Classical and Surround Receptive Field Structure in Cortical Area MT as Revealed by Reverse Correlation

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Biology with a specialization in Computational Neurobiology

by

Micah David Richert

Committee in charge:

Professor Thomas D. Albright, Chair
Professor E. J. Chichilnisky
Professor Virginia R. de Sa
Professor Bart Krekelberg
Professor Martin I. Sereno
Professor Pamela Reinagel

2008
The dissertation of Micah David Richert is approved, and it is acceptable in quality and form for publication on microfilm:

Chair

University of California, San Diego

2008
DEDICATION

This dissertation is dedicated to my parents, Dave and Carol Richert, for all of the love and support that they have provided.
# TABLE OF CONTENTS

Signature Page ...............................................................................................................iii
Dedication......................................................................................................................iv
Table of Contents ...........................................................................................................v
List of Tables ................................................................................................................ix
List of Figures .................................................................................................................x
Acknowledgements .....................................................................................................xii
Curriculum Vitae ...........................................................................................................xiii
Abstract of the Dissertation .........................................................................................xiv

Chapter 1: Introduction .................................................................................................1
  1.1 Overview ............................................................................................................1
  1.2 MT receptive field structure ...........................................................................3
    1.2.1 Classical Receptive Field ........................................................................3
    1.2.2 Surround ..................................................................................................5
  1.3 Object Motion ....................................................................................................8
  1.4 Maximally Informative Dimensions ...............................................................9
  1.5 Circular Statistics ...........................................................................................10
  1.6 References ......................................................................................................11

Chapter 2: The fine structure of receptive fields in cortical visual area MT .......... 13
  2.1 Abstract ..........................................................................................................13
  2.2 Introduction .....................................................................................................14
  2.3 Methods ..........................................................................................................16
    2.3.1 Subjects .................................................................................................16
    2.3.2 Surgical preparation ..............................................................................17
    2.3.3 Behavior ................................................................................................17
    2.3.4 Visual Display ......................................................................................18
    2.3.5 Visual Stimuli ......................................................................................18
    2.3.6 Electrophysiological Procedures .........................................................22
    2.3.7 Procedure ............................................................................................23
    2.3.8 Data analysis ........................................................................................24
      2.3.8.1 BMdots ........................................................................................24
      2.3.8.2 Latency ........................................................................................28
      2.3.8.3 Directional Preference and RF definition ..................................28
      2.3.8.4 GridRF ........................................................................................30
      2.3.8.5 PrefDir ........................................................................................30
      2.3.8.6 Patchiness ....................................................................................30
      2.3.8.7 Changing Direction Preference .............................................31
4.7 Conclusion ..................................................................................................97
4.8 Acknowledgements ....................................................................................97
4.9 Reference ....................................................................................................97

5.1 Abstract .......................................................................................................99
5.2 Introduction ..............................................................................................100
5.3 Methods ....................................................................................................106
  5.3.1 Optimization .......................................................................................106
  5.3.2 Approximate Mutual Information .......................................................107
  5.3.3 Comparing AMI to MI .........................................................................112
  5.3.4 Improve AMI Signal to Noise ............................................................113
  5.3.5 2D AMI ............................................................................................114
  5.3.6 Wavelets ............................................................................................119
  5.3.7 2D Search ........................................................................................122
  5.3.8 Significant Kernels ..........................................................................123
5.4 Results ......................................................................................................124
5.5 Discussion .................................................................................................128
5.6 Conclusion ................................................................................................133
5.7 Acknowledgements ..................................................................................133
5.8 References ................................................................................................134

Chapter 6: A non-parametric circular test for differences in mean direction with low circular concentrations .................................................................135
6.1 Abstract .....................................................................................................135
6.2 Introduction ..............................................................................................135
6.3 Methods ....................................................................................................137
  6.3.1 Example .............................................................................................140
  6.3.2 Unit Vectors .......................................................................................142
  6.3.3 False Positives ..................................................................................142
  6.3.4 Power ................................................................................................143
  6.3.5 2D Vectors .......................................................................................144
  6.3.6 False Positives ..................................................................................145
  6.3.7 Power ................................................................................................145
  6.3.8 Sample Sizes ....................................................................................146
  6.3.9 Large Sample Sizes ........................................................................146
  6.3.10 Small Sample Sizes .......................................................................147
6.4 Discussion .................................................................................................148
6.5 Acknowledgements ..................................................................................149
6.6 References ................................................................................................149

Chapter 7: Conclusions ...............................................................................................150
7.1 Classical Receptive Fields .......................................................................150
7.2 Surround Structure ...................................................................................151
7.3 Object Motion ..........................................................................................152
7.4 Maximally Informative Dimensions ............................................................ 153
7.5 Circular Statistics ...................................................................................... 153
7.6 References ............................................................................................... 154
LIST OF TABLES

Chapter 5
Table 5.I: Accuracy (mean correlation coefficient) ........................................... 125
Table 5.II: Execution Time (seconds) ............................................................. 126
Table 5.III: Accuracy for 2nd Kernel (mean correlation coefficient) ............... 127
Table 5.IV: Execution Times for 2nd Kernel (Seconds) .................................... 127

Chapter 6
Table 6.I: Comparing false-positive rates between WW and cKW. ............... 143
Table 6.II: Comparing false-positive rates between WW and cKW for 2D
  distributions .................................................................................................. 145
LIST OF FIGURES

Chapter 2
Figure 2.1: Example isolation for a representative unit (sj225-005-1) ...........23
Figure 2.2: BMdots stimulus and reverse correlation. .................................27
Figure 2.3: A “classical” spatial receptive field. .........................................33
Figure 2.4: Double-Direction preference cells. .............................................34
Figure 2.5: Double-Direction preference confirmation ..................................35
Figure 2.6: Subtle changes in direction preference. ....................................36
Figure 2.7: Subtle changes in direction preference and local vs. global .........37
Figure 2.8: Patchy receptive fields. .............................................................40
Figure 2.9: RF Gaps are not caused by retinal scotomas. ...........................42

Chapter 3
Figure 3.1: Center and Surround .................................................................54
Figure 3.2: BMdots stimulus and reverse correlation. .................................57
Figure 3.3: Example functions. .................................................................62
Figure 3.4: Surround Suppression. ...............................................................66
Figure 3.5: Off Direction Preference Suppression. .......................................68
Figure 3.6: Omni-modulation .....................................................................70

Chapter 4
Figure 4.1: The stimulus used for the psychophysics and most of the
electrophysiology. .......................................................................................81
Figure 4.2: The stimulus used for the third electrophysiology experiment.....83
Figure 4.3: Psychometric curves for unbiased motion perception for two
representative human subjects. .................................................................85
Figure 4.4: Psychometric curves for motion capture perception for two
representative human subjects. .................................................................86
Figure 4.5: Electrophysiological results for experiment one .....................90
Figure 4.6: Electrophysiological results for experiment two .....................92
Figure 4.7: Electrophysiological results for experiment three ..................93

Chapter 5
Figure 5.1: Approximate Mutual Information ..........................................111
Figure 5.2: AMI vs. MI. ..........................................................................113
Figure 5.3: 2 Dimensional AMI. ...............................................................118
Figure 5.4: Model nonlinearities. ...............................................................122

Chapter 6
Figure 6.1: Visual representation of the circular Kruskal-Wallis test ..........141
Figure 6.2: Power for different circular concentrations. ..........................143
Figure 6.3: Power for different circular concentrations for 2D distributions.146
Figure 6.4: Power as a function of N..............................................................147
Figure 6.5: Power as a function of small N...................................................148
ACKNOWLEDGEMENTS

I had the tremendous pleasure to work with many great people during my graduate career. Bart Krekelberg and Tom Albright were both excellent mentors. I am thankful for everything that Bart has taught me, and was instrumental in my joining the lab. It was a very fruitful collaboration for me and I hope as useful for you. Tom, thank you for steering me away from projects that surely would have failed yet giving me the freedom to still try something risky. Also, thank you for forcing me to stay more grounded and making me think of different ways to explain my work. I thank Virginia de Sa for a wonderful rotation and continued mentoring. I would have joined your lab had it not been for Bart. Thank you Sjeng for making learning to record so easy and Moe, we hated each other, but you still made me laugh about it.

I must acknowledge my friends who have kept me sane and happy throughout the years. In no particular order: Chris Adams and Kristy Sundberg (you two better get married soon…), Jeff Gauthier, Claire Discenza, Dan Hill, Tina Bakolitsa, Elyssa Burg, John Davidson, Julie Saye, Joaquin Ortiz and last but not least Emily Wiley. Also, everyone in my lab, you made it feel like we are a family.

Finally, I would not be the person I am today without the love and support of my family. My father, Dave, gave me my curious and questioning mind, my mother, Carol, gave me my gentle and giving heart and my sister, Lisa, gave me early intellectual competition (you were and still are a better speller than me…).

Chapters 2, 3, 5, and 6, in full, are being prepared for publication. Chapters 2-6 were co-authored with Bart Krekelberg, Tom Albright and the dissertation author. The dissertation author was the primary investigator.
CURRICULUM VITAE

Education
University of California, San Diego     09/2002-06/2008
   Ph.D. in Biology with a specialization in Computational Neurobiology
   Thesis Advisor: Tom Albright
   Lab: Albright, Salk Institute
   Department: Biology

University of California, San Diego     09/1997-12/2001
   B.S. in Computer Engineering
   Minor: Mathematics
   Area of Focus: Theater
   GPA: 3.52

Poster Presentations
Cosyne 2008   Poster: Maximally Informative Dimensions Using an Approximate
               Mutual Information Measure and Wavelets

SfN 2007    Poster: Excitatory and suppressive substructure of MT receptive fields

SfN 2005   Talk: A reverse-correlation method to assess fine spatial structure of
            MT receptive fields

Cosyne 2005  Poster: A reverse-correlation method to assess fine spatial structure of
               MT receptive fields

Programming Projects/Community Service
Utilities for reading, writing and playing movies in Matlab. The utilities are written in
C++ using Windows DirectShow Infrastructure and callable from both 32 and 64 bit
Matlab.
http://www.mathworks.com/matlabcentral/fileexchange/loadAuthor.do?objectType=au
thor&objectId=1094637

NIH CORTEX (http://www.cortex.salk.edu/): is a realtime behavior control program
written in C/C++. My main development was to take the existing source and make a
fully functional version that would run under Windows 2K/XP and remove specific
hardware dependence.

Neurostim (http://sourceforge.net/projects/neurostim/): is a stimulus presentation
package started by Bart Krekelberg that uses OpenGL and C++ to make dynamically
loadable stimuli.
ABSTRACT OF THE DISSERTATION

Classical and Surround Receptive Field Structure in Cortical Area MT as Revealed by

Reverse Correlation

by

Micah David Richert

Doctor of Philosophy in Biology with a specialization in Computational Neurobiology

University of California, San Diego 2008

Professor Thomas D. Albright, Chair

This dissertation is organized into two main parts: physiology and new techniques. The physiology is organized into classical receptive fields, surround properties and global object selectivity of area MT. The first two physiology chapters used a novel sparse motion stimulus to drive MT cells and used reverse correlation to analyze the data. For the classical receptive field the spike triggered average was used as an estimate of the field. For the surround, maximally informative dimension analysis as originally developed by Sharpee at el. (2004) and further optimized for the stimulus distribution was used in these studies (see Chapter 5). Chapter 6 covers a circular statistic derived for use in Chapter 2.
Using a new motion reverse correlation technique, we obtained high-resolution measurements of receptive field properties – spatial and directional selectivity – within cortical visual area MT. The standard, often implicit, view of these receptive fields is that they cover a contiguous area of the visual field and that the preferred direction is homogenous across this field. Contrary to this, we found that the receptive fields of many (19%) neurons were significantly patchy and that only half (48%) preferred only a single direction of motion within their receptive field. Both the spatial patchiness and directional preference variation were validated in single cells using more traditional stimuli.

In the second chapter we used a variant of Maximally Informative Dimension (MID; Sharpee et al. 2004; Chapter 5) in order to find mechanisms that are not directly implied by the Spike Triggered Average (STA). Using MID we found a second kernel (receptive field, RF2) that interacted with the STA. We found 3 categories for RF2 structure: Surround Suppression, Off Preferred Direction Suppression and Omni-modulation. A divisive nonlinearity is found to fit the surround and off preferred direction suppression data well.

In the third chapter we studied the response of area MT to a motion capture illusion. We first demonstrated a large psychophysical effect for humans, and then tested area MT’s response to this stimulus. We found no modulation in area MT consistent with the global object motion, i.e. consistent with the illusion.
Chapter 1: Introduction

1.1 Overview

The receptive field is a fundamental building block of the visual system, yet for higher cortical areas many studies gloss over the fine structure of receptive fields. For early visual areas the receptive fields have been studied more quantitatively, such that the local spatial variation in feature selection has been measured. In later visual areas, where feature selectivity generally is more complex, the receptive field is often assumed to be homogeneous in preference and approximately gaussian in shape. These assumptions to some extent are justified by the prohibitively long experiments that would be required to measure selectivity across the entire receptive field in a classical way when the feature space is large. To the best of our knowledge, direction preference has not been studied at a fine spatial scale. Furthermore, studies focusing on the fine spatial, but not directional, structure of MT receptive fields have been limited.

Receptive fields are often organized into an excitatory center and a suppressive surround that extends beyond the spatial extent of the excitatory center. These two structures are often viewed as being mediated by two separate mechanisms: the excitatory center is thought of as the feed forward signal form an earlier visual area, and the suppressive surround is often viewed as mediated by lateral inhibition from
within the same area. To disambiguate the center from the whole receptive field, the
excitatory center will be referred to as the Classical Receptive Field or CRF.

The surround in area MT is usually “silent”. A silent surround is characterized
by no response when only a single stimulus is used, but results in strong suppression
when there is a co-occurrence of stimuli in the center and surround, relative to a
stimulus in the center alone. This interaction is nonlinear and models of this
interaction have been made, yet this nonlinearity has not been systematically measured
in area MT. The normal paradigm to measure the surround requires a stimulus to fill
the CRF and since this central stimulus is normally not varied, it is an open question
whether the surround spatially overlaps with the CRF. Furthermore, since the central
stimulus is never varied, this leaves open the possibility of undiscovered modulatory
structures located entirely within the same region of space as the CRF. Finally,
Simoncelli and Heeger (1998) proposed a population model for area MT which
requires normalization of responses by the population, but to the best of our
knowledge there is no direct physiological evidence for or against this assumption in
area MT. Maximally Informative Dimensions as proposed by Sharpee et al. (2004) is
a method to address these issues. However, Maximally Informative Dimensions has
several issues, to this study the most important of which is that in the form proposed
by Sharpee et al. it does not function well for very sparse stimulus distributions like
the one used in this study (see Chapters 2, 3).
1.2 MT receptive field structure

This research focuses on the two main parts of the receptive field in area MT: the Classical Receptive Field (CRF) and the suppressive surround. For the CRF we will address what has been done and the associated limitations. We then propose a novel stimulus combined with the spike triggered average to estimate the receptive field. In the second part we address the surround structure observed within area MT. We demonstrate a technique to estimate the surround. Furthermore, this technique is not restricted to finding just surround structures. The technique will find any significant modulatory structures, such as structures consistent with population normalization and structures that spatially overlap the CRF.

1.2.1 Classical Receptive Field

In the past, the locations of Receptive Field (RF) boundaries have been approximated by hand, using the minimum response field approach (Barlow et al., 1967). Similar hand-mapping techniques have been used to estimate sensitivity to particular stimulus dimensions, such as orientation or direction of motion. Receptive field mapping became more precise with the introduction of quantitative measures, which have been most commonly used to assess the response to the average stimulus within the RF. One weakness to the average-stimulus approach is that it does not measure local variations in selectivity; the resulting RF thus has, by definition, a spatially uniform response profile. This problem has been overcome by an approach
that combines local pseudo-random stimulus presentations with the technique of reverse-correlation analysis of neuronal stimulus selectivity.

Most electrophysiological studies of local RF organization have focused on early stages of visual processing, where RFs can be simply characterized from responses to low-dimensional stimuli, such as randomly-positioned spots that vary in luminance or chrominance. This approach has not been commonly applied in higher visual areas, in part because the neurons are known to respond to higher-order stimulus properties, such as the change in a stimulus over space and time (i.e. motion), which increases the complexity of the experiment.

Cortical area MT is among the most well studied regions of visual cortex. Neurons in this area are highly selective for direction (Albright, 1984) and speed (for example Rodman and Albright, 1987) of visual motion and are believed to play a central role in visual motion perception (see Albright, 1992, for review). It is generally assumed that the response properties of MT neurons – such as the preferred direction – are uniform within the classical RF, although in truth there exists little evidence that bears on the subject.

Indeed, we know of only three published studies that have examined the substructure of MT receptive fields in any detail. In one case, Britten and Heuer (1999) stimulated MT neurons using small (<1 deg) stimuli on a 5x5 grid superimposed on the CRF and moving in the preferred direction. These investigators found that many MT neurons exhibited variations in sensitivity across the CRF, and they also noted response modulations that reflected nonlinear interactions between
stimuli in different regions of the RF. Because these small stimuli moved only in the preferred direction (assessed using larger stimuli), however, this study provides no insights into the spatial uniformity of preferred direction within the CRF. Perge et al. (2005) used a similar approach and obtained qualitatively similar results. Finally, Recanzone et al. (1997) examined responses of MT neurons to pairs of small patterns moving in different directions within the RF. These investigators found that the response to both stimuli was best predicted by the average of the two individual responses. Although these studies collectively reveal that the receptive field story is more complex than has been generally assumed, the conclusions one may draw remain limited by the spatial resolutions at which RFs were sampled, the small number of stimuli moving within the RF, and the small range of motions directions used.

