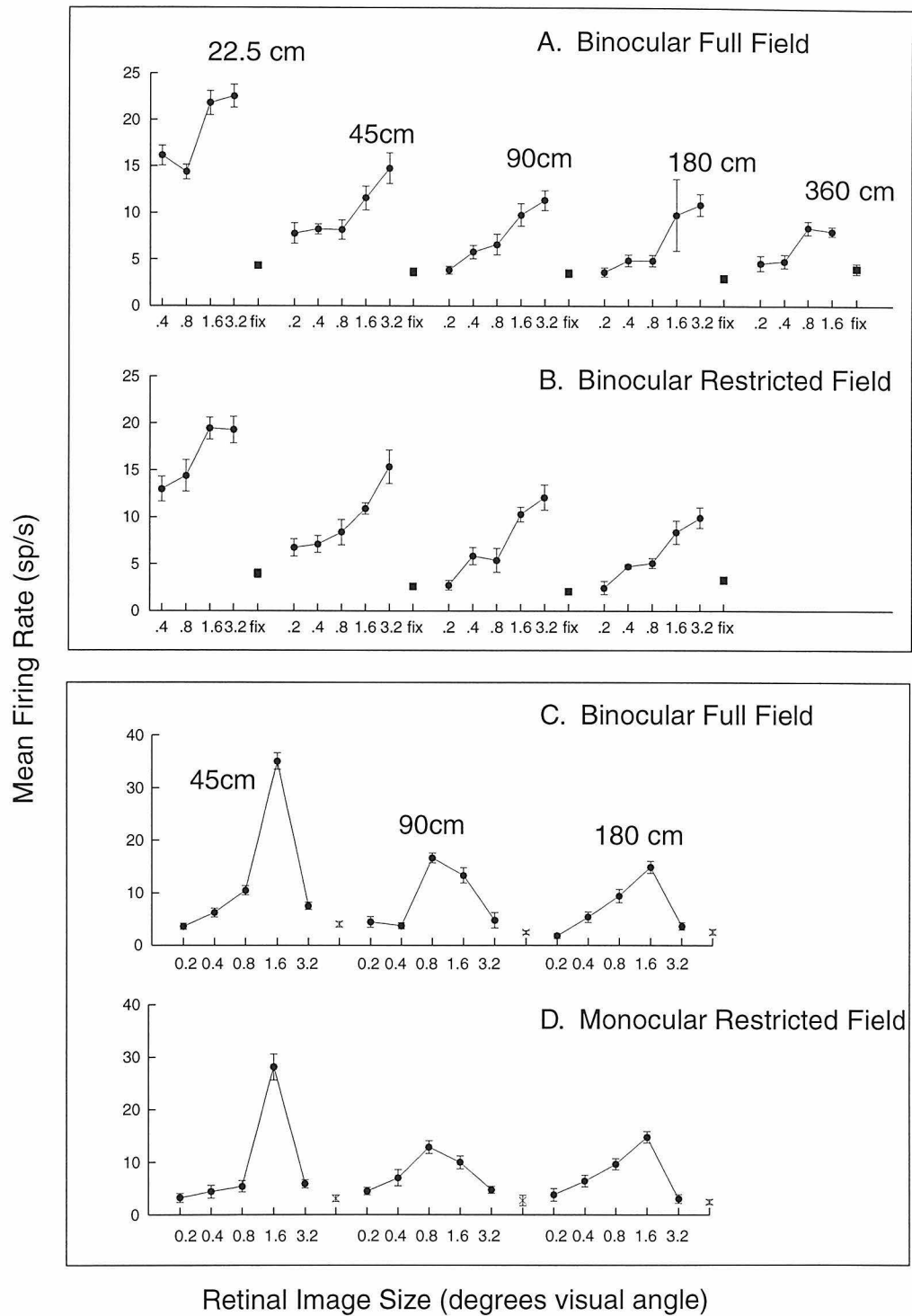


Figure 2.18: Examples of context independent cells. For these cells, restricted viewing conditions are sufficient for significant distance modulation. **A,B.** V1 cell that maintained significant distance modulation under both binocular full and restricted viewing conditions. **C,D.** V4 cell that exhibited distance modulation under both binocular full field and monocular restricted viewing conditions.