To overcome these limitations, we have developed a new method that probes all directions of motion and imposes no spatial resolution. This method allows us to make far more precise (in space and direction) measurements of MT receptive fields. Using this technique we were able to determine whether the direction preference is stable across the entire spatial receptive field as well as if all receptive fields are spatially contiguous.

1.2.2 Surround

Many studies have revealed a suppressive mechanism often referred to as the suppressive surround; this structure generally spatially surrounds the CRF, has a similar visual preference and reduces the response of the cell when stimulated. Often, this surround is only measurable when there is a stimulus located within the CRF,
such that without a stimulus within the CRF no response is elicited from within the surround: a silent surround. Since the surround is only induced when there is a corresponding stimulus within the center, it is viewed as a nonlinear interaction between two independent mechanisms: the center and surround. Xiao et al. (1997) demonstrated suppressive surrounds in area MT. However, the suppressive surround and the classical receptive field have not been studied simultaneously, where both the surround and center stimuli were varied. Furthermore, previous studies of the surround have used a relatively coarse spatial resolution and more importantly it is an open question whether the surround structure spatially overlaps with the classical receptive field. Finally, there are few physiological measurements of the exact nonlinear interaction between the center and surround beyond the 4 stimulus conditions of: stimulus or no stimulus at the center and surround.

Techniques have been developed to elucidate these nonlinearly interacting mechanisms, one of which is Spike Triggered Covariance (STC) and was employed by Rust et al. (2004) and others to study areas V1 and earlier in the visual system. The STC, however, requires a Gaussian distributed stimulus. Determining a Gaussian distributed stimulus for area MT has proven quite challenging and has inhibited the application of this technique to area MT and other areas. The stimulus used in this study was a sparse binary stimulus; therefore another analysis technique was required. Maximally Informative Dimensions (MID) as proposed by Sharpee et al. (2004) is the general solution to this problem, however, we use a variant (Chapter 5) that was optimized for the stimulus distribution used here (Chapters 2,3).
The approach of MID is to find a linear model that best predicts the response of the cell. The insight that Sharpee et al. (2004) had was that mutual information is the best measure of prediction ability; essentially the mutual information between the model and the spike train determines how well the model predicts the response of the cell. Thus it is natural to want to build a model that maximizes the prediction and therefore the mutual information. The model used by MID is of the form $F(RF_1*\text{Stimulus}, RF_2*\text{Stimulus}...)$, where $F()$ is a nonlinear function that maps the 1 or more linear terms into a firing rate. It can be demonstrated that the amount of mutual information is entirely calculated from the nonlinearity $F$. Furthermore, the nonlinearity $F$ is estimated from the 1 or more dot product values per response of the cell by combining similar dot product values and estimating the average response to those similar values. If there are 2 or more kernels, the nonlinearity represents the nonlinear interaction between the kernels.

While the true biophysical implementation could be different, one can visualize the kernels as receptive fields, and in our suppressive surround case, one kernel can represent the excitatory feed-forward receptive field, and the second kernel can represent the suppressive surround. A schematic is shown in Figure 3.1, where a simple model of a center surround receptive field is shown. Generally the center and surround are considered two separate mechanisms, where the center is suppressed by the surround and this suppression is often modeled as division (Simoncelli and Heeger, 1998). In this example, the surround is composed of many neighboring receptive fields that all individually and divisively suppress the response of the center
cell. Generally the center is thought of as a single mechanism, yet it is recognized as being constructed out of many smaller units. The surround should be viewed similarly; in this example, many neighboring receptive fields mediate the suppressive surround yet it is a single mechanism. One would expect the MID analysis to find two kernels: one consistent with the center and one consistent with the surround, or an equivalent subspace. Therefore we used MID to uncover the suppressive surround structure. We also set out to test whether a divisive model is a good model for the observed nonlinear interactions.

1.3 Object Motion

The previous section assumed a local motion centric view of motion processing; however, it is an attractive idea to think of area MT as responding not to just local motion but to object motion. There is some support for the idea that area MT encodes object motion and not just local: pattern vs. component motion in area MT (Movshon et al., 1986) indicates that some area MT cells encode the global motion of two superimposed gratings, while others only encode the individual directions. Furthermore, area MT is believed to be central to visual motion perception (see Albright, 1992, for review).

To test the hypothesis that area MT may respond to global motion even when no local motion existed, we developed a motion capture stimulus with these properties. Motion capture in general is the tendency of global motion to influence ones perception of local motion such that the local stimulus is perceived to move in
the global direction (MacKay 1961 and Ramachandran 1985). We first performed human psychophysics using this motion capture stimulus. We compared this to a very similar stimulus that imposed a different interpretation of figure and ground to construct a percept that does not result in strong motion capture. In order to measure a perceptual bias curve, we injected varying strengths and directions of true motion within the region of space where the motion capture was being induced. We then present area MT’s response to these stimuli to test to see if any MT responses are consistent with the global motion perception.

1.4 Maximally Informative Dimensions

Sharpee et al. (2004) developed Maximally Informative Dimensions (MID) in order to provide a general solution to finding a 1 or more dimensional linear model that best predicts the response of a cell. The linear model uses the dot product, or projection value, between a linear kernel (receptive field) and the stimulus to predict the response of the cell. This is the same form of model assumed by the Spike Triggered Average as well as implicitly assumed by many classical analysis techniques of receptive fields and therefore is both a very convenient but also intuitive model. For the model to predict the spike rate a nonlinearity must be estimated that maps the projection values to the response of the cell. It can be demonstrated that mutual information between the model and the response of the cell is the best measure of prediction. Sharpee et al. demonstrated a gradient ascent procedure to find the kernel that maximizes the mutual information.
While mutual information is the best measure of prediction, there are several practical limitations. First, mutual information does not take into account that the nonlinearity of the cell should be smooth. Second, to calculate mutual information requires binning, and this binning introduces additional noise into the optimization. Third, MID, as originally constructed, was optimized for natural scenes, which have a pink noise distribution. Unfortunately, MID as optimized for natural scenes does not perform well for binary sparse stimuli (the stimulus used in Chapters 2, 3). We proposed a heuristic approach to address all of these issues. First, we performed the optimization in the wavelet domain; the introduction of wavelets imposes a smoothness assumption on the linear kernel (receptive field). Second, we introduced a measure we termed Approximate Mutual Information (AMI). We demonstrated that AMI is related to mutual information for smooth nonlinearities. We compare these modifications to both the original MID analysis as well as to several variants to determine the individual contributions of the different heuristic approaches. We test all variants of MID with 3 different stimulus distributions and 3 different nonlinearities in order to determine which analysis techniques work best under which circumstances.

### 1.5 Circular Statistics

Two of the stimulus features studied most by visual neurophysiology are orientation and direction. It is well known that many neurons in early visual areas are
tuned for these stimulus features. Yet orientation and direction are circular variables, therefore, traditional statistical techniques cannot be applied to them.

The accepted test for determining if two (or more) circular mean directions are significantly different from one another is the Watson-Williams’ test (Watson and Williams, 1956). For the purposes described above, however, the Watson-Williams’ test has two significant shortcomings. First, it fails for low circular concentrations, even for an infinite amount of data. This means that the test cannot be applied to neurons that are either inherently weakly selective (which is the case in many visual areas) or are stimulated by weak stimuli (such as with a very low coherence motion stimulus, or the stimulus used in Chapters 2, 3). The second shortcoming is that the Watson-Williams’ test is only concerned with whether a neuron responded to a direction or not; by ignoring the level of response, much information on the properties of the neuron could be lost. To address these issues we propose a new test that is applicable for extremely low circular concentrations and uses weighted vectors (directions or orientations weighted by the response of the neuron). We compared the proposed test to the Watson-Williams’ test for both power and false-positive rates over a range of circular concentrations, angular differences and dataset sizes.

1.6 References


Chapter 2: The fine structure of receptive fields in cortical visual area MT

2.1 Abstract

Using a new motion reverse correlation technique, we obtained high-resolution measurements of receptive field properties – spatial and directional selectivity – within cortical visual area MT. The standard, often implicit, view of these receptive fields is that they cover a contiguous area of the visual field and that the preferred direction is homogenous across this field. Contrary to this, we found that the receptive fields of many (19%) neurons were significantly patchy and that only half (48%) preferred only a single direction of motion within their receptive field. Both the spatial patchiness and directional preference variation were validated in single cells using more traditional stimuli. The observed patchiness sheds light on how cells in area MT construct their relatively large receptive fields by sampling the input from neurons with smaller receptive fields, presumably in earlier visual areas. The complex nature of the directional preferences within individual MT receptive fields suggests that these neurons may represent information about spatio-temporal changes in stimulus direction. Such information could provide building blocks for analysis of the complex optic-flow fields that arise from natural movements through a dynamic environment.
2.2 Introduction

The receptive field is a fundamental building block of the visual system, yet for higher cortical areas many studies gloss over the fine structure of receptive fields. In the past, the locations of Receptive Field (RF) boundaries have been approximated by hand, using the minimum response field approach (Barlow, Blakemore et al. 1967). Similar hand-mapping techniques have been used to estimate sensitivity to particular stimulus dimensions, such as orientation or direction of motion. Receptive field mapping became more precise with the introduction of quantitative measures, which have been most commonly used to assess the response to the average stimulus within the RF. One weakness to the average-stimulus approach is that it does not permit assessment of spatially local variations in the effects of stimulus properties on neuronal responsivity; the resulting RF thus has, by definition, a spatially uniform response profile. This problem has been overcome by an approach that combines local pseudo-random stimulus presentations with the technique of reverse-correlation analysis of neuronal stimulus selectivity.

Most electrophysiological studies of local RF organization have focused on early stages of visual processing, where RFs can be simply characterized from responses to low-dimensional stimuli, such as randomly-positioned spots that vary in luminance or chrominance. This approach has not been commonly applied in higher visual areas, in part because the neurons are known to respond to higher-order stimulus properties, such as the change in a stimulus over space and time (i.e. motion), which vastly increases the complexity of the experiment.
Cortical area MT is among the most well studied regions of visual cortex. Neurons in this area are highly selective for direction and speed of visual motion and are believed to play a central role in visual motion perception (see Albright 1992, for review). It is generally assumed that the response properties of MT neurons – such as the preferred direction – are uniform within the classical RF, although in truth there exists little evidence that bears on the subject. Indeed, we know of only three published studies that have examined the substructure of MT receptive fields in any detail.

In one case, Britten and Heuer (1999) stimulated MT neurons using small (<1 deg) stimuli on a 5x5 grid superimposed on the CRF and moving in the preferred direction. These investigators found that many MT neurons exhibited variations in sensitivity across the CRF, and they also noted responses modulations that reflected non-linear interactions between stimuli in different regions of the RF. Because these small stimuli moved only in the preferred direction (assessed using larger stimuli), however, this study provides no insights into the spatial uniformity of preferred direction within the CRF. Perge et al. (2005) used a similar approach and obtained qualitatively similar results. Finally, Recanzone et al. (1997) examined responses of MT neurons to pairs of small patterns moving in different directions within the RF. These investigators found that the response to both stimuli was best predicted by the average of the two individual responses. Although these studies collectively reveal that the receptive field story is more complex than has been generally assumed, the conclusions one may draw remain limited by the spatial resolutions at which RFs were
sampled, the small number of stimuli moving within the RF, and the small range of motions directions used.

To overcome these limitations, we have developed a new method that probes all directions of motion and imposes no spatial resolution. This method allows us to make far more precise (in space and direction) measurements of MT receptive fields. Using our new technique, we find that receptive field structure is often far more complicated than previously reported. For example, our data reveal that many MT neurons possess receptive fields in which the preferred direction of motion varies as a function of position within the field. Additionally, some neurons exhibit RFs composed of multiple spatially disjoint but highly direction selective subregions, each of which is excitatory in nature.

2.3 Methods

2.3.1 Subjects

Electrophysiological recordings were performed in two adult male rhesus monkeys (Macaca mulatta), weighing 8.5-9.5 kg. Experimental protocols were approved by the Salk Institute Animal Care and Use Committee, and conform to US Department of Agriculture regulations and to the National Institutes of Health guidelines for humane care and use of laboratory animals.
2.3.2 Surgical preparation

Procedures for surgery and wound maintenance have been described in detail elsewhere (e.g. Dobkins and Albright 1994). In short, a head post and a recording cylinder were affixed to the skull using stainless steel rails, screws and dental acrylic. We estimated the anatomical location of area MT from structural MR scans and centered the recording chambers vertically above this area. The coordinates of the chambers were 4 mm posterior and 19 mm lateral in the first animal and 4 mm posterior and 20 mm lateral in the second animal. All surgical procedures were performed under sterile conditions using isoflurane anesthesia.

2.3.3 Behavior

Animals were seated in a standard primate chair (Crist Instruments, Germantown, MD). Head movements were constrained by a head post. Eye position was monitored continuously using an infrared video-based device (ISCAN, Burlington, MA) with temporal and spatial resolutions of 120 Hz and 30 arc min.

All visual stimuli were presented as the subject performed a simple fixation task. Each trial began with the appearance of a red fixation target (0.1° diameter). Once the subject directed his gaze to the target and maintained it there for 100ms, the visual stimulus appeared. This stimulus remained on for up to 3000 msec. The monkey was required to maintain fixation (within 2° of the fixation target) during the entire trial. Correct performance was rewarded with a small drop of juice. Failure to maintain fixation resulted in trial termination. Although our animals consistently
performed this task at high levels, the physiological data recorded were usable on all trials (and for all stimulus types) including those in which fixation was broken prior to the end of the trial.

The behavioral paradigm was controlled using the NIMH CORTEX program (NIH: http://www.cortex.salk.edu -VCortex 1.1 running under Windows 98 or VCortex 2.1 running under Windows 2000).

2.3.4 Visual Display

All visual stimuli were generated with an OpenGL-based library (Neurostim: http://sourceforge.net/projects/neurostim) using a high-resolution graphics display device (ATI Radeon 9600) operating in a Pentium-4 computer. Stimuli were displayed on a 21” analog RGB video monitor (either Sony GDM-2000TC or Sony GDM-C520). A range of refresh rates was used between 75 and 150Hz. The screen resolution was always 1024 by 768 pixels. Monkeys viewed the display from a distance of 57cm in a dark room (<0.5 cd/m²). The monitor subtended 39 by 29 degrees of visual angle.

2.3.5 Visual Stimuli

The visual stimuli used were of five types. The first of these was the novel stimulus we have created for use with reverse correlation. The remaining four stimuli were controls used in conjunction with more traditional analysis methods, which served to validate elements of our novel approach.
(1) **BMdots Stimulus**

The primary stimulus used in these experiments was a pseudo-Brownian motion stimulus using random dots. This stimulus was used in conjunction with reverse-correlation analysis (see below) to assess RF sensitivity. The stimulus was composed of 300 independently moving dots. Each dot was approximately 0.2 degrees in diameter and had a 2D gaussian luminance profile. The dots moved at 8 degrees per second. Dots moved in their assigned direction for 200ms, after which a new direction was chosen from a uniform circular distribution. The direction changes were interleaved such that only a portion of the dots changed direction on any one frame. The background was mean gray (18.3 cd/m²), and the dots were white with a contrast of 0.25 at the center. The luminance of the dots was constructed such that when two or more dots intersected the luminance of their intersection was brighter. This stimulus was similar to moving dot patterns used in other experiments (for example: Newsome and Pare 1988), but the speed of dots was fixed and dots did not have a limited lifetime. The stimulus was constructed from a seed chosen at the beginning of each trial, such that the whole stimulus (dot locations and directions) for that trial could be reconstructed at a later time.

(2) **GridRF Stimulus**

This stimulus was used in conjunction with a conventional response analysis method (see below), in order to assess the spatial profile of the RF. The results were used to validate the novel BMdots/reverse correlation method. The stimulus was structured on a grid subtending 11 x 11 degrees and centered on the classical receptive
field (assessed using BMdots; see below). Grid cells were 1x1 deg. Only one dot appeared on the screen at a time. The dot moved in the “average preferred direction” (assessed as the average of the local directional estimates obtained using BMdots; see below) at one of the 121 grid locations. On each appearance the dot moved for 200ms, disappeared, and immediately reappeared at a new grid location. When the dot reached the edge of the 1x1 degree grid location, it wrapped around to the other side of the grid. All other aspects of the stimulus (background, dot size, speed, etc) were identical to that of BMdots.

(3) PrefDir

This stimulus was used in conjunction with a conventional response analysis method (see below), in order to assess direction preference. The results were used to validate the novel BMdots/reverse correlation method. As with the GridRF, the stimulus was structured on a grid of 1x1 deg cells, and only one moving dot appeared at any point in time. The location and motion direction of the dot varied across appearances. For this stimulus, dot locations were limited to five pre-determined grid cells, which were selected based on results obtained using BMdots. Dot direction was selected from 64 possibilities (i.e. every 5.625 deg). Direction and location were chosen at random and the dot moved in the same direction for 200ms, after which a new direction and/or location was randomly chosen. All other stimulus attributes matched the BMdots stimulus.

(4) FlowField_local
The reverse correlation approach applied using the BMdots stimulus generates a prediction regarding the preferred motion stimulus at each location in the classical RF. This prediction can be tested using a CRF-sized dot-motion stimulus that simultaneously incorporates all of the local motion preferences. We term this the “FlowField_local” stimulus, and we evaluated its effectiveness relative to that for a similarly sized stimulus with all dots moving in the same direction – the global average of the local preferences – regardless of location (the “FlowField_global” stimulus; see below). The FlowField_local stimulus was constructed as follows: A neuron’s receptive field was first determined at a resolution of 1x1 deg using the BMdots data. At each 1x1 deg location the preferred direction was estimated. The FlowField_local stimulus was structured on a corresponding grid of 1x1 deg cells. One dot moved within each grid cell; and its motion direction conformed to the preferred direction for that location. The FlowField local stimulus was presented for 200ms on each trial and was randomly interleaved with trials of the FlowField_global stimulus.

(5) FlowField_global

This stimulus contained only a single direction of motion on each presentation, which reflected either the average motion preference within the classical RF (as determined using BMdots), or one of a range of directions around the average. Stimulus construction was similar to that for FlowField_local. One dot moved within each grid cell; the motion direction was the same in all grid cells and corresponded to either (1) the average of all local preferred directions, or (2) one of six additional
directions (5, 10 and 15 deg clockwise and counterclockwise from the preferred
direction). The FlowField global stimuli were presented for 200ms on each trial and
were randomly interleaved with trials of the FlowField_local stimulus.

2.3.6 Electrophysiological Procedures

We used tungsten microelectrodes (lacquer coated, FHC; glass coated, Alpha
Omega) with 1-4 MΩ impedance (measured at 1 kHz) to record the activity of single-
units in area MT. In each experiment electrodes were positioned using a hydraulic
micropositioner (David Kopf, model 650). We identified recordings as being from
area MT neurons by means of physiological criteria (i.e. strong directionally selective
responses, receptive fields (RFs) that were relatively small compared to those of
neighbouring area MST) and recording locations on the posterior bank of the superior
temporal sulcus. The coordinates and depths of the neurons so identified were
consistent with the expected location of area MT derived from MR scans.

We used the Plexon System (Plexon Inc., Dallas TX) to filter, store and sort
the neurophysiological signals. Information about stimulus parameters, and
behavioral data were stored in conjunction with spikes. Spikes were detected using a
box sorter at the time of the experiment. Offline, spikes were sorted using the
principal components of their waveforms (PCA space; Offline Sorter, Plexon Inc).

Very strict criteria were used to define single units: For a unit to be considered well
isolated, it had to be well separated from the noise waveforms in PCA space and have
very few spikes (<< 0.1%) with an inter-spike interval less than 1ms, for all cells
shown there were 0 spikes less than 0.9ms apart. When multiple units were recorded simultaneously, we imposed as an additional criterion that the units had to be well separated in PCA space from each other as well. Most recordings of single cells lasted at least 30 minutes. Over the recording time the waveforms normally changed, however, only the time range for which they were significantly separated from the noise and other units were used in the analysis. Figure 2.1 shows two examples of typical isolation.

![Figure 2.1: Example isolation for a representative unit (sj225-005-1). Panel a shows the isolation of the unit over time, each dot is a spike with the horizontal axis representing time and the vertical axis the projection onto the first principal component of the spike waveforms. Dots colored blue are considered spike waveforms, black dots are considered noise or multiunit activity. There is clear separation between the blue and black regions throughout the recording. Panel b shows the inter-spike-interval (ISI) histogram. Note, there are no spikes with an ISI less than 1ms.](image)

**2.3.7 Procedure**

After the guide tube had punctured the dura, the electrode was advanced to just before where area MT was expected. At this point a stimulus that moved in all directions over time (Hoffmann, Behrend et al. 1976) was turned on and the electrode was slowly advanced. Area MT could be identified easily due to the highly direction
selective response to this stimulus. The electrode was advanced until a direction selective single unit could be well isolated. Then, the BMdots stimulus was presented to the cell and online analysis began. Once sufficient data had been collected such that the estimate of the receptive field was stable, the control stimuli were started. Generally the GridRF stimulus was presented fist followed by the PrefDir stimulus and finally if the cell was still well isolated the FlowField stimuli were presented. At any point one of the stimuli could be turned off, thus providing more presentation time for the remaining stimuli. Whenever they were presented, all stimuli (BMdots, GridRF, PrefDir and FlowField) were randomly interleaved.

During the presentation of each of the stimuli, the animals fixated a small red dot for up to 2.4 seconds. At the end of the fixation period they received a drop of juice. The fixation dot was normally located at the center of the screen, but could be moved to more eccentric locations so that the visual stimulus would stimulate more of a peripheral receptive field. The required fixation window was 5 or fewer degrees square; only data recorded while the monkey fixated were included in the analysis.

2.3.8 Data analysis

2.3.8.1 BMdots

We used the BMdots stimulus to estimate the cell’s direction preference as a function of space. Using the seed of the random number generator that was associated with each trial, we reconstructed the sequence of dot locations and directions used in each experiment. On any given frame the centers of all of the dots as well as the
direction in which the dots moved on the next frame was known. To create a stimulus representation that was easier to analyze, we imposed a spatial grid on the dot locations; direction was also binned. The resolution of the grid and directional bins were arbitrarily set to 1 by 1 degree of visual angle for space and 64 bins for direction. To impose the spatial grid, all dot locations were rounded to the closest grid location and directions were assigned to the corresponding bin. A stimulus frame could then be represented as a 3 dimensional matrix; the first 2 dimensions corresponded to the spatial indices and the 3rd to the directional bin index. A visual representation of one of these matrices is shown in Figure 2.2d. These sparse spatial-directional matrices were then used for the reverse correlation estimate. To calculate the spike-triggered-average (STA), the correlation between the spike train and the binned space and direction representation of the stimulus was measured. This is traditionally done by averaging together all frames of the stimulus that preceded a spike by a certain time delay. However, to improve signal to noise, we used a model that takes the response to the stimulus onset and adaptation into account. We binned the spike train using bins the width of the frame duration (150Hz, 7ms; 120Hz, 8ms; 75Hz, 13ms) and then estimated the trial-locked, non-selective response of the cell by averaging all trails together. We smoothed this average temporal signal using a Gaussian filter (10ms width) and subtracted this signal from every trial to remove non-selective responses from the signal used for reverse correlation. As a final signal preprocessing step, we subtracted the mean firing rate in a trial from the response in that trial. This operation removes fluctuations in the response that vary on a time scale of trials. This final
signal – used for the reverse correlation analysis – contains no response changes due to slow or non stimulus-specific processes and allowed us to increase the signal to noise in the spike triggered average. To be precise, we calculated a response-weighted average, which is functionally equivalent to the spike-triggered-average and will still be referred to as the STA. The STA can be thought of as directional tuning curves measured at each bin location, measured over time; depicted in Figure 2.2e. To simplify analysis and visualization the directional tuning curves were reduced to a preferred direction (vector sum of the direction associated with each bin weighted by the value at that bin), this will be referred to as the STAv; shown in Figure 2.2f.
Figure 2.2: BMdots stimulus and reverse correlation. In panel a, the BMdots stimulus is shown. It was composed of 300 independently moving dots filling the entire monitor, which subtended 39 by 29 degrees. In b, the BMdots stimulus was constructed from a random seed that allow the dot location and direction to be reconstructed at a later time. To analyze the BMdots stimulus, an arbitrary spatial grid was imposed upon the dot locations (c) and a directional grid was imposed upon the dot directions (d). The spike triggered average (STA) was then performed on the data as visualized in (e) and a STA from an example cell is shown in (g-i). In (g) the STA is shown as a series of polar tuning functions. The response of the cell to many different directions of motion is shown at many different spatial locations and the radius from the center of each of these locations is proportional to the response of the cell. In (h) the vector average is shown from the circular tuning functions in (g). To visualize direction preference as well as response magnitude, pseudo-color images were used (i); the data is identical to that shown in (h). The color wheel is used to translate the pseudo-color images into a vector field of direction preferences. The Hue indicates direction, and Saturation indicates the magnitude of response.
2.3.8.2 Latency

Two measures of neural latency were used: a functional latency estimated from the reverse correlation and the onset latency measured directly from the spike trains. To determine the functional latency, we estimated the time-to-peak for each cell by testing multiple time shifts of the stimulus relative to the spikes. When analyzed at 1 by 1 degree, the STAv was a 39 by 29 matrix of mean direction vectors. To calculate the time shift that gave the strongest response (was most correlated with the stimulus); the summed mean vector length squared was calculated. The time shift that corresponded to the largest summed value (i.e. the time shift that resulted in the largest response) was used as the functional latency of the cell. The STAv corresponding to this latency was used for all analyses and visualizations.

The onset latency was estimated as the first time at which the cell’s response was 5 standard deviations above or below baseline. Due to the large number of trials (500+) this resulted in a reliable estimate of latency and gave qualitatively the same result as other methods. The onset latency was used for all analyses except BMdots (which used the time-to-peak).

2.3.8.3 Directional Preference and RF definition

Every grid location in the STAv (pixel) was tested to see if it was significantly direction selective; only statistically significant pixels were considered part of the Receptive Field (RF). The test we used was to determine a threshold mean vector length such that only 1% (p = 0.01) of all mean vectors would be that length or longer due to chance. The threshold vector length was determined using a Null-STAv. The
Null-STAv was calculated by reversing the response of the cell in time and then calculating the STA and STAv as normal. The assumption was that the reversed response of the cell could not be correlated with the stimulus while the spiking statistics and stimulus statistics were maintained. The Null-STAv was then used to estimate the distribution of vector lengths under the Null Hypothesis; specifically to estimate the variance to be used in a $\chi^2$ test with 2 degrees of freedom (a modified Rayleigh Test). To correct for multiple comparisons, we only considered significant those pixels that had 3 or more statistically significant neighboring pixels.

The preferred direction of the cell was estimated by the grand vector mean summed across the RF for the STAv. This assumes that there is a single direction preference for the cell and that every point in the RF is an estimate of this single preferred direction. Under these assumptions, a weighted average is the best estimator of this direction, where the more responsive pixels contribute more to the estimated direction. To allow for a suppressive surround, pixels with a direction preference greater than 90 away from the strongest pixel’s preferred direction were excluded from this analysis. The strongest pixel was the pixel which had the longest vector length (i.e. most responsive), and was assumed to be excitatory. Every pixel in the RF was also tested to see if it preferred a significantly different direction from the strongest pixel’s direction (using a circular Kruskal-Wallis test, Chapter 6).

The online analysis of responses to the BMDots stimulus was used to select spatial locations and directions to probe with the controlled stimuli. Using the binned direction STA allowed us to distinguish excitation from suppression (described
below). Only locations in the RF where excitation dominated were included for the offline GridRF and FlowField analyses. The locations that had a significantly different preferred direction (p<0.01, up to 4) than the strongest pixel were probed with the PrefDir stimulus.

2.3.8.4 GridRF

The mean firing rate per grid location was calculated, adjusted for response latency.

2.3.8.5 PrefDir

The mean firing rate per location and direction was calculated, adjusted for response latency. This method does not suffer from directional bias due to only sampling a few directions (64 directions were used), however to deal with the lower number of repetitions smoothing was employed. The mean responses were smoothed using a gaussian kernel with a sigma of 5 degrees.

2.3.8.6 Patchiness

To test whether receptive fields were not continuous in space (patchy), we used a test for non-monotonicity. In a non-patchy RF, the response along any line drawn from the most-responsive pixel (normally near the center of the RF) to any other part of the RF will decrease monotonically. If, on the other hand, the RF contains a gap, the response along a line connecting two parts of the receptive field would not be monotonic. This analysis could introduce false positives if pixels far away from the most-responsive pixel were erroneously considered part of the RF. To prevent this, we
used a more strict criterion for pixels to be included in the RF (p=0.005 instead of 
p=0.01). Furthermore, locations dominated by suppression (as described below) were 
excluded from the RF so that a spatially disjoint surround could be excluded. To test 
the Null hypothesis of non-patchiness, we compared all pair-wise combinations of 
pixels falling along such a line with a one-tailed ranksum test (closer>farther). Note 
that the included pixels along the line need not be in the RF (as defined above), but the 
endpoints were. The p-values of these ranksum tests were Bonferroni corrected for 
multiple comparisons. If a cell had one or more corrected p-values of less than 0.01 it 
was considered patchy.

**2.3.8.7 Changing Direction Preference**

We used the circular Kruskal-Wallis test to determine how many receptive 
fields were consistent with a uniform direction preference. To exclude parts of the 
receptive field which were part of a suppressive surround, a test based upon the binned 
direction STA was used. Specifically, a Null-STA was calculated as described above. 
The mean of this Null-STA was used to define suppression (less than the mean) vs. 
excitation (greater than the mean). Since the STA used 64 directional bins, we were 
able to measure excitation and suppression as a function of direction and space. A 
given pixel was excluded from the changing direction preference analysis, if there was 
greater suppression than excitation when summed across all directions. Then a 
circular Kruskal-Wallis test was performed on the set of pixels determined to be 
excitatory. The threshold for rejection was set to 0.01.
2.4 Results

We recorded from 322 cells from 2 hemispheres in 2 monkeys (Monkey S: 154, Monkey M: 168), 152 of these (47%) matched our criterion for single-unit isolation (see Methods); only these cells (73 from S and 79 from M) were included in this report. The average receptive field eccentricity, measured at the center of the receptive field, was 7.6 degrees (Range: 1.3 to 21.5).

In this section we first present quantitative receptive field maps that correspond to the classical view of an MT receptive field: a contiguous region of space in which a single direction of motion leads to the maximum response. The second part of the results describes the cells in MT that differ from this classical view.

Shown in Figure 2.3a are the data from a single cell that prefers rightward motion, and has an RF centered 5 degrees away from fixation (0,0) subtending approximately 5 degrees. This cell’s receptive field structure is consistent with the classical view of an MT receptive field inferred from qualitative or manual measurements reported previously (e.g. Rodman and Albright 1989). Specifically, the cell appears to prefer a single direction of motion across the receptive field and the receptive field is a single contiguous region in space. In 42% of cells, the RF structure was simple: one preferred direction and a non-patchy spatial receptive field. At the population level, we also quantified the relationship between eccentricity and receptive field size, and found similar linearity for the log-linear regression of the RF area to the eccentricity as (Perge, Borghuis et al. 2005) and (Raiguel, Van Hulle et al. 1995); specifically a slope of 0.033. These findings confirm that our quantitative RF
mapping technique provides an estimate of the receptive field that is consistent with classical ideas of receptive field organization. Our quantitative estimates of the receptive field, however, also revealed a significant number of cells whose receptive field properties did not match this “classical” view.

Figure 2.3: A “classical” spatial receptive field. The receptive field of unit sj249-003-1 is shown in panel a; it prefers rightward motion (cyan), and has an RF centered 5 degrees away from fixation (0,0) subtending approximately 5 degrees. This cell’s spatial receptive field structure is consistent with the classical view of an MT receptive field.

2.4.1 Changing direction preference

Figure 2.4 shows data from two cells, one from each monkey. The cell in Figure 2.4a clearly has two sub regions, one region prefers upward (yellow) motion and the other region prefers rightward motion (cyan). The cell in Figure 2.4b prefers down and to the left (magenta) as well as down and to the right (blue). These results indicate that some MT cells prefer different directions of motion in different parts of their receptive field.
Figure 2.4: Double-Direction preference cells. In panel (a) the results for unit sj225-005-1 (isolation shown in Figure 2.1a) are shown. This unit prefers upward motion in the yellowish region and rightward in the cyan region. In (b) the results from a second unit are shown (mo119-001-1). This unit prefers leftward (red) and downward (blue).

Even though the receptive field maps clearly demonstrate a changing direction preference, one might argue that this result is an artifact of the complex stimulus or even the reverse-correlation analysis method. To address such reservations, we used a more traditional method to confirm the finding that a single unit prefers more than one direction of motion in different parts of its receptive field. The PrefDir stimulus used for this purpose is described in detail in Methods, in brief: a single moving dot was used to measure the tuning properties of the cell separately at two or more locations within the receptive field.

Figure 2.5 shows the results for the first cell shown in Figure 2.4. Shown in (b) are the results of the PrefDir stimulus, the yellow-green curve is the firing rate elicited by a single dot moving in the corresponding directions within the pixel highlighted in black in the yellow-green subregion (preferring up and to the left) on the STAv image. The cyan curve is the direction tuning of the pixel highlighted in
black in the cyan subregion (preferring rightward motion). Arrows are superimposed upon the polar tuning curves to indicate the mean direction preference. This experiment clearly confirmed the difference in preferred direction across this cell’s RF: the upper subregion preferred upward motion, and the lower region preferred rightward motion using both the reverse correlation method as well as the polar direction tuning. Furthermore, the PrefDir stimulus confirms that both subregions were excitatory in nature (their responses were higher than baseline; baseline is shown as a red circle in Figure 2.5b).

Figure 2.5: Double-Direction preference confirmation. The PrefDir stimulus was presented for this unit at the two locations indicated by the black boxes overlaid on an enlarged version of Figure 2.4a. The results of the PrefDir stimulus are shown in (b); the responses from the two locations are shown in their corresponding colors. The red circle corresponds to the baseline firing rate of the cell, measured during the 200ms before stimulus presentation. The arrows are the mean direction of the response.

Not all cells showed such a large change in direction preference, examples of cells with more subtle changes in direction preference are shown in Figure 2.6 and Figure 2.7. Figure 2.6a shows the same cell shown in Figure 2.3a and appears to have the same direction preference across the entire RF. However, two subregions are highlighted by red and blue squares. The polar direction preference as measured by a
single moving dot (PrefDir) is shown in panel b; even though the two tuning curves are similar, it is clear that their mean preference is significantly different (superimposed arrows and p-value).

Figure 2.6: Subtle changes in direction preference. The unit shown in Figure 2.3a was also probed using the PrefDir stimulus. The two locations used in the analysis are shown with blue and red boxes in (a). The results of the PrefDir stimulus are shown in (b) in the corresponding color. The arrows represent the mean direction of the response. The two mean directions are significantly different (p=0.01, circular Kruskal-Wallis test).
Figure 2.7: Subtle changes in direction preference and local vs. global. In (a) a unit with more substantial changes in preferred direction than that shown in Figure 2.6a, is shown. The mean preferred direction slowly changes from upward to up (yellow) and to the right (green) across the receptive field. In (b) are the results from the FlowField stimulus. ‘Local’ corresponds to the response to the FlowField_local stimulus. The numbered bars correspond to the FlowField_global stimuli, 0 corresponding to the preferred direction. There is no significant difference in response to the Flow condition than to any other of the uniform conditions (p=0.76; Kruskal-Wallis), which is representative of the population.