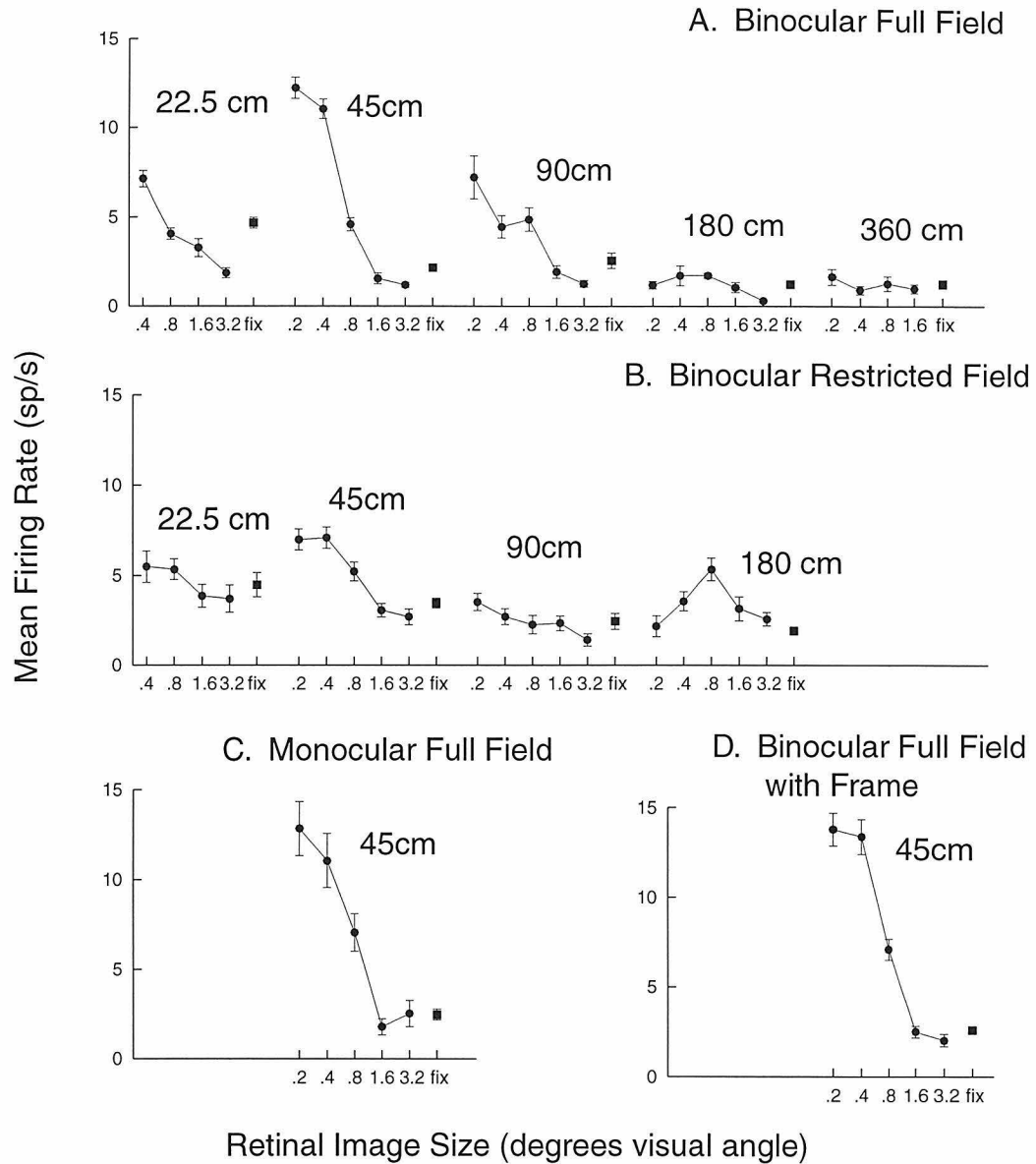


Figure 2.19: Context dependent V4 cell. **A.** Distance modulation under binocular full field conditions. **B.** Distance modulation was abolished by binocular restricted viewing. **C.** Responses at the preferred distance (45 cm) under monocular full field conditions were not attenuated compared to binocular full field, indicating that binocular disparity cues are not necessary for distance modulation. **D.** Results from frame test. Cell was measured at 45cm with a cardboard frame that matched the retinal dimensions of the monitor frame at 180cm. The frame alone did not suppress the neurons response.

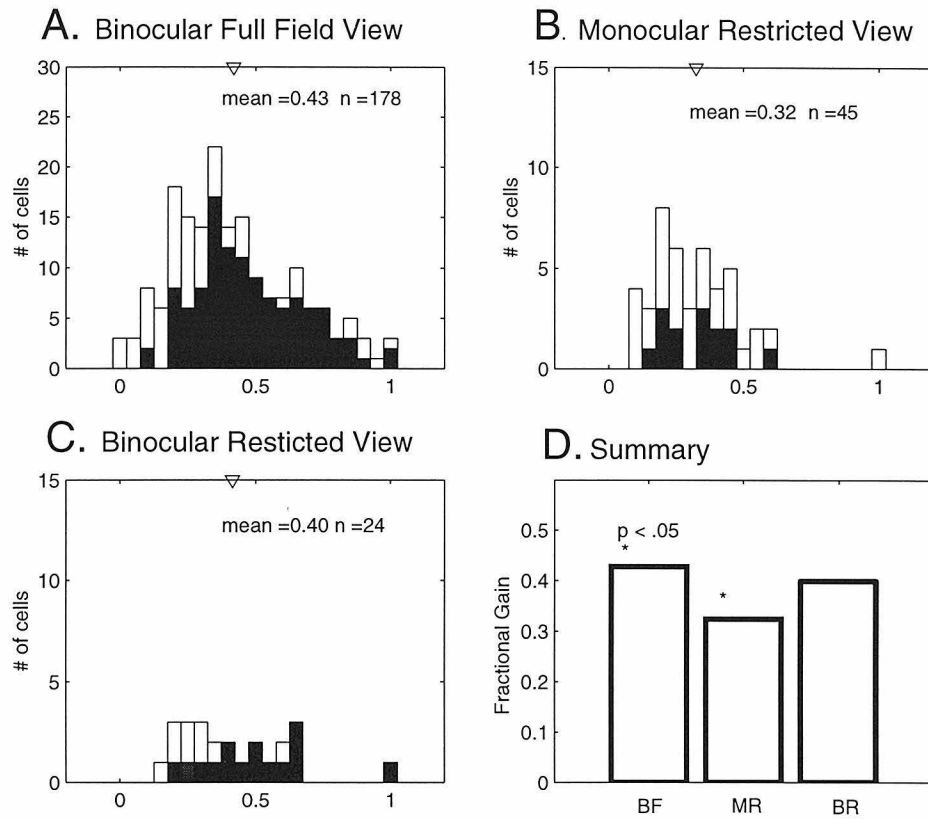


Figure 2.20: Fraction gain for different viewing conditions. **A.** Binocular Free. **B.** Monocular Restricted. **C.** Binocular Restricted. **D.** Mean fractional gain for each population. The star indicates significant effects ($p < .01$, t-test).

Chapter 3 Conclusions

The study of size constancy has provided an excellent intellectual framework for approaching the problem three-dimensional perception. Perhaps the most important advantage is that size constancy is very robust and is heavily utilized by the primate perceptual system in daily life. Fast and reliable scaling for distance and the accurate perception of object size are both extremely important for an animal to survive. Many animals, including macaque monkeys, have visual size constancy and can be trained to report the size of an object independent of viewing distance. Because size constancy is such a robust phenomenon, visual behaviors associated with size constancy are probably not artifacts of laboratory overtraining and may actually reflect some natural perceptual mechanisms utilized by the primate visual system.

Some other advantages afforded by the study of size constancy include an extensive psychophysical and developmental psychology literature and a wealth of robust visual illusions that are based on distortions of visual size.

A number of these advantages have allowed us to develop an experimental paradigm for the study of the neural mechanisms of size constancy. We utilized a very simple behavior that is directly related to the perception of size and distance (visual fixation at varying distances) and recorded neural responses during the performance of this behavior. This chapter will explore the implications of our experimental results and also highlight the limitations of our paradigm and recommend areas where additional study is warranted.

3.1 Cortical Visual Processing Mechanisms

A Common Three-Dimensional Representation

The principle finding of this study was that object distance modulates the gain of neural responses in V4. This relatively straightforward result has potentially far reaching implications for understanding parallel processing and the functional organization of the visual cortex.

The standard interpretation of the two stream hypothesis implies that distance is encoded by neurons in dorsal areas (the “where” stream) and that object size is encoded in ventral stream areas (the “what” stream). However, our experimental results suggest that spatial information is not strictly confined to the dorsal processing stream. Combined with results from previous lesion studies that have shown that ventral but not dorsal cortical lesions disrupt size constancy [Humphrey and Weiskrantz, 1969], our data indicates that spatial information necessary for size constancy is encoded by ventral stream cortical neurons. Thus, spatial processing mechanisms are carried out by ventral stream neurons independent of dorsal stream influence.

Many object vision processes, including size constancy, require processing of spatial information. We suggest that three-dimensional spatial representation is common to both the dorsal and the ventral visual cortical processing streams. This supposition is supported by recent results from fMRI experiments by Aguirre and D’Esposito [1997]. They found that separable dorsal and ventral areas were strongly activated by a spatial orientation virtual reality task, suggesting that the spatial processing necessary to move about in a virtual reality environment is subserved by both dorsal and ventral areas. We further speculate that an abstract three-dimensional representation of visual space may be common to all visual cortical areas.

Neural Mechanisms for Size Constancy

We originally set out to look for size constancy neurons, that is, neurons that respond best to particular object dimensions rather than retinal dimensions. Rolls and Bayliss [1986] reported that a few neurons in IT cortex encoded object size and were thus suggested to be size constancy neurons. However, these neurons were quite rare (four out of several hundred tested). We observed that only a small number of neurons in both V1/V2 and V4 exhibit significant interactions between size and distance. Our results indicate that neurons in V1/V2 and V4 do not shift preferred size tuning with changing distance as a population.