At the population level we found that 46% of cells preferred the same direction of motion for all positions within their receptive field. For the remaining 54% of cells at least two positions within the receptive field preferred significantly different directions of motion. The typical range of angular deviations of preferred directions for these cells was 9.2 to 80.3 degrees, median 40.0.

2.4.2 The optimal flow field

The STAv provides a prediction as to the optimal stimulus for a given cell. If MT cells were accurately described as a linear filter followed by a static non-linearity, the preferred global stimulus should be the stimulus that corresponds to the receptive field map determined by reverse-correlation. We tested this hypothesis by comparing
the response to various uniform flow fields to that evoked by the stimulus that perfectly matched the estimated receptive field (For details, see FlowField_local stimulus in Methods). Nine cells were isolated long enough to run this test. To avoid the complication of a suppressive subregion, cells that had only small direction preference changes across the receptive field were used, as exemplified in Figure 2.7. All cells were highly responsive to all conditions in the FlowField paradigm. All 8 conditions were presented for a minimum of 16 times (median 95). A Kruskal-Wallis test showed that for all but one cell there was no significant difference between the FlowField_global stimuli and the FlowField_local stimulus at $p < 0.05$. For the one cell that was tuned, a post-hoc test revealed that the FlowField_local stimulus did not evoke a significantly larger response than any of the FlowField_global stimuli.

2.4.3 Spatial Structure

Apart from the changes in direction preference, we also found surprising spatial structure in some MT receptive fields; they were often patchy (non-contiguous in space). Shown in Figure 2.8 are data from 2 cells, one from each monkey. Highly responsive regions (patches) are clearly separated by non-responsive regions (darker regions). For the cell shown in (a) there appear to be 7 or more isolated patches all preferring motion down and to the right. The patches are easier to identify in (c) which shows the vector length of the STA and has spurious pixels removed (ones without 3 neighbors being significant at $p=0.01$). In (b), there are 2, possibly 3, subregions preferring motion up and to the right. In the most responsive area, there are two small but highly responsive spots which are separated by 5 degrees.
Furthermore, there is a weak, but still significant region nearly 10 degrees above the more responsive area.
Figure 2.8: Patchy receptive fields. The results from two units are shown (a,c,e: sj248-005-1; b,d,f: mo101-002-1). In panels (a) and (b) the results from the BMdots analysis are shown. In (c) and (d) the vector length is shown in grayscale thresholded for significance. Shown in (e) and (f) are the results from the GridRF stimulus. Shown in grayscale is the firing rate at each location for a single dot moving in the estimated preferred direction for the cell. There is clear agreement between (b) and (c), and (e) and (f), thus confirming the patchy structure of the receptive fields.
To validate this result with a more traditional stimulus and analysis, we used the GridRF stimulus. In brief, the GridRF stimulus consisted of a single dot moving in the estimated preferred direction at 121 locations on an 11 by 11 grid (for details see Methods). The results for the two example cells are shown in Figure 2.8e,f. The firing rate of the cell for each location is shown as a gray level, the brighter the pixel the higher the firing rate. The 11 by 11 grid is positioned in the whole-screen panel for easy comparison to (c) and (d). Clearly, the patchy structure observed in (c) and (d) is reflected with near perfect agreement in (e) and (f), respectively.

One might argue that retinal scotomas could cause patchy receptive fields. To address this issue we estimated the receptive fields of two units from the same animal (sj239-012-1, sj248-005-1). The receptive field of the first unit is shown in Figure 2.8c, the second unit’s complete RF Map is shown in Figure 2.9 (a) and its receptive field outline in (c). Both units are highly patchy but they cover approximately the same range of visual space. Figure 2.9e shows an overlay of their two receptive fields; yellow represents the intersection of the two receptive fields. A majority of the gaps in the receptive field shown in (d) are filled in by the receptive field of the cell shown in (b). Because these cells are from the same animal and receive their input from the same retina, this shows that the patchiness cannot be explained by retinal scotomas.
Figure 2.9: RF Gaps are not caused by retinal scotomas. Receptive fields were estimated from two units from the same animal (sj239-012-1, sj248-005-1). The BMdots results are shown in (a) and (c) and the estimated receptive fields are shown in (b) and (d). The unit shown in (c) is highly patchy and is also shown in Figure 2.8a. The two receptive fields are then overlaid in (e); yellow is the intersection of the two receptive fields. Note that a majority of the gaps in (d) are filled in by (b); therefore the patchiness cannot be explained by retinal scotomas.
2.5 Discussion

Our fine-grained reverse-correlation methods allowed us to study MT receptive fields quantitatively, and at high resolution. The classical view of the receptive field as a contiguous region of the visual field in which the cell prefers a single direction of motion could be confirmed for approximately half the neurons. The other half, however, showed significant deviations from this view. More than 50% (81 out of 152) of cells had a significant change in their direction preference across the receptive field; by visual inspection: 7 showed double-direction preferences and another 16 showed receptive fields which were more complicated. A smaller percentage (19%; 29 out of 152 cells) had spatial receptive fields with significant gaps in them that could not be explained by retinal scotomas. There are several possible explanations for the patchiness and changing direction preference that we observed. Patchiness could be a biological phenomenon or a result of our electrophysiological technique, but it does not seem likely to be caused by eye movements. The changing direction preference could provide additional information for large-field optic flow selective areas such as area MST.

2.5.1 Patchiness

Previously, patchy visual receptive fields have been reported in the superior colliculus and the lateral geniculate nucleus during development ('Hot spot' cells: Tavazoie and Reid 2000; Carrasco, Razak et al. 2005 Fig 5D). They propose that imprecise connections are refined over the course of development, which results in
smaller and more precise receptive fields. Our results suggest that patchiness may be a normal phenomenon occurring in healthy adults.

In the results section we already demonstrated that the MT patchiness could not be due to retinal scotomas because such scotomas would show up in the same retinal location for each patchy cell. Our data (Figure 2.9) clearly show that the gaps in one cell’s RF are filled in by the RF of another cell. One could argue that the patchiness was caused by electrodes that sever part of the dentritic arbor. While this cannot be ruled out, it would require retinotopically organized dendritic branches, which have not been demonstrated in area MT.

Finally, eye movements cannot explain the patchiness observed. Such an explanation would require consistent error in fixation of greater than 5 degrees for only approximately 20% of recordings. Furthermore, when subsamples of the data were analyzed the same degree of patchiness was observed (data not shown); this implies that the mis-location must be randomly interwoven over the course of the recording session.

Given these arguments, we conclude that these patches are real; many spatial receptive fields in MT are not contiguous. It seems possible that patches arise from a developmental process in which a coarse initial connectivity between MT and V1 input neurons is fine-tuned by experience. The gaps in the RF we observed could then be interpreted as examples in which the initial connectivity was too broad, or the experience driven fine-tuning process removed relevant parts of the RF. In a noisy, non-ideal biological tuning process, such errors are not too surprising. The prevalence
of 19%, however, does seem rather large for an explanation that relies on errors in development. However, while precise laminar information is not available from our recording technique, we found the simplest and least patchy receptive fields in recordings from what we estimated to be layer 4. This is consistent with Raiguel et al. (1995) who demonstrated that the center-surround organization of MT cell receptive fields is least complex in layer 4. This suggests that the patchiness of MT receptive fields may arise from within MT and not from sparse V1 input.

2.5.2 Changing direction preference

To our knowledge, spatially changing direction preferences have not been reported for area MT before. In theory, these changes in direction preference could serve as building blocks for the large-field optic flow analysis taking place, for instance, in area MST. Many models construct MST flow-field responses from the sampling of single-direction preferring MT neurons. (Eg. Perrone and Stone 1994). Duffy and Wurtz (1991), however, could not find support for a model of MST receptive fields constructed out of purely translation selective MT cells. Our data may resolve this issue; rather than providing flow-field building blocks that represent pure translational motion, the MT cells with changing direction preferences may represent building blocks for locally divergent and rotational flows.

2.5.3 Suppressive surrounds.

MT cells are known to have quite complex suppressive surrounds. Surrounds are normally much larger but weaker than the excitatory center. Surrounds have been
found which are radially and bilaterally symmetric as well as asymmetric or patchy (Raiguel, Van Hulle et al. 1995; Perge, Borghuis et al. 2005).

The changing direction preferences we report here, however, are not suppressive surrounds. This is clear from the data in Figure 2.5 that show that the regions of the receptive fields with different preferred directions are both excitatory. In fact, we observed very few receptive fields consistent with a suppressive surround. This could be due to the fact that surrounds are generally weaker than the excitatory center and therefore harder to detect. Furthermore, our stimulus is not optimal to detect such surrounds; if a cell had a strong suppressive field, it would be suppressed while the BMDots stimulus was presented. Consistent with this, we noted that a fair number of cells were entirely non-responsive to the BMDots stimulus. For the few cells that showed suppressive surrounds, we excluded their surrounds from all direction preference analyses.

2.5.4 The Preferred Flow Field

We used the locally estimated preferred stimulus directions to construct the FlowField_local. Comparing the response to the FlowField_local stimulus with the response to FlowField_global stimuli revealed no significant difference. This could lead one to conclude that the changing direction preferences are not relevant for the response of the cell. Apart from the fact that the absence of proof should not be interpreted as the proof of absence, we point out that our prediction of the optimal flow field suffered from some limitations. First of all, the simple combination of locally preferred directions assumes linearity of spatial interactions, which is unlikely.
to be the case (Britten and Heuer 1999). Second, we used the average (STAv) as the best estimate of the locally preferred direction; it is possible however that the mean of the circular tuning distributions did not evoke the maximum response. To truly estimate the optimal flow field these issues would need to be addressed. As it stands, our FlowField control experiment merely shows that uniform flow fields (over a 25 degree range) and the globally preferred flow field drive the cells equally well.

2.6 Conclusions

We demonstrated that MT receptive fields often do not have the simple structure that is commonly assumed. Receive fields were found that preferred very different directions of motion in different parts of the receptive field. We also found receptive fields that were patchy, or composed of highly responsive regions separated by non-responsive regions. These results suggest that area MT receptive fields are more complicated than previously thought, and that new models need to be developed to explain these results.

2.7 Acknowledgements

This chapter was co-authored with Bart Krekelberg, Tom Albright and the dissertation author; it is being prepared for publication.

2.8 References


Chapter 3: Modulatory Receptive Field

Structure of Area MT Revealed By

Maximally Informative Dimensions

3.1 Abstract

We took data from our previous reverse correlation study and applied a variant of Maximally Information Dimension (MID; Sharpee et al. 2004) to find mechanisms that the Spike Triggered Average (STA) could not reveal. Using MID we found a second kernel (receptive field, RF2) that interacted with the STA. We found 3 categories for RF2 structure: Surround Suppression, Off Preferred Direction Suppression and Omni-modulation. Surround Suppression has been demonstrated for area MT before, which validates the technique. Moreover, the analysis reveals that a divisive nonlinearity describes the interaction between the STA and the surround. Off Preferred Direction Suppression is suppression within the receptive field that is not on the preferred axis of motion; this nonlinear interaction is similar to surround suppression and half were well fit by a divisive nonlinearity. This off preferred direction suppression could explain the change of direction preference found previously in some receptive fields (Chapter 2). Omni-modulation is modulation due to all directions of motion; this structure may reflect population normalization.
3.2 Introduction

Receptive fields have been studied to the point where the term is now ambiguous. The receptive field has been probed in many different ways (for example Barlow et al. 1967, and Chichilnisky 2001) and all reveal different aspects of response. Many techniques measure predominantly the excitatory structure of the receptive field and this is often referred to as the classical receptive field (CRF); essentially the region of visual space that elicits a response. The Spike Triggered Average (STA) has been a very fruitful technique for studying different regions of the brain such as the retina, LGN, V1, MT and A1 and is often a good estimate for the classical receptive field.

Many studies, however, have revealed a suppressive mechanism often referred to as the suppressive surround; this structure generally spatially surrounds the CRF with a similar visual preference and reduces the response of the cell. Often, this surround is only measureable when a stimulus is located within the CRF, such that without a stimulus within the CRF no response is elicited from within the surround: a silent surround. Since the surround is only induced when there is a corresponding stimulus within the center, it is viewed as a nonlinear interaction between two independent mechanisms: the center and surround. Xiao et al. (1997) demonstrated suppressive surround in area MT. However, no one has studied the suppressive surround and the classical receptive field simultaneously, where both the center and surround stimuli were varied. Furthermore, no one has studied the surround in fine spatial detail and more importantly no one knows the structure of the surround where
it spatially overlaps with the classical receptive field. Finally, the exact nonlinear interaction between the center and surround, to the best of our knowledge, has never been directly measured in area MT.

Techniques have been developed to elucidate such nonlinearly interacting mechanisms, one of which is Spike Triggered Covariance (STC) and was employed by Rust et al. (2004) and others to study areas V1 and earlier in the visual system. This technique however, requires a Gaussian distributed stimulus. Determining a Gaussian distributed stimulus that drives area MT has proved challenging and has limited the application of this technique to area MT. The stimulus used in this study was a sparse binary stimulus; therefore another analysis technique was required. Maximally Informative Dimensions (MID) as proposed by Sharpee et al. (2004) is the general solution to this problem, however, we use a variant that is optimized for the stimulus distribution used here (Chapter 5). The approach of MID is to find a linear model, where the linear part is the dot product of the stimulus with one or more kernels that are being estimated (RF1 and RF2 in our examples; see below), that best predicts the response of the cell. The insight that Sharpee et al. (2004) had was that mutual information is the best measure of prediction ability; essentially the mutual information between the model and the spike train determines how good the model is at predicting the response of the cell. The model used by MID is of the form F(RF1*Stimulus, RF2*Stimulus…), where F() is a nonlinear function that maps the 1 or more linear terms into a firing rate. It can be demonstrated that the amount of mutual information is calculated entirely from the nonlinearity F, and does not depend
upon anything else. Furthermore, the nonlinearity $F$ is in fact estimated from the 1 or more dot product values and the response of the cell by combining similar dot product values and estimating the average response to those similar values. If there are 2 or more kernels, the nonlinearity represents the nonlinear interaction between the kernels.

While the true biophysical implementation could be different, one can visualize the kernels as receptive fields, and in our suppressive surround case, one kernel can represent the excitatory feed-forward receptive field, and the second kernel can represent the suppressive surround. Furthermore, for these receptive fields to be considered separate mechanisms there must be a nonlinear interaction between them, otherwise, they are indistinguishable from a single linear receptive field. A schematic is shown in Figure 3.1, where a simple model of a center surround receptive field is shown. Generally, the center and surround are considered two separate mechanisms, where the center is suppressed by the surround and this suppression is often modeled as division (Simoncelli et al. 1998). In this example, the surround is composed of many neighboring receptive fields that all individually divisively suppress the response of the center cell. Similarly to how the center is generally thought of as a single mechanism, however, is recognized as being constructed out of many smaller units, the surround should be constructed out of many subunits, but considered a single mechanism. One would expect the MID analysis to find two kernels one consistent with the center and one consistent with the surround, or an equivalent subspace. We set out to test whether a divisive model is a good model for the observed nonlinear interactions.
3.3 Methods

3.3.1 Electrophysiology

The experimental design and all electrophysiological data used for the current study were described elsewhere (Chapter 2). In brief, using a juice reward, awake-behaving monkeys were trained to fixate a red fixation dot while a swarm of hundreds of independently moving dots were moving about the entire screen. While the monkeys were fixated electrophysiological recordings were made of cells in area MT using tungsten coated with either lacquer (FHC) or glass (Alpha Omega) electrodes.
with an impedance of 1-2Mohms. Area MT was found based upon a structural MRI and the predominance of direction selective cells within area MT. Only extremely well isolated units were included from the two monkeys studied. Isolation was based upon the separation of the waveforms in a 3D space defined by the first 2 principal components of the waveforms and time, as well as based upon the inter-spike interval histogram. The same criteria were imposed as previously (Chapter 2), only continuous time intervals for where the waveforms where well isolated visually, within the 3D space, from one another and from noise were used. To ensure that there were sufficient data to measure a second kernel, we only included cells recorded for over 1,000 seconds using the reverse correlation stimulus (roughly 400 trials) and had 10,000 spikes. Out of the 152 cells that were well isolated only 50 met this further requirement.

3.3.2 Stimulus and Spike Triggered Average

The stimulus used was composed of 300 independently moving dots simulating approximately Brownian motion. The stimulus was represented by binning the dot motion in both space and direction as shown in Figure 3.2 and as described in Chapter 2. The spatial resolution was 1 degree by 1 degree of visual angle and the directional resolution was 45 degrees (8 directional bins); these values were chosen to keep the size of the kernels relatively small due to the computational expense of large kernels. The Spike Triggered Average (STA) was also calculated identically to previously; all stimulus frames were weighted by the response of the cell before being averaged then the baseline firing rate of the cell was subtracted so as to visualize anti-
preferred direction suppression as a negative number (blue in Figure 3.4a). The latency of the cell was estimated from the time shift of spikes relative to the stimulus that resulted in the greatest signal in the STA; all analyses were performed at this time shift and all other temporal aspects of the receptive field were ignored. The analysis was restricted to a rectangle that contained the receptive field as defined in our previous study. Essentially, each spatial location within the entire whole-screen STA was tested to determine whether it was direction selective using a Rayleigh Test but this study used a stricter significance threshold of 0.005 so as to minimize the total number of pixels included in the analysis.
Figure 3.2: BMdots stimulus and reverse correlation. In panel a, the BMdots stimulus is shown. It was composed of 300 independently moving dots filling the entire monitor, which subtended 39 by 29 degrees. In b, the BMdots stimulus was constructed from a random seed that allow the dot location and direction to be reconstructed at a later time. To analyze the BMdots stimulus, an arbitrary spatial grid was imposed upon the dot locations (c) and a directional grid was imposed upon the dot directions (d). The spike triggered average (STA) was then performed on the data as visualized in (e) and a STA from an example cell is shown in (f) as a series of polar tuning functions. The response of the cell to many different directions of motion are shown at many different spatial locations and the radius from the center of each of these locations is proportional to the response of the cell.

3.3.3 Maximally Informative Dimension Analysis

The Hybrid search using approximate mutual information and wavelets as defined by (Chapter 5) was then applied to these data in order to find a highly informative second kernel; the first kernel being the Spike Triggered Average (STA). The STA is often the best first linear model with one kernel. Since the stimulus used for this study was not Gaussian distributed, Spike Triggered Covariance (for an example application see Rust et al. 2004) could not be used so another method was
required; we chose to use a variant of the Maximally Informative Dimensions (MID)
analysis originally proposed by Sharpee et al. (2004). The basic premise of MID (both
Hybrid and original) is to find the best linear model for the response of a cell, where
the optimization criteria is mutual information between the model and the response of
the cell. The linear model can be a function of 1, 2 or N inputs, where each input is
the dot product of a kernel with the stimulus at each instance of time (frame); for this
study 2 linear kernels were found: RF1 (STA) and RF2. Therefore, MID searched for
a value of RF2 that maximized the mutual information between
F(RF1*Stimulus,RF2*Stimulus) and the response of the cell for all stimuli, where F()
is a 2 dimensional nonlinearity that maps the two linear terms into a firing rate for the
cell. Kernels can be thought of as receptive fields that have distinct interactions with
one another. An example of what 2 kernels would be for MT is one kernel could be
the feed-forward excitatory receptive field (Classical Receptive Field), and the second
kernel could be the suppressive surround.

For the Hybrid method a 3 dimensional wavelet was used, 2 spatial and 1
directional dimension. Since start configurations influence the results and in order to
remove algorithm noise, 8 different wavelet configurations (forward and flipped for all
3 dimensions) were used with 4 repetitions for a total of 32 runs of the Hybrid search
per cell. These 8 different configurations were a convenient way of using 8 different
variants of the same search. For cells with a strong signal for the 2nd dimension, all 8
configurations resulted in essentially the same final answer with similar levels of
mutual information; however, for cells with a very weak signal a few of the start
configurations may result in more mutual information than others. These 32 runs were then combined by calculating the principal components of these 32 kernels weighted by their respective information gain. If the first principal component was the most informative of all components then it was used as the second kernel (RF2); 13 cells were rejected (37 remained) at this point because the first principal component was not the most informative, generally when this happened no consistent pattern was found by the 32 runs and therefore there were no meaningful kernels other than the STA.

Since the sign of the kernel is arbitrary due to the nonlinearity $F$ 

$F(RF1*Stimulus,-RF2*Stimulus) = G(RF1*Stimulus,-RF2*Stimulus)$ where $G$ is another nonlinearity but with equal mutual information), for the second kernel we adopted the convention that the mean of the kernel should be positive. To remove kernels that were dominated by noise, we further constrained the dataset such that the ratio of the sum of the positive pixel values to the sum all the absolute value of all pixel values must be greater than 2/3; in other words select results that were predominantly of one sign and therefore potentially the easiest to understand mechanistically. This selection reduced the number of cells being analyzed to 20.

### 3.3.4 Fitting a Divisive Nonlinearity

The nonlinear function that maps the pair of projection values (the projection of the stimulus on to the STA and to the second kernel) to a firing rate was estimated for all of these 20 cells using the Hybrid method described earlier. We wished to
compare the nonlinearities found here to that which others have used, so we fit the
found nonlinearities to the form:

\[
F \left( \frac{RF1 \ast Stimulus}{x + (RF2 \ast Stimulus)^2} \right),
\]

where \( F \) is a static nonlinearity that maps the result of the
inner equation to the average, estimated from the data, and \( x \) was being optimized,
\( x > 0 \). The fitting procedure was to find the value of \( x \) that resulted in the maximal
mutual information between

\[
\frac{RF1 \ast Stimulus}{x + (RF2 \ast Stimulus)^2}
\]  \hspace{1cm} (1)

and the response of the cell. Divisive normalization of this form has been proposed by
others (Simoncelli et al. 1998) and fit most of the measured nonlinearities well.

To quantify how well this model fit our data, we used Akaike information
criterion to compare the amount of explained variance between the fit model and that
of a model based solely upon the STA. We estimated appropriate nonlinearities for
the fit model and the STA and measured the residual sum squared error between these
two models and the cellular response. We considered the data well fit by the above
equation when Akaike information criterion for the fit model was less than the STA by
at least 25. This is an arbitrary threshold since it is difficult to estimate the number of
free variables between the two models so as to do an appropriate comparison. If we
were to use the number of elements in \( RF2 + 1 \), the upper bound on the number of free
variables over the STA model, all fits would be rejected, where as by eye it is obvious
that this is often a good fit of the data. At this threshold, 12 of the 20 nonlinearities
were well fit by this model.
3.3.5 Nonlinearity Illustration

The 2 dimensional nonlinearity indicates the nature of the interaction between the two kernels (or receptive fields); for example divisive or subtractive half rectification. To develop an understanding of a two dimensional nonlinearity, a simple model was constructed. Two linear kernels (or receptive fields) were used, one a Gabor function (RF1) and the other a 2D Gaussian (RF2) at a resolution of 16 by 16; both kernels were normalized to be unit length. The stimulus was sparse binary noise, similar to that of the representation of the physiology stimulus; the probability of a 1 was 0.05, otherwise 0, at any given spatial location. Equation 1 was used as the nonlinear interaction for this model with $x = 0.1$. 50,000 random stimuli were generated. A 2 dimensional histogram was then calculated where the vertical axis corresponds to the projection onto RF1 and the horizontal corresponds to the projection onto RF2 and the mean response within each bin was calculated. This histogram is a visualization of the nonlinearity (Figure 3.3a). Grayscale is used to represent the mean response, white being larger positive values and black being large negative values and iso-contours are used to improve visualization. As one can see as one progresses vertically that responses monotonically increase, this is due to the fact that Equation 1 is approximately linear with regard to RF1. However, as one progresses horizontally, the structure becomes more complicated. For positive projection values onto RF1 as one progresses from left to right the more responses are reduced, due to the division by the projection onto RF2. For negative projection values onto RF1, progressing from left to right responses increase, this is because
negative numbers divided by a large positive number will approach 0 and therefore be increased. To further help understand the visualization, two other functions, or neural models, are shown: $RF1 \cdot \text{Stimulus} - \lfloor RF2 \cdot \text{Stimulus} - 0.5 \rfloor$, where $\lfloor \rfloor$ is half rectification, and $RF1 \cdot \text{Stimulus}$ (Figure 3.3b,c respectively). The exact shape of the plot should be ignored and is determined by the two kernels and the stimulus distribution, the important aspect is the curvature of the iso-contours.

![Figure 3.3: Example functions.](image)

Figure 3.3: Example functions. RF1 is a Gabor function and RF2 is a 2D Gaussian. Shown in (a) is a visualization of Equation 1 with $x = 0.1$ and $F$ being linear. The axes are the projection values onto RF1 and RF2, the reason that the RF2 dimension is entirely positive is due to the fact that Gaussians are entirely positive. The black lines are iso-contours where the output of $F$ is constant and the gray scale values are used to represent the value of $F$; dark values are negative, light values positive. To note is that the iso-contours are away from 0 on the vertical axis, or equivalently moving from left to right all values are slowly converging to 0 (mean gray). Shown in (b) and (c) are two other functions $RF1 \cdot \text{Stimulus} - \lfloor RF2 \cdot \text{Stimulus} - 0.5 \rfloor$, where $\lfloor \rfloor$ is half rectification, RF1*Stimulus respectively. (b) demonstrates what a subtractive half rectifier interaction would look like in this form and (c) demonstrates what one would expect if RF2 were irrelevant to the response, for example, if there where no surround.

### 3.3.6 RF2 Categories

Three categories were observed in the data: suppressive surround, off preferred direction suppression, and omni-modulation. Classification was preformed manually, and was based upon visual inspection of the second kernel and the spike triggered
average; the nonlinearity was not taken into account during classification. Once classification has been performed, the results from the previous study (Chapter 2) were used to determine if there was any previous evidence consistent with either a suppressive surround or changing direction preference. To determine the existence of a suppressive surround a more classical stimulus was used to probe the spatial extent of the receptive field: a single moving dot stimulus; GridRF (Chapter 2). The GridRF results occasionally suggested a receptive field larger than that estimated by the spike triggered average, this was used as evidence in favor of a suppressive surround (results not shown). Furthermore, the STA would infrequently suggest the existence of a surround with weak suppression (blue in the color tuning functions) in the region surrounding the strong excitation but in the same direction as the excitation; for example see Figure 3.4a, left hand edge there are small blue curves pointing to the right. To assess the changing direction preference the same criteria were used as Chapter 2; see the Changing Direction Preference section in the methods. The circular Kruskal-Wallis test (Chapter 6) was applied to the STA and a significance threshold of 0.01 was used. Once changing direction preference was confirmed, the direction and location of the change were compared to the second kernel results (RF2) to confirm that it was consistent with this change; i.e. spatially overlapping the changing region and in the same direction as the changing preference.
3.4 Results

Three classes of second kernels were found: suppressive surround, off direction suppression, and omni-modulation. These three classes will be addressed.

3.4.1 Surround Suppression

It has been known for a while that suppressive surrounds exist in area MT (Xiao et al. 1997). Eight cells fell into this category, 7 of the cells had other evidence suggesting a surround (see methods). Interestingly, there was only a small suggestion of suppressive surrounds in our previous study. Occasionally, the STA would have a very weak suppression to the preferred direction surrounding the excitatory center (Figure 3.4a, blue curves in region near -6, -8 degrees); however, due to how weak the suppression was often it would not be visible within the STA. A large number of second kernels were found that were consistent with a suppressive surround (Figure 3.4c); they had a greater spatial extent than the excitatory center of the receptive field as well as both components selective to the same direction (Figure 3.4a and c both have strong rightward components) and having a suppressive response for the same direction of motion as the center (Figure 3.4b, showing similar divisive curvature as Figure 3.3a). The suppressive nature of the nonlinearity is apparent by the fact that as one moves from the left to the right along any plane that the values converge to a similar value (medium gray in this case) or equivalently that the iso-contours arc away from approximately 0 on the vertical axis. Zero on the vertical axis corresponds to roughly no stimulus within the classical receptive field, and as one can see there is
very little modulation in response (change in color) horizontally at this point; i.e. presenting a stimulus that moves to the right in the surround does not change the response much when there is no stimulus in the center. However, if there is a preferred stimulus in the center, the more rightward motion there is in the surround, the greater the response drops. The fact that we found these suppressive surrounds is not surprising; however, the fact that they are found provides credibility to the method. Furthermore, all 8 of these cells were well fit by the divisive model (see methods) and it provides evidence for divisive normalization in area MT.
Figure 3.4: Surround Suppression. Shown is data from a cell with a strong suppressive surround. In (a) the Spike Triggered Average is shown, the plot is composed of many polar tuning functions spaced every 1 degree; red is excitation (greater than baseline) and blue is suppression (less than baseline). This cell was excited by rightward motion and suppressed by leftward motion within the center of the RF. The cell was also suppressed by rightward motion on the leftward edge of the RF (near -6, -8 degrees) as seen by the blue curves. In (c) the second kernel, as found by the new MID method, is shown in the same style as (a). This second kernel is highly selective to rightward motion and spatially overlaps the rightward suppressing region of the STA. In (b) the estimated and smoothed nonlinearity is shown, which demonstrates the interaction between the two kernels, and it should be noted, resembles Figure 3.3a. The exact shape of this function is irrelevant, and has to do with the exact stimulus distribution and kernels; the important aspect is that the iso-contours curve in a similar manner as Figure 3.3a. The axes do not have numbers because the absolute scale does not matter, but relative magnitudes do.
3.4.2 Off Preferred Direction Suppression

The second category of receptive field structure found was the off preferred direction suppression. Eight cells were in this category. Cells in this category have a second kernel that is spatially restricted to be within the classical receptive field (Figure 3.5a, c); i.e. these kernels are not consistent with a traditional suppressive surround. Furthermore, the motion direction that the second kernel was selective for was different from that of the STA. Generally the nonlinearity’s structure was similar to that of the suppressive surrounds (Figure 3.4b), and was consistent with a divisive interaction. However, 4 of the 8 cells were not well fit by the divisive model (see methods). Specifically for the cell shown in Figure 3.5, the second kernel (RF2) was highly responsive to predominantly rightward motion whereas the STA (RF1) preferred predominantly upward motion. Note, however, that the direction preference in RF1 was not constant across the receptive field: in the lower left the cell preferred upward motion, whereas, on the upper right it preferred slightly more leftward motion. Further, the strongest parts of RF2 overlap with the upper right region of RF1, where the slightly different direction preference occurred. Six of the eight cells in the category had changes in RF1 similar to Figure 3.5a and similar spatial and directional relationships as between RF1 and RF2.
Figure 3.5: Off Direction Preference Suppression. The format is the same as in Figure 3.4. In (a) the STA is shown, which exhibits a changing direction preference from the lower left (upward preference) to the upper right (preference for up and to the left). In (c) the second kernel is shown and is most modulated by rightward motion. It should be noted that the most responsive region of RF2 spatially overlaps with the upper right part of RF1, where there is a change in direction preference. In (b) the smoothed nonlinearity it shown; this demonstrates that the second kernel was suppressive in nature and specifically was consistent with a divisive interaction.
3.4.3 Omni-modulation

The third category is the omni-modulation; these cells are modulated by all directions of motion within a localized region of space. Four cells were in this category. This modulation is evident by the “circles” at each spatial location within the polar tuning plots (Figure 3.6c), meaning that the cell is equally modulated by every direction of motion at that location. None of these cells were well fit by the divisive model (see methods). The nonlinearity shown in Figure 3.6b, for instance, is not consistent with the divisive model; the iso-contours are not arcing out from the origin as they are in Figure 3.3a, 4b, 5b and the predominant structure is more “v” shaped.
Figure 3.6: Omni-modulation. The format is the same as in Figure 3.4. The STA is shown in (a), note that the most responsive regions of the RF are not grouped together, but clumped into 2 or more subregions (lower left vs. middle right). In (c) the second kernel is shown, it is striking that at nearly every spatial location, the kernel is not direction selective but instead responsive to every direction of motion, as evidenced by the “circles.” In (b) the nonlinearity for the interaction between (a) and (c) is shown; notice that the structure is substantially different from that of Figure 3.4b and 5b and not well fit by Equation 1.
3.5 Discussion

Using Maximally Informative Dimensions, we found modulatory structures that were consistent with a suppressive surround, off preferred direction suppression and omni-modulation. We will discuss the implications of finding suppressive surrounds has on the validity of our other results. Furthermore, we discuss the implication on the biophysical implementation. We then discuss the off preferred direction suppression structure and how this could possibly explain the subtle changing direction preference results found in our previous work (Chapter 2). Finally, we discuss the omni-modulation results and how this structure may be consistent with population normalization and how the nonlinearity for these cells is more complex than that of equation 1.

The surround suppression cells are not surprising; this structure of MT receptive fields has been known for many years (Xiao et al. 1997). However, the fact that these surround can be measured using this technique is new and provides credibility to other results found this way. This is also the first direct confirmation that a divisive normalization model fits the data well. Furthermore, the spatial extent of the surround is also interesting, in Figure 3.4c, the surround spatially overlaps the center. The area where the surround intersects the CRF approximately, -3,-7 degrees also seems to have a qualitatively different selectivity and is virtually omni-modulation. Though, the strongest modulation, longest radius, is actually for vertical motion and only weakly for the anti-preferred direction. This further suggests that the
cell receives some of the strongest suppression within the classical receptive field, and that this suppression was not measurable using previous techniques.

The changing direction preference observed in our previous work (Chapter 2) was somewhat of a surprise, particularly when other methods did not confirm these findings. These off direction preference suppression cells can explain a lot of this. Since this is a suppressive and interactive mechanism, it requires two or more stimuli to be present to be able to observe it. The data is consistent with a model where the feedforward input to MT prefers one direction of motion; however, there can be suppressive mechanisms that are modulated by different directions (approximately RF2). When the feedforward and suppressive mechanisms interact as they would for the reverse correlation stimulus used, the estimate of direction preference will be a combination of these two mechanisms. This could explain why the uniform flow fields generated the same level of response as the locally optimized stimulus based upon the spike triggered average (FlowField_global vs. FlowField_local; Chapter 2). The suppressive mechanism (RF2) had a direction preference substantially different than that of the STA and therefore all of the flow fields were sufficiently far away in direction so as to not induce the mechanism.

Furthermore, if we were to assume the uniform feedforward direction preference model, the STA would be biased in the direction opposite to that of the suppressive mechanism (since a suppressive mechanism is observed as a subtracted effect in the STA). Therefore, we can not rule out the possibility of predominantly uniform direction preference for the feed forward excitation. Yet, our results are still
consistent with the receptive field containing a change in direction preference if one were to use a broader definition of receptive field, a definition that encompasses both linear kernels.

Omni-modulation is consistent with a few different models. The most straightforward interpretation of the nonlinearity is that cells have a preferred density, or number of dots, within the RF. Deviations from this preferred density result in reduced firing rate. This is not a very appealing model from a biological perspective. Another model that is more interesting is that these responses are consistent with population normalization. The Simoncelli and Heeger model (Simoncelli et al. 1998) requires normalizing individual cell’s responses by the entire population; the entire population when combined is not direction selective, hence such population normalization would reveal itself in our analysis as omni-directional second kernels since these kernels are spatially selective but not directionally selective.