When combined with data from Rolls and Bayliss [1986], we suggest that size constancy is represented as a population code in ventral cortical areas. Neurons that encode both size and distance in V1/V2 and V4 could serve as the underlying neural basis for size constancy. However, the study by Rolls is the only other experimental examination of the interaction between object distance and size, directly related to the problem of size constancy. Further examination of neurons in V1, V2, V4, and new experiments in areas VP and IT are necessary to directly elucidate the mechanisms of size perception and size constancy.

Network models [Zipser and Andersen, 1988; Pouget and Sejnowski, 1994, 1997] based on the properties of parietal cortex neurons where gaze direction or gaze distance modulate retinal position or disparity signals can achieve coordinate transformations and egocentric distance computation. Our results, and those of Trotter et al. [1992, 1996], imply that such computations can occur as early as primary visual cortex, and that neurons in downstream areas may simply inherit these properties from V1 neurons. Further theoretical work, including developing more biologically plausible models of size constancy, needs to be performed and could lend insight into the neural mechanisms of perceptual constancy and also drive future electrophysiological experiments.

The Binding Problem

Our hypothesis, that an abstract representation of three-dimensional visual space is common to all areas of the visual cortex, has implications for many aspects of cortical visual processing and the functional organization of the visual cortex. One particular application of our hypothesis involves the separation of processing and recombination or “binding” of visual processing information.

It has been established that the dorsal and the ventral visual pathways are not completely independent of each other and the scope of the behavioral contributions made by each pathway is not fully understood (for a review, see Merigan and Maunsell [1993]). The distinctions between the two pathways has proven to be a valuable framework for evaluating the functional differences between cortical visual areas [Goodale and Milner, 1992; Ferrera et al., 1992, 1994; Milner and Goodale, 1993; Merigan and Maunsell, 1993; Schiller, 1993].

However, the separation of processing function and especially the handles of “what” and the “where” pathways have led some researchers to believe that object and spatial information are exclusively processed by each respective pathway, and the outputs of the pathways are later recombined. This concept of separating different types of visual information creates a binding problem, since the divided visual information necessarily must be recombined. Our results suggest that solutions to the binding problem are not necessary — the spatial information necessary for size constancy is present along with the object information. Thus, information from dorsal and ventral cortex does not need to be recombined for size constancy. This suggests that solutions to the binding problem might also be unnecessary in other systems where anatomical separation of processing function and downstream binding have been postulated.

Gain Modulation in Cortical Neurons

Change in response gain was the most commonly observed change in the firing pattern of neurons that encoded distance in V1/V2 and V4. A large body of

experimental evidence suggests that neurons in dorsal visual cortex modulate the gain of response as a function of distance and angle of gaze [Sakata et al., 1980; Wise and Desimone, 1988; Andersen and Mountcastle, 1983; Galletti and Battaglini, 1989; Colby et al., 1993; Gnadt and Mays, 1995]. We suggest that gain modulation might be a general coding mechanism implemented by cortical neurons in both dorsal and ventral visual processing streams. Moreover, gain modulation may be a general coding strategy implemented by the mammalian neocortex.

Changes in neural response as a function of attention has been an active area of investigation and might lend insight into potential neural mechanisms of size constancy. One of the primary mechanisms for attentional modulation appears to involve changes in the gain of the neural response [Connor et al., 1996; McAdam and Maunsell, 1996; Connor et al., 1997; Luck et al., 1997; Salinas and Abbott, 1997]. It is unknown how the mechanisms of gain control utilized in attention interact with mechanisms related to changes in viewing distance.

Additionally, spatial attention also involves mechanisms other than gain modulation and work in this area might lend insight into some other potential and testable mechanisms of size constancy. Physiological studies have shown that gating within the receptive field in area V4 [Moran and Desimone, 1985] is an important factor in attentional modulation. Several theoretical models have been developed that explore possible neural circuitry involved in attentional modulation. Olshausen et al. [1993] developed a biologically plausible model of attentional modulation based on a dynamic routing circuit, that remaps selected portions of an input array into an object-centered reference frame. Olshausen et al. [1995] later generalized the dynamic routing model for forming size- and position-invariant representations of visual objects. Such models achieve coordinate transformations in a very different manner than do models based on basis functions [Pouget and Sejnowski, 1994, 1997].

To what degree mechanisms beyond gain are important in size constancy remains unanswered. In the experiments presented here, interactions between retinal size tuning and distance beyond gain modulation were complex and not easily inter-

puted. The presence of modulatory interactions beyond gain suggest that multiple distance cues that influence the cell's response may exert differential effects at different viewing distances. Mechanisms of interaction between various cues to distance and other factors, such as the animals attentional state, are not known.

Neuroethological Approaches

Size constancy probably results from interactions between visual spatial processing and object vision. In most previous studies, these aspects of visual processing were considered separately. Our results, as well results from many neuroethological studies, indicate that such a separation of function is highly unlikely. Separation of visual function into independent processing modules ignores a major function of the visual system — the control of behavioral output.

Neuroethological studies have suggested that the frog visual system is composed of independent, parallel visual modules, each with specific behavioral outputs [Ingle, 1980, 1982; Ewert et al., 1983]. Because the frog visual system has been approached with the natural behavior of the animal in mind, these parallel systems have not been postulated to be processing different types of visual information which later converge and form a unified perception of the world. The frog has at least five separate visuomotor channels [Ewert et al., 1983] and it would be unlikely that a single visual representation would mediate all five parallel systems. Instead each system is involved in the processing information specific to different behavioral outputs, and all the visual information necessary for that behavior is locally represented.

Similarly, in primate species, dorsal cortical areas are considered to be involved in visuomotor behavior, such as reaching and grasping. This behavior requires extensive spatial information, and therefore spatial information is well represented in dorsal areas. However, just because spatial information is processed in primate dorsal visual areas, does not necessarily suggest that these areas are the exclusive source of spatial processing.

If we view the visual system as a means of controlling behavioral output, spatial information necessary for behaviors is likely to be represented locally. For example,

information necessary for spatial attention and size constancy is represented in ventral visual cortex along with information about object identity. Our results highlight the need for considering the biology of the animal under investigation, rather than simply focusing on the inputs to the visual system.

Neural Coding of Natural Scenes

Our experiments can be viewed as an potential paradigm for exploring the mechanisms of natural vision. Olshausen and Field [1996a,b] have suggested that the visual system is optimized for coding natural scenes. Gallant et al. [1998] reported that the overall responsiveness of a neuron is attenuated when free viewing natural images compared to responses of the neuron to optimized bars and sinusoidal gratings. Gallant suggested that non-classical surrounds might be suppressing neuronal responses and that a wealth of other excitatory or inhibitory extraretinal signals (eye position, the animal’s attentive state, etc.) are probably in operation as well.

In our experiments, we found that the natural image (the actual, physical room surrounding the computer monitor) is often involved in modulating the responses of a neuron to a somewhat unnatural stimuli (a bar or spot on a computer screen). Our approach of real physical space was inspired by work in the owl auditory system [Knudsen and Konishi, 1979; Konishi, 1986] where physically moving a sound source was an effective approach in understanding the mechanisms of auditory sound localization.