It is interesting to note that 2 of the 4 cells in the omni-modulation class were measured to be significantly patchy by our previous study (see Chapter 2 Patchiness section in methods) where as none of the other cells in the other categories were significantly patchy. Patchiness, or “hot spots”, is when different parts of the receptive field are highly responsive with weak or non-responsive regions in between. The STA in Figure 3.6a had an isolated “hot spot” located near -8, 4 degrees that is surrounded by a slightly less responsive region and then followed by a more responsive region. It would be interesting if this omni-modulation caused the patchiness observed. One possibility is that these patchy cells represent a later stage in
the cortical processing; it could be constructed out of relatively few smaller MT receptive fields that are then being normalized by the local population before being sent out to another cortical area, such as MST.

For the cells that were not well fit by the Equation 1, some would have been better fit by a model of the form $\frac{RF1 \times Stimulus}{x + (RF2 \times Stimulus - c)^2}$, where $c$ is a constant that shifts the “zero point” for where divisive normalization is minimal. It would result in a “v” shaped nonlinearity more similar to that of Figure 3.6; however, even for Figure 3.6 this would not fit all of the dynamics observed in the plot. In particular, several nonlinearities instead of having iso-contours progressively arcing up as one progresses from left to right, the iso-contours flatten out (as seen in Figure 3.6) or even arch down, suggesting far more complex dynamics than a simple divisive interaction because for large projection values onto the second kernel (for omni-cells this is equivalent to a large number of dots within the receptive field) the second dimension becomes excitatory again or at least less suppressive.

Some may wonder about the choice of squaring in the denominator, aside from this model being used by others it provides a convenient form that ensures that no division by 0 occurs. While some nonlinearities would be better fit by allowing this power to vary, this was not extensively tested.

Also, none of the nonlinearities were consistent with a subtractive half rectifier as shown in Figure 3.3b; all nonlinearities suggested either a divisive or a more complex nonlinear interaction.
A new variant of Maximally Informative Dimensions was required mainly due to the sparse stimulus used in this study. As demonstrated in (Chapter 5) the use of wavelets substantially improves the performance of MID optimization for sparse stimuli. The optimization used here started with the spike triggered average and only allowed the second kernel to be varied during optimization. In theory the STA may not be the optimal kernel in 2 dimensions; however, in practice for the stimulus distribution used it seemed to be optimal. First, in simulation with a 2 dimensional spiking model where both kernels are known, using the STA and a free second kernel consistently converged to the correct subspace as more and more data was included. Second, running the search once to find the optimal RF2 and then starting the search over again, but instead of starting from the STA using RF2 instead consistently found a kernel within noise of the STA. While neither of these techniques is absolutely conclusive, they suggest that the STA is the optimal kernel for higher dimensional models when using this stimulus distribution; however, this should be investigated further.

3.6 Conclusion

We applied a new Maximally Informative Dimension technique that was specifically optimized for the stimulus distribution used for this study. Using this technique we found 3 categories of structures. First, we found results consistent with surround suppression. Second, we found off preferred direction suppression; this mechanism could explain the change in direction preference across the receptive field.
observed in our previous study. Third, we found omni-modulation, which could be consistent with population normalization.

3.7 Acknowledgements

This chapter was co-authored with Bart Krekelberg, Tom Albright and the dissertation author; it is being prepared for publication.

3.8 References


Chapter 4: Object Motion Recognition in Area MT Probed with Motion Capture

4.1 Abstract

The question, does area MT code for object motion in the absence of motion within the classical receptive field, was probed using a motion capture stimulus. A difference between foreground and background was demonstrated in the magnitude of capture using human psychophysics. This difference was then used as a controlled comparison in neuronal responses from area MT in two male macaques. No large modulation was found that was consistent with the motion capture illusion. Therefore, it is reasonable to conclude that area MT only represents local motion, and not object motion.

4.2 Introduction

Recognizing the motion of an object as a whole instead of the motion of the constituent parts is arguably a goal of the visual system. It has been shown that area MT has a subpopulation of cells with responses that correspond to perception when probed with more complicated object motion signals (plaids, barber pole illusion, etc.). However, these more complicated stimuli all contain local motion cues, specifically one or more surfaces that locally define motion are within the receptive field of the
MT cells studied. What is not clear is does MT have a subpopulation of cells that will respond to a globally defined motion signal when there is no coherent local signal? To probe this question, a variant of an illusion called motion capture was used.

Motion capture was first reported by MacKay (MacKay, 1961) and later popularized by Ramachandran and Inada (Ramachandran and Inada, 1985). In essence, motion capture is the perception of motion in random dot flicker in the same direction as unambiguous motion signals. In Ramachandran and Inada’s paper they described a two-frame stimulus where two uncorrelated random dot matrices, one on each frame, are shifted horizontally with respect to each other. When these two frames are displayed in succession, it generated a strong perception of motion for the random dots; the perceived motion corresponds with the apparent motion of the matrix. The more commonly studied form of capture was also demonstrated in the same study; it is constructed from a compound stimulus of dots superimposed upon a moving sinusoidal background. Using stimuli similar to this compound stimulus, Murakami and Shimojo argue that the motion capture effect is most effective for stimuli that are on the order of the receptive field of a MT cell (Murakami and Shimojo, 1995).

These studies indicate that MT may be mediating this illusion and therefore may respond to purely global motion. Using a stimulus similar to Ramachandran and Inada’s random matrix stimulus, we set out to see if area MT responds exclusively to local motion, albeit sometimes locally ambiguous, or global object motion with no local motion cues.
4.3 Stimuli

Two versions of capture stimuli were used in this study: one that uses a red and green color mask and the other was a stimulus constructed entirely out of white dots. There are two configurations for the color mask stimulus; the color mask can either define a rectangle, titled “box”, or another shape titled “two bars.” Both configurations are shown in Figure 4.1. Two variants of the color mask stimulus were tested.

For the color mask stimuli each dot was circular in shape and 16 pixels (0.45 degrees) in diameter. Dots were rendered either red or green; the luminance was fixed for both colors to be approximately 15 lumens. The visible aspect of the stimulus was constructed to be 29 x 29 degrees, so that the vertical size matched the horizontal. A white or blue fixation dot appeared in the center of the screen. A color mask determined the color of each dot and the mask defined either a box or two bars, shown in Figure 4.1a and b respectively. The distance between the two vertical edges of the box or bars was set to 29 degrees, and one of the edges started off screen. The edges were 10 degrees tall. In reality, the two edges of the box or both of the two bars did not appear on the screen at the same time except for one frame. The reason for having the edges start off screen was so that a large motion signal could be defined, but also avoiding a large region of the stimulus (14.5 degrees wide). The magnitude of the coherence of the dot motion could be varied between 0.0 (flicker) and 1.0 (a uniform surface moving in a specific direction). The dot motion was controlled independently of the color mask motion. All dots were identical except for color, specifically the
dots that define a box move in the exact same manor as the surrounding dots. The dots were randomly placed with a mean density of 1.5 dots per degree squared. When a dot moved, the distance traveled was fixed, but the direction was pseudorandom. Dot motion was similar to (Williams and Sekuler, 1984; Newsome and Pare, 1988; Downing and Movshon, 1989; Newsome et al., 1989; Britten et al., 1992, 1993) and had a lifetime of 4 movements. All versions of the stimulus have a 333ms static period, with only the first stimulus frame being displayed, followed by 480ms of motion. The static phase was introduced when subjects reported that they were not able to interpret the visual scene and therefore could not perform the task. The mask moved at 30 degrees per second for a total of 7.25 degrees.
The two different variants of the color mask stimuli that were tested probed different aspects of apparent motion of the color-defined edges and dots. For the psychophysics and one of the monkey experiments the dot motion occurred every third frame and all dots and the two edges moved on the same frame. For the other monkey experiment, the dots and edges moved every frame. Regardless of the apparent motion setting, the average speed for both dots and edges was constrained to be 30 degrees per second.
The other version of the capture stimulus defined a rectangle 24 degrees wide similar to the box defined above but using only white dots on a black background. A given dot was moved every fourth frame, however the dots were interleaved such that only a quarter of the dots updated on a given frame. Edges were moved every frame. This stimulus also had the 333ms static phase, but then had 2 full cycles of forward and back edge motion. The total distance traveled by the edges was 12 degrees. Only the 0.0 coherence level was tested. The dots were the brightest white possible, and no lookup table was used. Two other configurations were used as controls, one where two white lines were drawn in the same location as the edges, and another where the dots were stationary and the edges moved. The dot density was increased to 6 dots per degree squared and the diameter reduced to 4 pixels (0.11 degrees). A schematic of these two configurations is shown in Figure 4.2. This stimulus was used because the edge motion signal is stronger than the color mask, and therefore might generate a stronger response in area MT.
4.4 Human Psychophysics

4.4.1 Methods

Stimuli were displayed on a Sony Multiscan E500 21’ monitor (75Hz, 1024x768) viewed binocularly 56cm away in a dimly lit room, using custom display software. For these experiments the dot and edge motion occurred every third stimulus frame. For a baseline test, subjects were presented a stimulus where the color-defined edges did not move, and only the dot coherence was changed. Coherence values that were tested in the principal experiment were 0.1, 0, -0.1, -0.2, -0.5, and -1.0 for two subjects or 0.1, 0, -0.1, -0.2, -0.4, and -0.8 for 5 subjects. For the
baseline experiment, the same coherence magnitudes were used. Negative coherence values indicate that the dot motion is in the opposite direction as that of the color-defined edges.

Subjects were asked to report the direction that they perceived the dots moving within a 5-degree radius around the fixation point. This was well within the region where the color-defined edges never entered. They were instructed to maintain fixation, but no external verification was used. The task was a forced choice between left or right, once the subject report a direction the next condition started. Further more, subjects were instructed to choose a direction at random if they did not perceive coherent motion. There was no time limit for response. All 5 coherence levels were tested with every combination of left, right; red center, green center; and box, two bars.

4.4.2 Results

For the baseline experiment two subjects’ data are shown in Figure 4.3. Data is collapsed across all conditions for the specified coherence, and the x-axis is reversed so that it matches corresponding negative coherences tested in the principal experiment. It is important to note that both subjects are reasonably good at the task and that at 0.5 and 1.0 coherence levels the subjects are nearly perfect.
Figure 4.3: Psychometric curves for unbiased motion perception for two representative human subjects. (a) shows a diagram of the stimulus as well as the response area used by subjects to report the direction of motion, the blue dot indicates fixation. The box color mask configuration was used, however the edges never moved. This experiment was used to determine the subject’s baseline motion perception abilities. The curves decaying down to 0 as the coherence increases indicates that subjects were nearly perfect for high coherence levels. Shown in (b, c) are two different subjects, the coherence is plotted on an inverted axis so that it will match that negative coherence values shown in Figure 4.4.

The results of the two subjects for the principle experiment are shown in Figure 4.4. As one can see the curves are significantly higher for the -.5 and –1.0 test conditions for both the box and two bars as compared to the corresponding conditions in the baseline experiment (compare Figure 4.3 and 3.4). This means that subjects were more likely to perceive the dots moving in the same direction as the color-defined edges even at high coherence levels. More importantly though, the box configurations have a stronger capture effect than the two bars configurations: the blue line is always above the green line. It should be noted that the amount of motion is
identical in the corresponding box and two bars conditions, and the most significant
difference is in what is perceived as figure.

Figure 4.4: Psychometric curves for motion capture perception for two representative
human subjects. (a) shows a diagram of the stimulus as well as the response area used
by subjects to report the direction of motion, the blue dot indicates fixation. The
dashed vertical lines indicate the extent to which the edges move. Two conditions are
shown, “box” (blue) and “two bars” (green). These two conditions exhibit motion
capture, since their curves are above the corresponding curves in Figure 4.3 b, c. Also
note that the “box” condition has a stronger capture effect, as demonstrated by being
above the “two bars” curve.

The box configuration was constructed to generate the perception that the dots
near the fixation point are part of a foreground object. Where as, the two bars
configuration was designed to give the impression of background. For 6 of the 7
subjects this foreground / background configuration was what was perceived. A few
subjects reported perceiving the two bars configuration as a box that wrapped around
the screen, but this perception is still compatible with the desired percept. The seventh
subject had a very strong capture effect, but both configurations were perceived as foreground, and therefore there was no difference between the box and two bars configurations. A difference between figure, ground and the magnitude of capture has been demonstrated before (Ramachandran, 1996).

4.5 Monkey Electrophysiology

4.5.1 Methods

Two male macaque monkeys were used in this study, both were given head posts and had recording chambers located over the parietal lobe to access area MT as described in (Thiele et al., 1999). The monkeys had their fluid intake controlled. For the task they were required to maintain fixation and were rewarded with a drop of juice at the end of the trial. The Salk Institute Animal Care and Use Committee approved protocols for all experiments.

Stimuli were displayed on a Sony GDM-F520 monitor (75Hz, 1024x768) using the same custom software used in the psychophysics. The version 5.2 of CORTEX (CORTEX, NIMH, Salk Institute) was used to control the graphics computer as well as a Plexon data acquisition machine (Plexon Inc., Dallas, TX). Tungsten electrodes with 1-4M ohm resistance were used. Box sorting was performed online. Later, spikes were sorted offline using visual PCA clustering and template matching. Cells were found and their direction selectivity determined by using a circular mapping stimulus (Hoffmann et al., 1976). Receptive fields were mapped used a sparse motion stimulus composed of 5x5 degree patches of coherent random
dots moving the in the preferred direction of the cell appearing in pseudorandom order at 1 of 16 positions. Once the receptive field and preferred direction were known, the fixation point was positioned to align the center of the receptive field to the center of the screen. The direction of the stimulus was set to the closest of eight possible directions to the preferred direction of the cell.

Each monkey was shown a different variant of the same color mask stimulus. For the first monkey, the variant with dot motion occurring on every frame was used. In addition, different coherence levels were tested to be able to construct a response curve comparable to the psychophysics. Coherence levels tested were, 0.2, 0.0, -0.2, -0.5 –1.0. 4 conditions were used with the dots stationary and only the color-defined edges moved, and 7 conditions with the edges stationary and the dots moving. In the stationary edge conditions, the same coherence magnitudes were tested but varied between preferred and non-preferred directions. To keep the number of conditions manageable only the green center conditions were tested, for a total of 31 conditions.

For the second monkey, the stimulus was identical to that as described in the psychophysics but had additional control conditions and only the 0.0 coherence conditions were tested. 4 flicker conditions were added where the color mask was stationary and 8 conditions with stationary dots were used with a moving color mask. There were a total of 20 conditions. The white box stimulus was also tested on this monkey.
4.5.2 Results

18 cells were studied in the first monkey; data from one cell is shown in Figure 4.5. Multiple coherence levels were tested and the box, two bars, and stationary conditions are compared to one another. The stationary conditions are where the color mask that defined a box was displayed, but the edges never moved. Also, dots were moved on every frame. The reason for deviating from the motion type used in the psychophysics was that most MT cells lost a majority of their direction selectivity with that type of motion. This was somewhat of a surprise since the temporal (40ms) and spatial (1.2 degrees) aspects of the motion signal are within the direction selective range of MT cells as measured with solid bars by (Mikami et al., 1986). Additional psychophysics was done to confirm that capture was still possible with this configuration, though the magnitude of the effect is not quite as large (data not shown). As one can see there is no large modulation in the response of the cell in comparison to all three conditions. In fact no single coherence level has a significant difference between the three configurations. However, there is a very small but significant effect in that the two bars configuration is consistently and significantly higher than the box with the non-preferred edge motion when using all coherence levels. This difference is surprising because even though it is consistent with the capture illusion, it is not of the magnitude one would expect from the psychophysical data. Furthermore, this could be due to some small luminance or attentional difference between red and green. This is why we then tested using the red and green center configuration for the second monkey.
Figure 4.5: Electrophysiological results for experiment one. In panel (a) the stimulus is depicted with the classically defined receptive field shown in red and the movable fixation dot in blue. The dashed vertical lines indicate the extent to which the edges move. (b, c) demonstrate the response of a single cell (mo65e) to different coherence levels and edge motion configurations. Negative coherence means non-preferred dot motion. The plots show that for the “box” (blue), “two bars” (magenta) and a “stationary” (black) edge case there is no significant difference between any of the coherence levels.

For the second monkey experiment 27 cells were studied. Only the 0.0 coherence level was tested, and the dot and edge motion was synchronized occurring every third frame. In this configuration all of the dots and the color mask moved every 40ms (3 frames), but the average velocity was matched to the original configuration. The reason for trying this variant is that perceptually capture was strongest when using more apparent motion. This was tried in order to maximize any capture effect. It was observed that the capture effect seems to be stronger with longer inter-motion duration than 40ms and larger movement steps, however to keep the
times and speeds within a physiological range for MT cells no longer times or
distances were tested.

An example cell from this second experiment is shown in Figure 4.6. Again,
stationary means that the edges did not move, but the dots were flickering. Since there
were no preferred and non-preferred versions of the stationary edge conditions the
data is duplicated across the two panels. As one can see there is no significant
difference between any of the conditions, and that the responses seem to only be
driven by the flicker, this was the trend for all cells recorded. One issue with this
particular variant is that a large number of the cells were entrained by the 40ms jumps,
and it was thought that this might be reducing direction selectivity.
Figure 4.6: Electrophysiological results for experiment two. In panel (a) the stimulus is depicted with the classically defined receptive field shown in red and the movable fixation dot in blue. The dashed vertical lines indicate the extent to which the edges move. Shown in (b,c) is a single cell (sj70e) for the 0.0 coherence level and for all color and edge motion configurations. The stationary cases are duplicated between the preferred and non-preferred panels. GR stands for green center, and RG stands for red center. Again no significant difference is observed between any of the conditions. Except in the moving GR preferred box case, but because the pattern is not replicated for RG this difference must be caused by something other than motion capture.