A method of systematically testing the influences of different features in the surrounding visual context would be useful to further explore the mechanisms of neural coding of distance and size perception. Before such experiments can be performed, it may be necessary to rigorously describe the characteristics of the surrounding visual context. A statistical description of the inherent characteristics of natural scenes of near and far objects or landscapes remains undefined.

Role of V4 in Color Vision

Our findings add further evidence to the large body of data that contradicts the idea advanced by Zeki [1980] that V4 is exclusively or primarily devoted to the processing of color [Desimone and Schein, 1987; Heywood et al., 1992; Schiller, 1993; Heywood et al., 1995; Merigan, 1996]. V4 in macaque monkeys does not correspond to the cortical area on the ventromedial side of the occipital lobe in humans that, when damaged, produces achromotopsia [Allman and McGuinness, 1988; Damasio et al., 1980; Heywood et al., 1995].

3.2 Development of Size Constancy

“...when I was a boy going past the garrison chapel in Potsdam, where some people were standing in the belfry, I mistook them for dolls and asked my mother to reach up to get them for me. The circumstances were impressed on my memory, because it was by this mistake that I learned to understand the law of foreshortening in perspective”.
[Helmholtz, 1925]

The quote above, taken from Helmholtz [1925], illustrates the role of learning in the development of size constancy. A number of studies in the developmental psychology literature have shown that learning may play a role in this early development of the perception of size constancy. Psychological experiments suggest that size constancy for far distances is learned during childhood; eight year old subjects tend to underestimate the size of distant objects [Zeigler and Leibowitz, 1957]. The development of near and far mechanisms for size constancy seems to progress at different rates; size constancy for near objects is established early in life and is based primarily on vergence and accommodation cues for distance [Frank, 1926; Klimpfinger, 1933; Cruikshank, 1941; Leibowitz, 1974; Granrud, 1986]. However, even at close distances, children were much more dependent than adults on binocular disparity and motion parallax for accurate size constancy [Yonas and

Hagen, 1973]. Piaget [1969] observed a similar developmental time course in depth discrimination and size constancy in children.

Visual illusions of size differences may be instances in which the constancy mechanism are engaged inappropriately [Gregory, 1963; Aglioti et al., 1995]. Leibowitz [1971] found that the perceived magnitude of the Ponzo illusion increased in children between ages 5 and 10 years in the same period in which they acquired size constancy for distant objects.

In our experiments, we found that the majority of neurons in primary visual cortex exhibited their highest response rates for distances of less than 1 meter. A very small proportion of cells in our sample preferred distances of greater than 1 meter in primary visual cortex. However, at an intermediate level of visual processing, in area V4, a much larger proportion of cells responded best for far distances (greater than 1 meter). These results suggest that the perception of size constancy for distances greater than 1 meter and the representation of far distances arise as a result of higher levels of cortical processing.

When our electrophysiological results are combined with data from numerous developmental psychology studies, we suggest that the representation of near distances not only develops earlier in a primate's life, but that the representation of near space reflects an early stage of visual processing. The representation of far space, on the other hand, must be learned through visual experience (and is slow to develop) and may be the result of higher levels of cortical processing. Additionally, restricted view experiments suggest that neurons in area V4 are more dependent on the surrounding visual context for distance modulation than neurons in V1. This result is consistent with the suggestion that the representation of far space in higher visual areas is based on learned visual cues.

In summary, the distinction between near and far mechanisms of size perception and size constancy is supported by several lines of evidence. First, the physical nature of the various cues for distance and behavioral results suggest that different mechanisms are operational at near and far ([Holway and Boring, 1941; Leibowitz and Moore, 1966], discussed at length in section 1.2). Second, previous work on

the development of size constancy suggests that the time course for the acquisition of size constancy is different for near and far distances. Finally, we found that proportional representation of near and far space and the proportional contribution of retinal and extraretinal cues differs between V1 and V4.

3.3 Future Studies and Limitations

This work explored interactions between spatial processing and object recognition mechanisms, using electrophysiological techniques in awake monkeys. We have shown here that neurons in ventral areas are sensitive to spatial aspects of vision (such as distance) as well as object vision aspects such as retinal size, color, orientation etc. From this simple result, we have suggested that a three-dimensional representation of visual space is characteristic of visual cortical areas; such a three-dimensional representation might be similar in nature to retinal topographic maps, and form the underlying framework for cortical processing circuits. However, this hypothesis is not yet established and further investigation and experiments need to be performed in order to test the hypothesis.

Because neurons in dorsal areas modulate their response gain with changes in the direction of gaze, an interesting and straight forward experiment would be to test if neurons in ventral areas are also sensitive to direction of gaze. We observed, qualitatively, that V4 neurons often changed their response gain between trials as the monkey made eye movements around the experiment room. However, these changes could be due to attentional shifts or from changes in the light pattern on the monkey's retina and receptive field. The experiment need to be completed under controlled conditions to establish whether or not angle of gaze modulates neural responses in ventral areas.

Our experimental paradigm involved training the animal to fixate at different distances. We did not use an active size discrimination task and the monkey was only required to fixate for several seconds in order to receive a juice reward. Size discrimination tasks could be implemented to measure the animal's reports of stim-

ulus size. This behavioral data could then be combined with the electrophysiological data and might give further insight into the mechanisms of size perception. Visual size illusions, such as the Ebbinghaus and the Ponzo illusions (see Figure 1.3 and Figure 1.4) might provide a good paradigm to examine how changes in perception are manifested at the single neuron level. More natural implementations of the illusions could also be developed and manipulated experimentally.

The study of size constancy at the single neuron level has been a productive approach to understanding the problem of three-dimensional perception. While the work presented here represents a significant advance in the understanding of size perception in the primate visual cortex, many questions regarding the mechanisms of three-dimensional perception remain unanswered.

3.4 Specific Contributions

1. Object distance modulates neural activity in cortical visual areas V1/V2 and V4. Distance is explicitly encoded in V4, indicating that spatial processing is not confined to parietal cortex.
2. Both retinal and extraretinal cues contribute to distance modulation in V1/V2 and V4.
3. Single neurons are present in V1/V2 and V4 that encode both retinal size and distance information. This is consistent with these neurons serving as a basis for size constancy.
4. Contrary to previous work separating the visual cortex into a dorsal "what" and a ventral "where" pathway, our results suggest that 3-dimensional spatial information is coded in some ventral stream neurons. We further suggest that like retinotopic maps, 3-dimensional spatial coding is ubiquitous to visual cortical processing.
5. Gain modulation is a general coding mechanism implemented by cortical neurons in both dorsal and ventral visual processing streams.

Appendix A Cortical Cytochrome Oxidase Topography in Two Lemur Species

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Abstract

We had the unique opportunity to study fresh post-mortem brain tissues from two lemuroid primate species: the brown lemur (*Eulemur fulvus*) and the mouse lemur (*Microcebus murinus*). The brains were removed, physically flattened, cut parallel to the cortical surface and stained for cytochrome oxidase (CO) activity. CO staining revealed a system of dark staining CO blobs in area V1 of both *Eulemur* and *Microcebus*. Area V2 of *Eulemur* showed some patchy CO staining, but a stereotyped system of prominent, dark staining, thick and thin stripes (present in old and new world monkeys) was not evident. *Microcebus* did not show any evidence of V2 stripes; however, the absence of CO stripes in *Microcebus* V2 could be attributed to the condition of the brain tissue at the time of histology. In *Eulemur* we were able to identify area MT, primary auditory cortex (A1) and primary somatosensory cortex (S1), based on dark cytochrome oxidase staining patterns. These findings indicate that two characteristic features of the visual cortex in anthropoid primates, namely the cytochrome oxidase blobs in V1 and cortical visual area MT, are also present in lemuroid primates.

A.1 Introduction

The functional organization of the visual cortex in primates has been intensively investigated, but the majority of the work has been performed on only a few species and very little is known about the visual cortex of the lemurs of Madagascar. We studied fresh post-mortem brain tissues from two lemuroid primates species, the brown lemur (*Eulemur fulvus*) and the mouse lemur (*Microcebus murinus*), using cytochrome oxidase (CO) staining techniques.

In anthropoid primates, staining for the mitochondrial enzyme cytochrome oxidase reveals a system of periodic dark and light staining regions in the supergranular layers of primary visual cortex [Wong-Riley, 1979]. The presence of CO “blobs” or “puffs” is among the strongest evidence for visual processing modularity because they have been anatomically correlated with processing functions not directly related to metabolism, including a number of physiological and connective properties [Horton and Hubel, 1981; Horton, 1984; Livingston and Hubel, 1984; Tootell et al., 1985, 1988; Condo and Casagrande, 1990; Allman et al., 1990; Blasdel, 1992; Yoshioka et al., 1996].

Anatomically, the presence of CO blobs has been demonstrated in all old and new world anthropoids examined thus far [Horton and Hubel, 1981; Horton, 1984; Tootell et al., 1985]. Some information exists on the cortical organization of a few strepsirine primate species including the Slow Loris (*Nycticebus*), the Dwarf Lemur (*Cheirogaleus*) and several Bushbaby (*Galago*) species [Condo and Casagrande, 1990; Preuss et al., 1993; Preuss and Kaas, 1996], all of which have CO blobs in primary visual cortex. Recently, the presence of CO blobs has also been reported in cats [Murphy and Van Sluyters, 1995], challenging the theory that CO blobs are unique to primates [Horton, 1984]. Thus, the examination of unstudied primate taxa (such as the lemurs) is necessary in order to answer phylogenetic questions, such as the origin of CO blobs in mammals.

Although the distribution of CO activity and the corresponding physiological function of the CO system in lemuroid primates is of comparative phylogenetic

interest, the endangered species status of lemurs in the wild prohibits electrophysiological study. Because the distribution of CO activity can be studied in fresh, post-mortem tissue, we examined the brains of two rare species of lemurs soon after they died in captivity (from causes unrelated to these experiments) as a step towards understanding the functional organization of the visual system in lemuroid primates.

Preliminary versions of this work have been previously reported [Jeo et al., 1997].

A.2 Methods

A.2.1 Histology and Flattening

We examined 4 hemispheres from 2 brown lemurs (*Eulemur fulvus*) and 4 hemispheres from 2 mouse lemurs (*Microcebus murinus*). The mouse lemurs were found dead in their cages and their brains promptly removed and prepared for flatmounting. One of the brown lemurs was also found dead in its cage. The second brown lemur developed a large testicular tumor. The tumor was deemed inoperable and under the advice of the attending veterinarian it was decided that the animal was to be killed. We deeply anesthetized this animal and perfused transcardially with buffered saline.

We removed the unfixed brains, quickly photographed, and physically flattened the neocortical hemispheres [Tootell et al., 1985; Sereno et al., 1994]. This was accomplished by gently dissecting away the underlying white matter with dry cotton swabs. A cut was made in the fundus of the calcarine sulcus to allow the cortex to lie flat. The cortex was fixed (either 4% glutaraldehyde or 10% formalin) between large glass for several hours. The tissue was then allowed to float freely in a 30% sucrose solution until it sunk. The flattened hemispheres were cut in 50 μ m sections parallel to the pial surface on a freezing microtome [Sereno et al., 1994]. Sections were stained for cytochrome oxidase activity [Wong-Riley, 1979; Tootell et al., 1985]

and the entire flattened sections were mounted whole, on large glass slides.

A.2.2 Reconstruction of Cytochrome Oxidase Topography

Physically flatmounted sections cut approximately parallel to cortical laminae reveal subtle features in two dimensions. Such features are often visible in one dimension in conventional sections but are extremely difficult to reconstruct in two dimensions from (a much larger number of) conventional sections, especially if these features are small or have undulatory borders. Single sections from flatmounts, however, can pass through more than one cortical layer in different parts of the section. Because of this, we made 10x pencil drawings of the overall density of the cytochrome oxidase stain by superimposing all the sections from one hemisphere using a projecting microscope. We used the radial blood vessels to align the flatmounted sections thus keeping CO features in precise registration.

A.3 Results

Area V1

We were easily able to identify the primary visual cortex (V1) at the occipital pole of all CO stained hemispheres. Area V1 of both *Eulemur* and *Microcebus* was characterized by a system of dark staining CO blobs.

CO blobs were visible in both superficial and deep layers of the cortex. CO blobs were quite large compared to those present in anthropoid primates (Figure A.2), and resembled blobs reported in *Galago* species.

Area V2

Anthropoid primates exhibit a stereotyped pattern of alternating thick-, thin- and interstripe CO regions [Tootell et al., 1983; Horton, 1984; Tootell et al., 1985; Olavarria and Vanessen, 1997]. Area V2 of *Eulemur* showed some patchy CO staining (Figure A.3, arrows), but a stereotyped system of prominent, dark stain-

ing, thick and thin stripes (present in old and new world monkeys) was not evident (see Figure A.2 for comparison).

Some irregular dark staining regions were noted in a number of flatmounted sections, but we were not able to consistently identify stripe-like activity in area V2 in every histological section. Through reconstruction of the CO staining in all sections, an overall, patchy and irregular organization of CO activity in area V2 is evident Figure A.5.

The stripes in V2 have also been defined by anatomical connection patterns in the absence of strong CO staining in *Galago* species [Krubitzer and Kaas, 1989, 1990]; we cannot rule out the presence of connectionally defined stripes in V2 in *Eulemur*.

Microcebus did not show any evidence of V2 stripes Figure A.4; however, the absence of CO stripes in *Microcebus* V2 could be attributed to the condition of the brain tissue at the time of histology.

Other Cortical Areas

In *Eulemur* we were able to identify area MT, primary auditory cortex (A1) and primary somatosensory cortex (S1), based on dark cytochrome oxidase staining patterns Figure A.5.

Mouse Lemur

Results from the mouse lemur were less conclusive because the tissue studied was not in optimal condition at the time of histology. However, clear periodic regions of dark and light staining were identified in primary visual cortex of two mouse lemurs Figure A.4. Area V2 did not show any indications of stripes. However, the absence of CO stripe could possibly be attributed to the suboptimal state of the tissue at the time of histology. The blobs in the mouse lemur were qualitatively similar to those observed in the brown lemur and the galago.