For the white box experiment, performed on the second monkey, 28 cells were studied. An example cell is shown in Figure 4.7. The stimulus was composed of either random white dots, or two white lines. The random dots were interleaved such that only a third of them moved on a given frame. Since there was no motion-matched control for this stimulus, the white bars and stationary dots conditions were used. The white bars were positioned in the same place as the edges of the white box and moved in preferred and non-preferred directions. The stationary dots condition had moving edges but the dots were stationary. There were two capture conditions, one where the edges started in the preferred direction, and one where they started in the non-
preferred. It became apparent very quickly that even though the stimulus was positioned fairly close to the center of the classical receptive field, we still found significant modulation for the white lines condition (Figure 4.7d), but not for the other conditions. Also note that for the two capture conditions, the magnitude of modulation is vastly diminished in comparison to the white lines condition (compare Figure 4.7a,b to 3.8d). This trend of superior direction selectivity for the white lines condition compared to the capture conditions was maintained for the population.

Figure 4.7: Electrophysiological results for experiment three. All panels are peristimulus time histograms for different conditions of an example cell (sj76e). (a) the white box condition with the edges moving in the non-preferred direction first. (b) the white box condition with the edges moving in the preferred direction first. (c) The white lines condition, where two lines in the place of the edges from the white box configuration is moved in the same pattern as in (a). (d) random dots are generated but do not flicker, while the edges move in the same pattern as in (a). What is surprising is that the white lines condition is much more direction selective than either of the other conditions and that none of the other conditions are significantly modulated.
4.6 Discussion

It came as a surprise when we realized that the white lines control condition had higher direction selectivity than either the stationary dots or capture conditions. The first surprise is that the receptive fields were larger than originally believed. The second was that responses were reduced so much in the presence of random dots. One explanation for the stationary dots case is that stationary objects within the receptive field seem to suppress the cell. In regards to the dot flicker, Churan and Ilg demonstrated that flicker in the background significantly reduced direction discrimination in MT, MST and perceptually (Churan and Ilg, 2002). In addition, because this directional modulation is not apparent in the responses to the stationary dots condition it suggests that the controls used in the previous experiments may not be sufficient. Considering the two stimuli have different widths, it is not certain that if the white lines conditions were spaced 29 degrees apart we would find the same effect. However it seems likely that the color-defined edges were in fact within some aspect of the receptive field.

One very significant aspect of motion capture that indicates that it might not be mediated by area MT is that, as mentioned earlier, the strength of capture increases with greater spatial jumps and temporal gaps. Most capture paradigms use 200ms or greater inter-frame intervals with several degree jumps. From our own experimentation, longer delays and greater distances increased the magnitude of the capture illusion, but a confound is that true dot motion become more difficult to detect. Therefore, it is difficult to say if the increased strength of capture is due to a
stronger illusory effect, or a weaker true motion signal. None-the-less, due to the fact that area MT has a limited spatial, temporal range over which it is direction selective and the most capture paradigms are out of this range, suggests that area MT may not be involved. Area MT is unable to selectively respond to the type of motion normally used in capture paradigms, therefore it is difficult to image it would respond to the object motion.

Furthermore, the requirement for the 333ms duration static phase suggests that attentional and higher-level mechanisms are needed for the illusion studied here. The duration was not systematically varied, so the exact minimum time for subjects to be able to perform the task is not known. However, it is clear from the subjects, that they needed the extra time in order to interpret the visual scene.

After review of the literature, there appears to be two types of motion capture. The first and more common, is the configuration where dots are superimposed onto a moving surface. The second type is where the random dots define the moving object, as demonstrated by McKay, Ramachandran, and this chapter. For the first type of motion capture, Murakami and Shimojo demonstrate that this has a center, surround antagonism that changes motion capture into induced motion with increasing stimulus size relative to eccentricity and they argue that this likely occurs in area MT or MST. However, no reversal to motion induction was ever seen for the stimulus used here for any stimulus size. Due to this inconsistency with stimulus size and motion induction, it is likely that there are two phenomena, one mediated by a center, surround receptive field possibly in area MT or MST and another which is performing object motion.
recognition and inappropriately binding motion to the dots. Furthermore, we tested
the effect of different frame durations and found that longer durations increased the
perception of capture, both qualitatively and quantitatively. The qualitative difference
was that for longer durations, and curiously for higher magnitude coherence levels, the
capture was seen as a surface of coherently moving dots in the captured direction. In
contrast to the low coherence levels and short durations, the dots were seen as moving
every direction with only a small bias towards the captured direction. Finally, two
subjects reported on occasion for the highest magnitude coherence levels the
perception that the dots moved in both the captured direction and the true dot motion
directions simultaneously. It was not the perception of two surfaces with a subset of
dots moving in each direction, but the exact same set had the contradictory and
simultaneous perception of both directions. The closest perceptual correlate is if one
is looking through a moving aperture with dots in the distance moving in the opposite
direction, but the aperture is defined by the dots and thus the dots must be moving
with the aperture. This suggests that two or more different areas, not just populations,
are signaling opposite directions. Thus, the motion capture type studied here seems to
be inconsistent with the characteristics of area MT, both in the lack of surround-
agonism and the spatial, temporal settings that generate the strongest illusion.

Taking into account that area MT is not tuned for the type of motion that
generates the strongest capture suggests a model with area MT giving a very
unreliable motion signal. Since MT’s signal is too weak, another area would then be
needed to compensate since perceptually the unbiased dot motion is unambiguous.
This other area should be tuned for longer duration apparent motion and presumably more complex motion signals (such as object motion), as well as be highly influenced by attention (Culham and Cabanagh, 1996; Ramachandran, 1996).

### 4.7 Conclusion

The data presented suggests that cells in area MT may not be significantly biased by the surround stimulus used in these experiments. Random dot flicker seems to reduce direction selectivity for most MT cells; therefore the random dot flicker most likely will occlude any response in MT consistent with capture. Due to the spatial and temporal aspects for generating capture, it seems less likely that MT would exhibit responses consistent with this illusion. It seems quite likely that responses in MT are mediated solely by local motion.

### 4.8 Acknowledgements

This chapter was co-authored with Bart Krekelberg, Tom Albright and the dissertation author.

### 4.9 Reference


Chapter 5: A Heuristic Approach to Maximally Informative Dimensions

5.1 Abstract

A new algorithm is presented to improve upon the Maximally Informative Dimensions (MID) method proposed by Sharpee et al. (2004). The MID method is a general solution, which is less biased by the stimulus distribution, to the problem of finding a linear model that best predicts the response of a cell. Some of the issues with MID are that it does not always converge to the correct answer and what is most important for us, does not function well for sparse binary stimuli. Our new method uses an approximate mutual information measure that does not require binning; this imposes a plausibility constraint on the nonlinearity, specifically, it must be smooth. Further, it uses a Hybrid search based upon a non-gradient based optimization (Nelder-Mead Simplex Optimization) and the numerical gradient optimization approach proposed by Sharpee et al. (2004). The method also uses wavelets in order to further improve the optimization. The new algorithm (Hybrid) was compared to the original method (MID) for several nonlinearities and stimulus distributions for one and two linear kernels. Various combinations of approximate mutual information vs. mutual information and wavelets vs. no wavelets were tested to determine the contribution of the various approaches. The accuracy of the methods was measured
using a simple spiking model and the computational times were also recorded. The Hybrid approach performed similarly or significantly better than the MID method for most cases except for a pink noise distribution. For finding 2 linear kernels, variants of the Hybrid approach were compared and the use of approximate mutual information and wavelets were justified by significant performance benefits particularly for the sparse binary stimulus distribution. The new approach is a general approach that works well for many stimulus distributions and nonlinearities; in particular it demonstrates a massive benefit for sparse binary noise for the 2 kernel cases and for the Even nonlinearity in the 1 kernel case.

5.2 Introduction

Visual electrophysiologists are interested in structure and behavior of receptive fields. In order to acquire a greater understanding of receptive fields, one needs methods that elucidate more aspects of the receptive field than a single structure (i.e. classical receptive field or the Spike Triggered Average). An example of a more complex structure would be a suppressive surround. A suppressive surround can be probed in many different ways, but generally requires placing a preferred stimulus within the classical receptive field. However, if the surround spatially overlapped, partially or otherwise, with the classical receptive field, one would be unable to measure it where they overlap. Furthermore, generally stimuli that are constructed specifically to study the surround are designed to only probe one aspect of the surround in at most a few spatial locations. For example, in area MT only the
preferred direction is generally tested in the surround in maybe 10 different locations. The number of conditions is constrained by the fact that they are presented one at a time. However, if one wanted to map the interaction of directions within the classical receptive field and surround and get a spatial profile, this would become prohibitively large. For example 8 different directions at 10 different surround locations with 8 different directions within the classical receptive field would be 640 conditions and thus would not be practical.

The only way around this massive data requirement is to begin to make assumptions about how signals are integrated within the receptive field. The assumption that reverse correlation (Spike Triggered Average, Spike Triggered Covariance, the method proposed in this chapter, etc.) uses is to assume that signals interact linearly within the receptive field. Therefore, the receptive field can be represented by a linear kernel. Assuming this, the dot product between this linear kernel and the stimulus can be used to predict the response of the cell. Assuming linear interactions within the receptive field does not imply that the response of the cell must be linear: a static nonlinearity is assumed in the model; for more information see Chichilnisky (2001), where how to calculate the spike triggered average for Gaussian white noise stimuli is explained and then how to use the spike triggered average to estimate the nonlinearity. The technique is easily generalized to finding more than one linear kernel or receptive field, such as finding a kernel consistent with the classical receptive field and another consistent with the suppressive surround. Spike Triggered Covariance is an example of a technique that finds more than one
kernel (for example Rust et al. 2004); however, it requires Gaussian distributed stimuli. Gaussian white noise provides many advantages to more classical methods; however the requirement of Gaussian stimuli is also one of its greatest downfalls. Not only is a Gaussian distribution hard, if not impossible, to construct for certain stimuli, it often also suffers from low contrast and therefore may not drive cells well. Sharpee et al. (2004) introduced Maximally Informative Dimensions as a technique that liberates the experimenter from requiring Gaussian stimuli but still allows one to find more than one structure in a non-parametric way, unlike the Generalized Linear Model (Paninski 2004), which is a parametric solution to the problem. Therefore, experimenters are able to use stimuli that drive the cell well and/or are more biologically relevant, and still measure complex receptive field properties. Another immediate benefit is that this technique automatically generates a model for the cell, since its optimization procedure is to find a linear model that maximizes the mutual information between the model and the response of the cell.

The general principle for Maximally Informative Dimensions (MID) is to find a linear model that best predicts the response of a cell. To do this we make a linearity assumption, and approximate the receptive field of the cell by one or more linear kernels. These linear kernels represent the structures or features that modulate the response of a cell. Examples of features could be feed-forward excitation, lateral suppression, feedback from other cortical areas or a mixture of these. The linear model is based upon the dot product of 1 or more linear kernels with a stimulus frame; this is also known as the projection of the stimulus onto the linear kernel; in other
words a measure of similarity. When the stimulus is similar to the linear kernel, the
dot product will be a large number. A stimulus frame can be thought of as the
stimulus on the screen during one refresh of the monitor, or can be more complex.
Therefore, if we have \( L \) frames in our stimulus movie, we will have \( L \) projection (dot
product) values. We also discretize the response of the cell into \( L \) bins; for visual
datasets this would generally be the refresh frame duration. Therefore, for every
stimulus frame, there is a corresponding response of the cell. These are the same steps
taken before calculating the Spike Triggered Average (STA), and in fact the STA is
often the best first linear kernel.

In general MID is a nonlinear optimization problem. We wish to find the
linear kernel that results in projection values that best predict the response of the cell.
For a Gaussian distributed stimulus this is a simple problem: STA for one kernel or
Spike Triggered Covariance for more than 1; however, in general this is a very hard
problem. The optimization technique taken by Sharpee et al. (2004) was simulated
annealing. An analogy would be to imagine a ball falling down into a valley. The
valley walls may be very rough, and the ball could get stuck, but if the ground were
shaking while the ball was falling, it may then get out of local minima to then fall to
the valley floor. Sharpee et al. (2004) also used gradient line optimization, in the
analogy this is equivalent to gravity. In the analogy, the location of the ball is the
linear kernel and the depth of the ball is the measure of how good of an answer we
have found. The ball is shaken around for a while until no deeper locations are found;
if conditions are good, the ball should be located at the bottom of the valley.
The insight that Sharpee et al. (2004) had was that mutual information is the best measure of prediction ability. Specifically, a model that best predicts the response also maximizes the mutual information between the output of the model (projection values) and the response of the cell. Therefore, one can use mutual information as the optimization criteria for the nonlinear search.

However, this optimization also has a few limitations. The largest limitation is that there is no guarantee that the search will converge to the global optimal solution. There are several reasons for this. First, calculation of mutual information usually requires binning the data, which results in extra noise, and second, simulated annealing with line-optimization is not always the best algorithm for avoiding local minima. A second limitation of the original algorithm is that there is no obvious stopping criterion, which results in an unconstrained computational cost. While mutual information should theoretically be the optimal optimization criteria, in practice there are some implementation limitations. The binning noise is one limitation and the second is that it treats all nonlinearities equally. One could imagine a nonlinearity, for example a high frequency sine wave, which is highly non-biological that has the same amount of mutual information as a monotonically increasing nonlinearity (a more biologically plausible nonlinearity). Both of these examples would potentially be highly informative and thus construct a predictive model, however, the sine wave would be almost certainly rejected by an electrophysiologist as not being plausible. Therefore, making a smoothness assumption on the nonlinearity
could under weak or noisy circumstances substantially improve the accuracy of the search.

Our new approach still uses the gradient ascent as used by Sharpee et al. (2004); however, it is embedded within a non-gradient based method: Nelder-Mead Simplex Optimization. Our Hybrid approach uses two heuristic techniques to reduce the number of local maxima. The first technique is to use an approximate measure of Mutual Information (MI). This Approximate Mutual Information (AMI) is based upon the sum of the low frequency power of the nonlinearity of the cell; the idea being that biological nonlinearities are most likely to be smooth, or equivalently composed predominantly of low frequencies. Using this measure of mutual information ensures that more biologically plausible nonlinearities (or models) are found. Also, Pillow et al. (2006) demonstrated that assuming a functional form of the nonlinearity could improve accuracy; in their case they assumed the nonlinearity was a ratio of Gaussians. Note, Paninski (2003) discussed a non-parametric mutual information estimator that also assumes smoothness, which is related to work done by Victor (2002) that discusses a bin-less information calculation technique.

The second technique aims to reduce the dimensionality of the search space without sacrificing resolution. Wavelets are used in image compression algorithms such as JPEG2000; these algorithms exploit the fact that there is normally local structure in images. As receptive fields (RFs) tend to have similar spatial (and/or temporal) structure, the RF, or linear kernel, should be highly compressible by using wavelets. Specifically, the linear kernel should be well represented by a relatively
small number of non-zero wavelet weights. Therefore, we can search for the wavelet weights that maximize information, as compared to searching for pixel values that maximize information as the traditional MID method does.

5.3 Methods

The Hybrid approach taken here has several parts. First, the optimization algorithm is a modified Nelder-Mead Simplex Optimization with an embedded gradient based search. Second, we maximize Approximate Mutual Information (AMI); we will define this for 1 and 2 linear kernels. Finally, we perform the search within the wavelet domain. We then state how the Hybrid method was compared to the original MID method.

5.3.1 Optimization

At the core, we are performing a nonlinear optimization; we wish to find the kernel (receptive field) that maximizes a certain value, in our case approximate mutual information. The search algorithm used was a Hybrid approach. The main search algorithm was based upon the Nelder-Mead Simplex Optimization, which is a non-gradient based iterative optimization algorithm. It is essentially able to estimate the gradient by maintaining a mesh (or simplex) of kernels that are able to approximate the surface being optimized. In the valley analogy given above, this would be analogous to using a large number of balls. This simplex optimization uses a series of rules based upon perturbations of the worst performing kernel in the simplex. The algorithm was always started from a kernel of all 0’s, instead of the spike triggered
average as the original MID algorithm was. The most commonly executed rule is the “reflection” rule, which reflects the worst kernel about the center of the simplex. The Nelder-Mead algorithm was then modified such that 1 in every $N^2$ reflections, where $N$ is the length of the kernel, a gradient search is performed from the centroid of the simplex instead of the reflection. The gradient search algorithm used the same gradient as proposed by Sharpee et al. (2004); however, AMI was maximized instead of MI during the line-optimization. The advantage of this Hybrid approach is that the simplex method performs well when the start position is far from the optimal solution; whereas the gradient based method often does not. Furthermore, when the gradient is stuck in a local maxima the simplex method will normally continue to search outside of this local region. We do not assert that this is the optimal or even fastest solution, merely that it performs similarly or better than that proposed by Sharpee et al. (2004). The search was stopped once AMI for the test set as calculated with the best kernel found so far was significantly worse over the 30 most recent iterations (over fit). This stopping criteria does not work for the original MID method because it rarely, if ever over fits the data. The test set was $\frac{1}{4}$ of the data and the training set was the remaining $\frac{3}{4}$ of the data.