A.4 Discussion

The lack of detailed comparative information from the majority of primate species makes hypothesis regarding the evolution of the primate visual system difficult to develop and test. This dearth of information is especially acute in lemuroid species, which make up a significant portion of the primate evolutionary tree and have not been well studied. This study is one of the few investigations of the organization of the visual cortex in lemuroid primate species.

Figure A.5 summarizes results from reconstruction the entire map of CO activity, done with 10x pencil tracings of each flatmounted section. Several patterns emerged from this reconstruction. Visual areas MT and DL were identified from dark and light staining regions respectively. These findings together with recent data from the dwarf lemur (*Cheirogaleus medius*) indicate that two characteristic features of the visual cortex in anthropoid primates —a system of CO blobs is present in area V1 and a number of cortical visual areas, including area MT — are also present in lemuroid primates [Paolini et al., 1994; Preuss and Kaas, 1996]. Additionally, we were able to reconstruct the locations of primary auditory and somatosensory areas based on dark CO staining patterns (Figure A.5).

Our results suggest that there remains a high degree of similarity of the functional organization of the visual cortex between lemuroid and anthropoid primate species. Our data are consistent with the hypothesis that CO blobs evolved once in primate evolution and that CO blobs in V1 are characteristic features of all primates including the lemurs.

Relatively little is known about the functional significance of the CO system in lemuroid species because electrophysiological studies have not been performed. Livingston and Hubel [1984] suggested that the CO blobs are specialized for color processing, based on studies in macaque and squirrel monkeys. However, further comparative results imply that the processing of color information is probably not carried out by the CO blobs in all species. The blobs are well developed in nocturnal primates with limited color vision [Horton, 1984; Allman et al., 1990; Condo and

Casagrande, 1990], and the earliest primates were likely to be nocturnal as well [Martin, 1990]. Additionally, cats have a well developed CO blob system [Murphy and Van Sluyters, 1995], but poor color vision [Guenther and Zrenner, 1993]. *Microcebus* is an example of another nocturnal primate with a well developed system of CO blobs; this finding further supports the hypothesis that CO blobs are not specialized for color vision in prosimian primates.

Area V2 of *Eulemur* showed some patchy cytochrome oxidase staining, but a clear system of prominent thick- and thin- stripes was not evident (Figure A.3). The absence of CO stripes in Lemur V2 does not discount the possibility that the stripes are defined architectonically. Connection patterns from area V1 to area V2 are likely to be similar to those found in *Galago* species, where stripes in V2 do not show distinct CO activity but are well defined by architectonic connectivity [Condo and Casagrande, 1990; Krubitzer and Kaas, 1990]. However, the reduction of CO activity in *Eulemur* V2 reported here (as well as in *Galago* and *Nycticebus* [Preuss et al., 1993]) might reflect that area V2 of primitive primates is serving a different or reduced functional role that demands less metabolic energy.

Similarly, staining flattened tree shrew primary visual cortex for myelin using the Gallyas silver stain [Gallyas, 1979] reveals a pattern of alternating light and dark bands akin to the blob like pattern following cytochrome oxidase stains in primate V1 [Lyon et al., 1996, 1997]. In primates, myelin stains darkest in the area surrounding the blobs [Krubitzer and Kaas, 1989]. Myelin blob-like patches in tree shrews could be the equivalent of interblob regions in primates. Though tree shrews do not show evidence of cytochrome oxidase blobs, they show that at least architectonically tree shrew V1 is modularly organized in a similar fashion to primate V1.

The exact functional significance of the CO blobs in most primate species remains unknown. However, modular organization is likely to be a general feature of the mammalian visual system — CO blobs may simply represent a subset of the many types of spatially blob-like cortical processing modules.

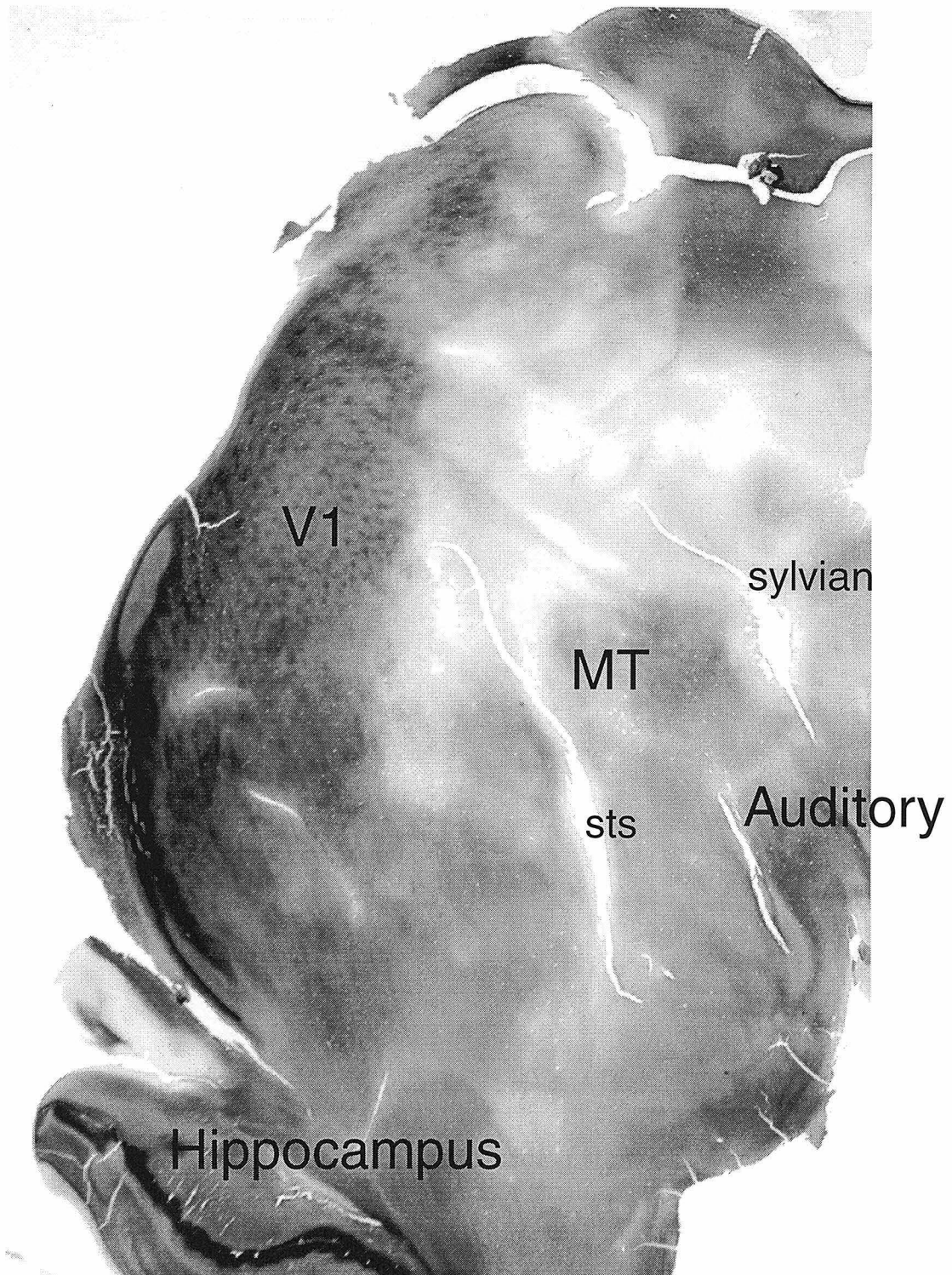


Figure A.1: Photomicrograph of flatmounted section through superficial layers of *Eulemur* visual cortex. Staining for CO reveals many characteristic features of cortical anatomy including a system of CO blobs in primay visual cortex.

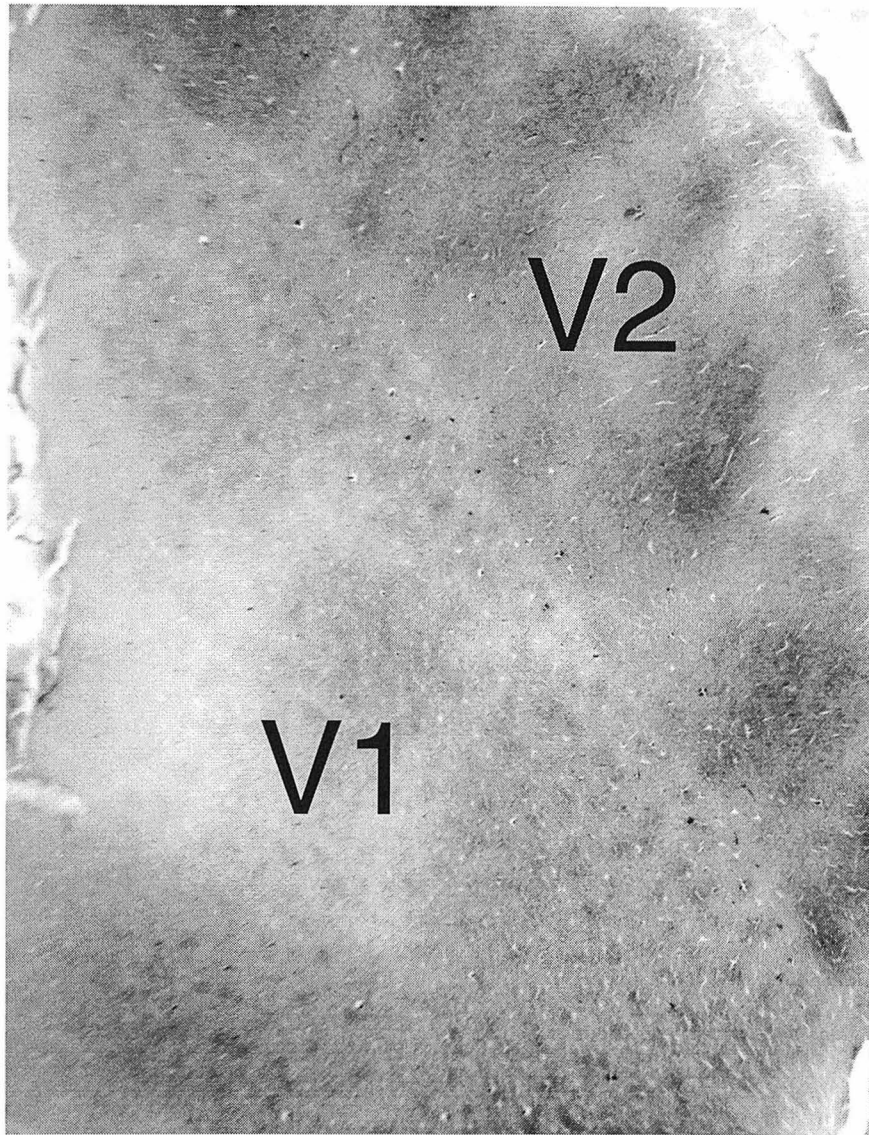


Figure A.2: Cebus monkey cytochrome oxidase stained flatmount. Anthropoid visual cortex is characterized by a system of small, punctate CO blobs in V1 and clear alternating stripes in V2. CO blobs in V1 of the Cebus monkey are much smaller than those identified in either Lemur species. The functional significance of blobs size is not well understood.

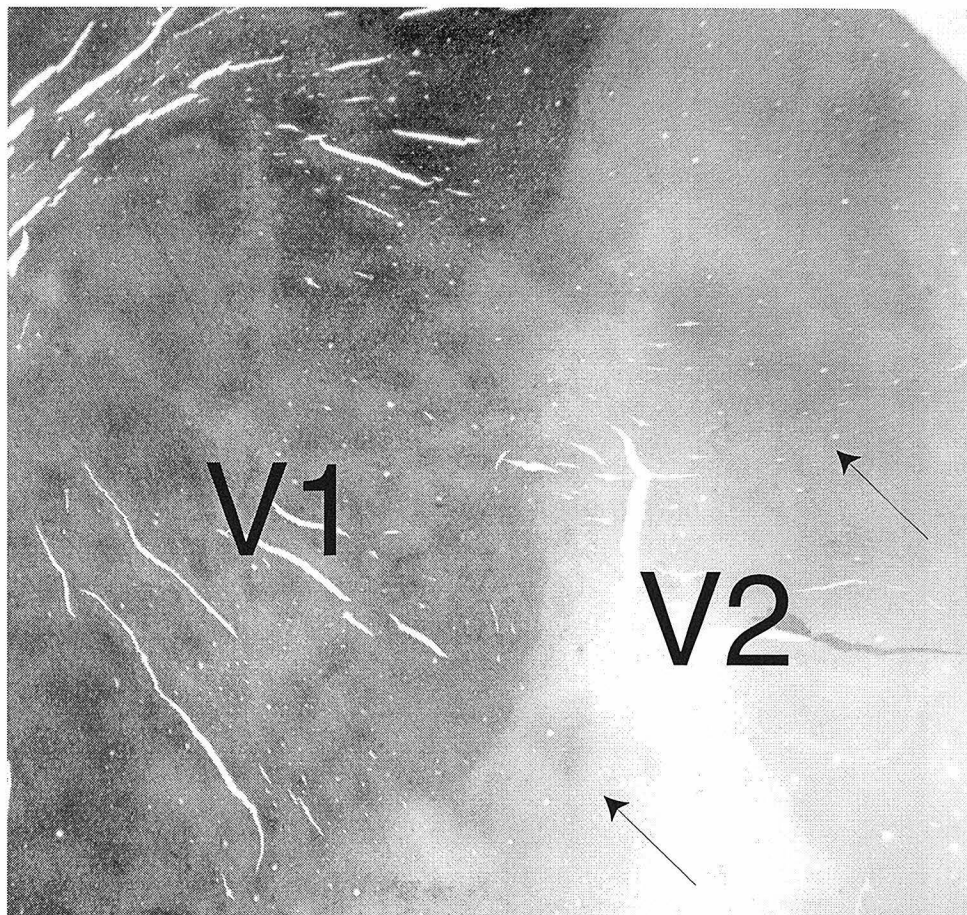


Figure A.3: Lemur V2.

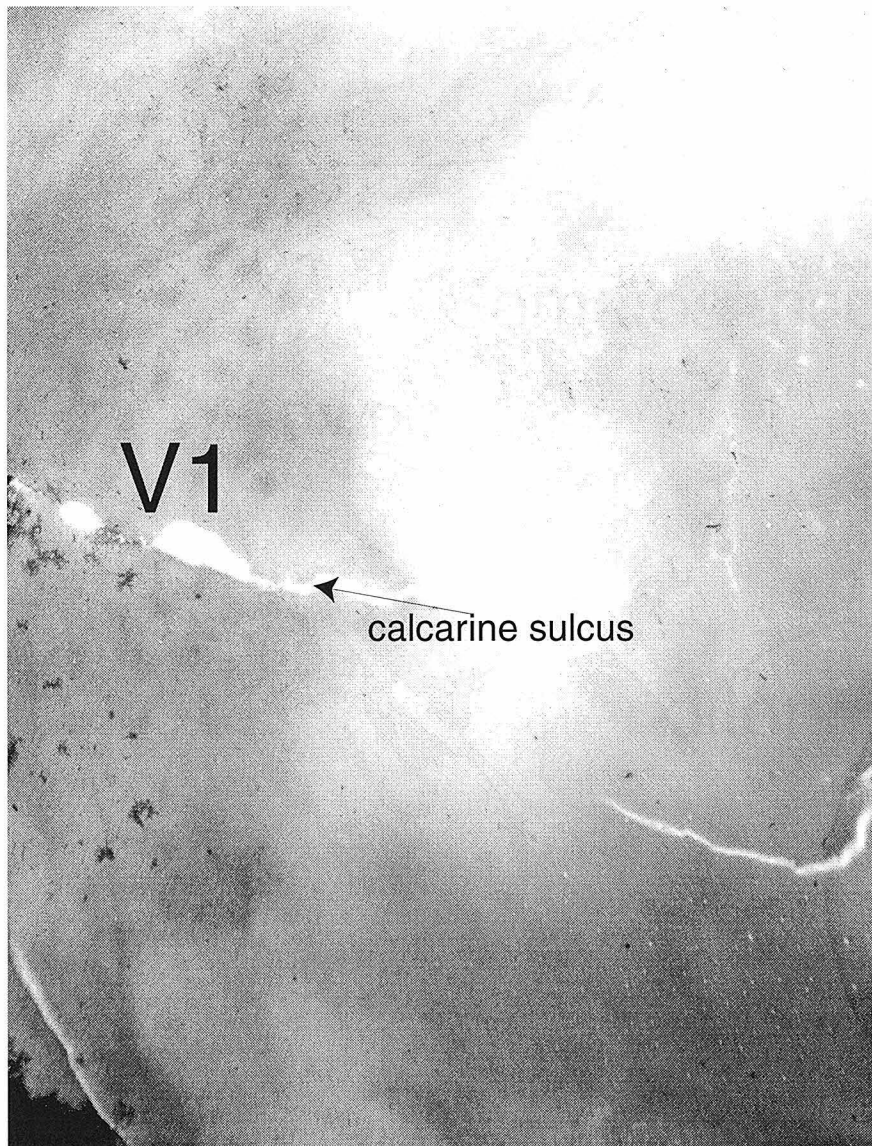


Figure A.4: Microcebus CO blobs.

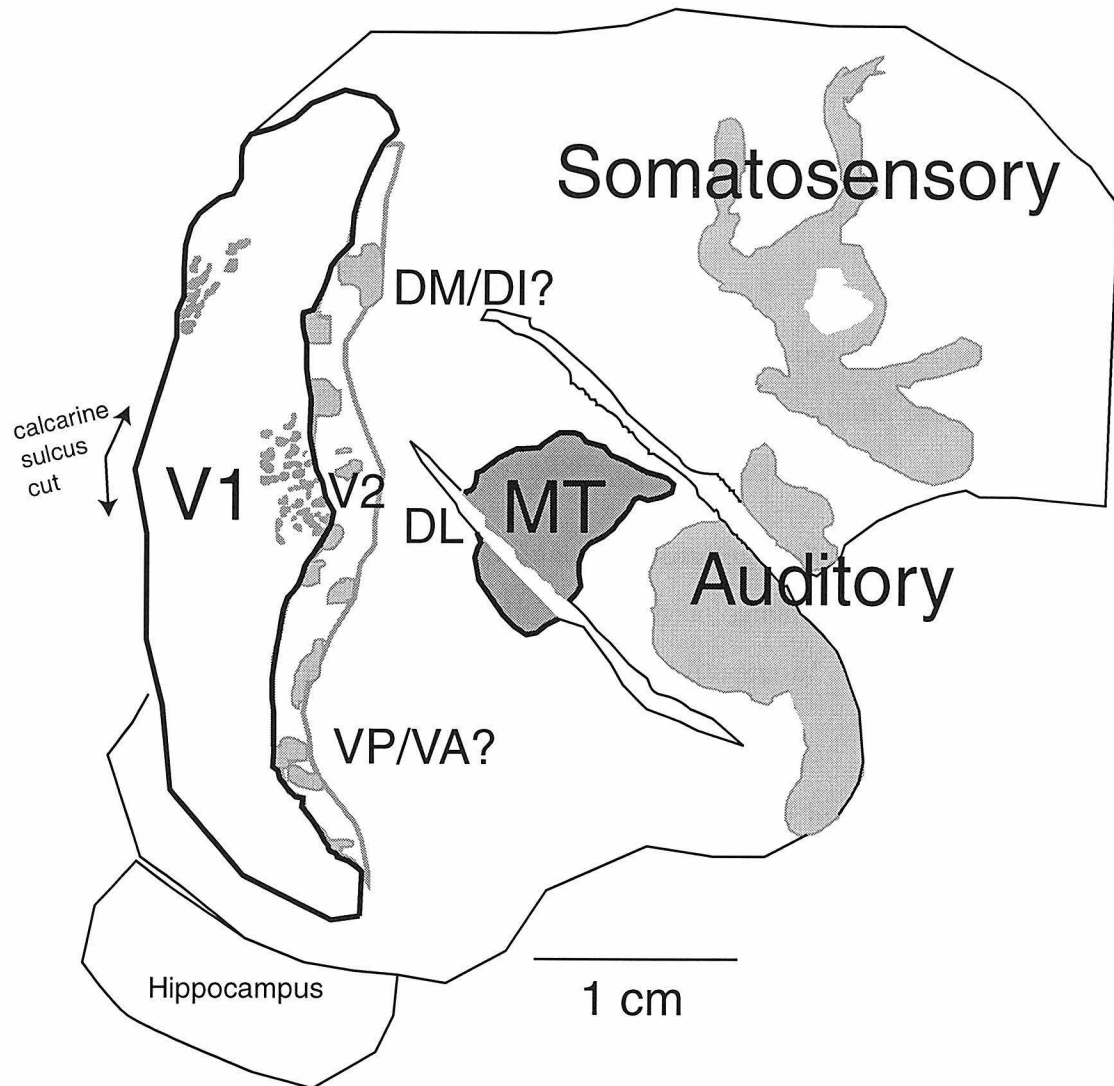


Figure A.5: Summary of reconstruction.

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