5.3.2 Approximate Mutual Information

We begin by explaining Mutual Information (MI) and then define Approximate Mutual Information (AMI) and how it is calculated. Mutual information comes from the intuition that a model should predict as many spikes as possible. We use a linear model, specifically, the dot product of a given stimulus
frame with our linear kernel (receptive field) should in some way predict the probability of the cell spiking to that frame. Since the frame and response pairs are known, the projection values can be calculated so that the projection, response pairs can be used to estimate the function that maps projection values to probability of spiking. The general approach to calculating this function (or nonlinearity) is to bin projection values, and count how many projection values fall within each bin, and how many corresponding spikes fall within that bin to then calculate the probability of spiking given a projection value (a specific bin); this can also be thought of as the division of two 1 dimensional histograms. An example nonlinearity and visualization of this calculation is shown in Chichilnisky (2001) Fig. 4; the projection value is called generator signal and the dots on the plots in (c) and (f) correspond to the bins. The insight is that the measure of how good any nonlinearity is at predicting the response of the cell can be directly measured from this nonlinearity and is in fact the mutual information. Specifically, the nonlinearity is the function \( p(\text{spike} \mid \text{projection value}) \), where \( p() \) is the probability and mutual information is then the Kullback–Leibler divergence between \( p(\text{spike} \mid \text{projection value}) \) and \( \text{p(spike)} \). Basically, the less flat the nonlinearity is, the better it is at predicting spikes. However, there are two issues with this formulation. One issue is that the KL divergence is not sensitive to the order of bins. Therefore, it is possible to have a smooth nonlinearity have the same amount of mutual information as a pathological nonlinearity (think of the smooth version but each bin randomly scrambled with each other). The second issue is that the number of bins must be chosen, and the choice of number of bins has a
significant affect upon the calculation of mutual information. Too few bins and more subtle changes in the nonlinearity will be averaged over, thus underestimating the amount of information. Too many bins and the information calculation will be dominated by noise. For these reasons an alternative measure of mutual information is proposed: Approximate Mutual Information (AMI).

To begin constructing Approximate Mutual Information, we assume that the nonlinearity should be smooth. Most nonlinearities are modeled as either a sigmoid, half rectifier, or squared function; all smooth. We also realize that binning is not necessary. If we use the rank of the projection values, i.e. sort them, then binning is not required. To construct the measure of approximate mutual information, we begin by projecting all stimuli onto the current best estimate of the linear kernel and constructing a vector of neural responses ordered by the rank of the projection values; we refer to this as the ranked-response. To be precise: $S_i$ (N by 1) is the stimulus at time (frame) $i$ and $RF$ (1 by N) is the linear kernel and $p_i$ is the projection. The response at time $i$ ($r_i$) is put into the ranked-response (RR) vector at the index corresponding to the rank of the projection value:

$$p_i = RF * S_i$$

$$RR_{rank(p_i)} = r_i$$

(1)

The ranked-response is the estimate of the nonlinearity of the neuron, see Figure 5.1a and b. Ordinarily the nonlinearity is estimated in the projection space (as defined for Mutual Information see above), however, there always exists a monotonic
function that maps projection-space into rank-space and visa versa; therefore, this is an
equivalent representation of a nonlinearity for the cell. Specifically: $f(RF*Si) = f(h(\text{rank}(RF*Si))) = g(\text{rank}(RF*Si))$, where $f, h, \text{and} g$ are arbitrary nonlinearities. This
procedure can also be thought of as analogous to histogram equalization in image
processing; in histogram equalization all pixel intensity values are made to have the
same number of pixels in the image (or as close as possible). For example, if there
were 1000 pixels in the image and 100 pixel values (gray scale values) then this
algorithm would try to have any given pixel value appear in 10 pixels. Furthermore,
we note that for a biologically relevant nonlinearity, the ranked-response should be
smooth, but not flat. Therefore, there should be substantial power in the low spatial
frequencies, see Figure 5.1c, and this assumption should make AMI more sensitive to
smoothness than MI. Specifically, we define the non-binned Approximate Mutual
Information (AMI) as the sum of the low frequencies (both positive and negative) in
the Fourier power spectrum of the ranked-response (excluding DC); we arbitrarily
choose the 5% lowest frequencies. Including more or less frequencies in the
summation does not change the results of the optimization much, unlike changing the
number of bins for MI; data not shown.

$$P = \| \text{fft}(RR - \text{mean}(r)) \|^2$$

$$AMI = \sum_{f=1}^{L*0.05} P_f + \sum_{f=-L*0.05}^{-1} P_f$$

(2)

where $L$ is the number of stimuli or projection values. For convenience, we use the
notation where $f$ is negative to correspond to the negative frequencies.
Figure 5.1: Approximate Mutual Information. Mutual Information is calculated from the nonlinearity for the cell. The nonlinearity is estimated by first calculating the number of projection values per bin, and then counting the number of spikes associated to each bin. An example spiking and stimulus histogram is shown in (a), the total height of the bars (black + white) is the number of projection values per bin and the black bars correspond to the number of spikes associated to stimuli in that bin. The nonlinearity is estimated by dividing the spiking histogram (black bars) by the bin count histogram (sum of black plus white); shown in (b). Shown in (c) is the ranked-response vector shown as black dots, a 0 corresponds to no spike, and a 1 is a spike. Superimposed is the smoothed ranked-response vector so that the low frequency structure is more apparent. Shown in (d) is the low frequency power of the ranked-response. Note that the power for the 0 frequency (DC) is also 0; the mean firing rate was subtracted from the ranked-response before calculating the power.
5.3.3 Comparing AMI to MI

Since the mutual information is calculated entirely from the nonlinearity of the cell, a family of nonlinearities was simulated to compare AMI to MI. Specifically, the family of a pair of hyperbolic tangents was used, with random slopes (flat 0 to 10) and shifts (flat -0.5 to 0.5):

\[ f(x) = \sum \frac{\tanh((x - shift1) * slope1) + \tanh(-x - shift2) * slope2)}{2 + 0.5} \]

\( x = -0.5 \) to 0.5 in 1000 steps. A large variety of functions are contained within this family; specifically, pseudo-linear, even, sigmoid and approximately delta. We normalize by the sum to keep the area under the curve constant; this is important because the area under the curve is proportional to the number of spikes. Since the number of spikes is constant for any given cell, we must normalize our functions such that they can be thought of as being caused by the same number of spikes. Or equivalently we can use \( f(x) \) as a probability distribution to simulate spiking with a fixed number of spikes and stimuli, for qualitatively the same result. 100,000 functions were simulated and plotted in a scattergram: Figure 5.2.
Figure 5.2: AMI vs. MI. A set of two hyperbolic tangents were combined to simulate spiking nonlinearities; a large variety of functions are contained within this family; specifically, pseudo-linear, even, sigmoid and approximately delta. The amount of Approximate Mutual Information and Mutual Information were calculated for 100,000 functions and plotted in a scattergram. One can clearly see that there is a monotonic relationship between these two measures.

5.3.4 Improve AMI Signal to Noise

In order to improve the signal of the AMI calculation, we can further constrain the frequencies included. We are most interested in the frequencies with large power, and there is a certain level of power than one would expect just due to chance or noise. Therefore, one could discount any frequencies below a certain chance level. Since the Fourier power follows approximately a chi2 distribution with 2 degrees of freedom a
significance threshold can be applied to the lowest 5% of frequencies in order to constrain the search, particularly with very weak signals. Specifically the threshold can be subtracted from the power and then half rectified before then being summed together for the AMI calculation (excluding the lowest frequency). This effectively removes insignificant fluctuations in power from contaminating the search.

Specifically:

$$\frac{2 \cdot Pi}{\text{var}(r) \cdot L} \approx \chi^2_{n=2}$$

and therefore a significance threshold ($th$) can be calculated ($th = \chi^2_{n=2}\text{inv}\left(1 - \frac{0.01}{0.05 \cdot L} \cdot 2\right)$) and

$$AMI = P_i + \sum_{f=2}^{L_0.05} [P_f - th] + \sum_{f=-L_0.05}^{-1} [P_f - th],$$

where $[$ denotes half rectification.

### 5.3.5 2D AMI

For higher dimensions, one runs into the issue of how to do an N dimensional ranking. We will discuss 2 dimensions and from that it should be clear how to implement N dimensions.

For the traditional 2 dimensional MID analysis, two linear kernels are used: RF1 and RF2. These two kernels are then used to calculate pairs of projection values (associated to a response). The idea being that if there are two mechanisms, such as an excitatory input and a suppressive surround mechanism, they both influence the response of the cell. We wish to estimate the probability of spiking given these two projection values, instead of just 1 in the 1 dimensional case. To estimate this probability we calculate two 2 dimensional histograms, the bin counts (i.e. the number
of projection value pairs that fall within a bin) and the spike count per bin, then divide
the spike counts by the bin counts; this is analogous to the 1 dimensional case. The
major issue here is that these 2 dimensional histograms are even more sensitive to the
number of bins chosen; the 2 dimensional nonlinearity needs to average over enough
data so that it is not dominated by noise but not so pixilated that fine structure is lost.
Furthermore, the 2 dimensional structure is not constrained and could be any shape,
such as a diagonally oriented, elongated distribution, which would result in a majority
of the bins being empty. Therefore, we propose a 2 dimensional version of the
Approximate Mutual Information that is less influenced by the absolute shape of the
distribution.

In order to construct a 2 dimensional AMI a 2 dimension ranking is proposed.
In order to do a 2D ranking, two types of ranks are needed: a course grain and a fine
grain. The idea being, that if we assume one signal is slowly varying, small local
groups could be thought of as being relatively constant. Then each small local group
could be ranked by the second signal; the local groups can be a single row in a matrix
and the first signal can determine the order of all of the rows. In order to implement
this, we must choose the size of the 2D matrix; ideally we want this to be as square as
possible such that both dimensions are equally represented. However, the number of
data points (responses, or stimulus frames; L) is often not a perfect square. Therefore,
one must construct a 2D matrix of responses with dimensions similar to each other,
such that the number of elements is as close to the number of stimuli (L) as possible.
Let us assume the dimensions are m by n, where both m and n are close but may not
be exactly equal to the square root of L. In order to do the 2D ranking, we first do a
course grain sort of the projections of RF1; group the data into m groups of size n
(grouped rank). Within each group sort the n values by the projection values of RF2
(rank within group) and this defines the ranked-response matrix. Specifically:

\[
p_{1i} = RF1 * S_i \\
p_{2i} = RF2 * S_i \\
group_i = \left\lceil \text{rank}(p_{1i})/n \right\rceil \\
sp_{2i, \text{mod(rank}(p_{1i})-1,n)+1} = p_{2i} \\
RR_{\text{group}, \text{rank}(sp_{2i, \text{groupi}})} = r_i
\]

where \(RR\) is the ranked-response matrix (m by n), \(sp2\) is a matrix (m by n) of \(p2\)
values ordered by \(p1\), \(\text{mod()}\) is for modular division, \(\left\lceil \ \right\rceil\) is the ceiling function and
\(\text{rank}(sp_{2i, \text{groupi}})\) is the rank of \(sp_{2i, \text{mod(rank}(p_{1i})-1,n)+1}\) within the vector \(sp_{2i, \text{groupi}}\). The
rest of the notation is the same as equation 1.

This is equivalent to taking the 1D ranked-response vector, shown in Figure
5.1c, and breaking it into m sized pieces and then stacking them on top of each other
row-wise (Figure 5.3a), but then sorting each row by the second projection value
(Figure 5.3c). The assumption is that within each m sized piece, the stimulus can be
thought of as being relatively constant; this is the same assumption used by the
binning for MI, however, the bins used here tend to be much smaller. The fact that
smaller bins are used means that there are fewer binning artifacts and since AMI is
calculating the low frequency power across these bins, it does not suffer from noise
like MI would with small bins. Therefore, all values into a group are given the same
rank for the first projection (grouped rank). Then each value is sorted by the second
projection value within its group (rank within group). If the second kernel is informative, there should be horizontal structure from (i.e. low frequencies). Shown in Figure 5.3a is an example ranked-response matrix, however the second (horizontal) dimension is not informative; this matrix can be thought of as the 1D ranked-response vector squashed into a matrix. In Figure 5.3c an informative second dimension is used, this causes a majority of the spikes to cluster into one region (low frequency structure). Approximate Mutual Information is now calculated from the low frequency power in the 2 dimensional Fourier transform of the RR matrix analogously to the 1 dimensional case; this is shown in Figure 5.3 (b) and (d). The amount of power is identical in the left column between both panels, therefore, summing the amount of power in (d) results in a larger number than (b). Therefore, AMI for 2 dimensions is calculated as:

\[ P = \| \text{fft2}(\text{RR} - \text{mean}(r)) \|^2 \]

\[ AMI = \sum_{i=1}^{0.05n} \sum_{j=1}^{0.05n} P_{i,j} + \sum_{i=-0.05n}^{0.05n} \sum_{j=1}^{-1} P_{i,j} + \sum_{i=0}^{0.05n} \sum_{j=-0.05n}^{0.05n} P_{i,j} + \sum_{i=-0.05n}^{0.05n} \sum_{j=-0.05n}^{-1} P_{i,j} \]

, where \( \text{fft2} \) is the 2 dimensional Fourier transform. The same significance threshold rule for 1 dimensional AMI can be applied here as well (see Section Improve AMI Signal to Noise), and is not being shown for simplicity.
Figure 5.3: 2 Dimensional AMI. A spiking model was constructed from two linear kernels. To show the intuition of the AMI calculation for two dimensions, first only one informative kernel is used so as to be compared to the complete 2 dimensional space. In (a) is the pseudo 2D sorted, ranked-response matrix for an informative first dimension (vertical) and an uninformative second dimension (horizontal). The responses (black squares are spikes) are first coarsely sorted by the first dimension, exactly as in Figure 5.1c, and broken into groups. Each group is considered to be relatively constant with regards to the first dimension, and therefore all values in the same group are given the same first dimension rank (grouped rank). Then within each group the responses are sorted by the projection of the second dimension (rank within group). In (b) is the 2 dimensional low frequency powers of the matrix in (a); to be correct the square root of power is shown, so that weaker powers can be seen. The 2nd dimension is not informative and therefore there is no horizontal structure in (a) and no power aside from the left hand edge in (b); the lighter the pixel the greater the power. For an informative 2nd dimension, the exact same spiking data was used, but now the second dimension is sorted by an informative kernel. One can see that in (c), there is the same structure vertically, but now there is horizontal structure, which can be seen in the plot of the power in (d). Note that the left hand column for both plots (b,d) is the same; therefore the summed power will be higher for (d).
5.3.6 Wavelets

Wavelet analysis can be thought of as an alternative linear basis set, one which is composed of different spatial frequencies. The advantage of this basis set is that most images (or receptive fields) have spatial structure and wavelets are able to represent this structure to a reasonable approximation with a relatively small number of non-zero values; in other words most images and receptive fields are highly compressible using wavelets. Therefore, we represent the linear kernel in wavelet space and search for the weights that result in the maximum AMI. The wavelet set used has a large influence on the success of the search algorithm; we found that the Vaidyanathan wavelets worked the best of the options tried, but we do not assert that this is the best wavelet in general. Wavelets are defined for more than one stimulus feature dimension. For example, most images are composed of 2 spatial dimensions therefore they are compressed with a 2 dimensional wavelet. The dimensions of the wavelet were set to match that of the stimulus representation, such as 2 spatial dimensions and 1 temporal, for a 3 dimensional wavelet transform. In order to calculate the projection values used in the information calculation, an inverse wavelet transform was required.

Since the simplex optimization is nonlinear, searching the in wavelet domain is not equivalent to searching in the pixel domain even though they are a complete basis sets for each other. The advantage of wavelets is that the low frequency structure of receptive fields is concentrated in a few wavelet weights of large value; therefore a nonlinear search is able to optimize these large values first. The gradient used in the
optimization was calculated in the pixel domain, which also required performing a forward and inverse wavelet transform; this transformation to and from the wavelet domain is required since the simplex optimization is being performed in the wavelet domain, otherwise there is no advantage to this particular transform.

In order to compare the new method (Hybrid, written in Matlab) to the Sharpee method (MID, written in C), we simulated a spiking model with 1 linear kernel and ran all search algorithms. The accuracy and speed of the two algorithms were measured. To address the lack of an adequate stopping criterion for the original MID method, we ran the simulated annealing algorithm N times, where N is the length of the kernel; qualitatively, no more beneficial kernels were found after this. 64 bins were used for all MID tests, 32 bins gave qualitatively similar results but are not shown here. Three nonlinearities were used in the spiking model: mild, even and sigmoid, as well as, 3 stimulus distributions: a flat distribution between -0.5 and 0.5 (Rand), a binary sparse distribution where the probability of having an event at any given location is 5%, and a pink noise distribution. All stimulus values were transformed to be integer values between 0 and 255 so as to conform to the stimulus representation assumed by the MID code. All simulations used 10,000 frames (or responses) and model was constrained to spike approximately 2,500 times. All three nonlinearities were modeled from the same form:

\[ p(\text{spike} \mid \mathbf{S}_i) = p(\text{rank}(\mathbf{RF} \ast \mathbf{S}_i)^\text{power} + \text{Rand}(-\text{scale},\text{scale}) > 7500) \], where \text{Rand}(-\text{scale},\text{scale}) is a flat probability distribution between -\text{scale} and \text{scale}. This form of nonlinearity can be thought of as a neuron with a spike threshold but with random
fluctuations on top of the membrane potential. In order to ensure that our model always had a comparable number of spikes between stimulus distributions, we used ranks. This can be thought of as a spiking threshold that was automatically recalibrated depending upon the statistics of the input distribution so as to always generate 2,500 spikes. For the mild nonlinearity, power=$1$ and scale = 20,000, which results in an approximately linear function that saturates at 0 for large negative projection values. For the even nonlinearity, power=2 and scale = 10,000, which results in a ‘v’ shaped nonlinearity. For the sigmoid nonlinearity, power=1 and scale=5,000, which strongly saturates at both extremes but the slope of the transition is still relatively slow. These nonlinearities are plotted using the Rand distribution in Figure 5.4. To simulate a realistic receptive field, a 2D Gabor function orientated at 45 degrees was used, at a resolution of 16 by 16. All results were run 25 times with 4 jackknifes of the same dataset, for a total of 100 repetitions. Accuracy was measured as the correlation coefficient of the true Gabor function to the estimated kernel, averaged over all 100 repetitions. In order to tease apart the contribution of the different aspects, wavelets, AMI and starting from the STA, 6 search algorithm variants were run: 4 variants of the Hybrid search (with or without wavelets and AMI or MI, in all combinations) and 2 for MID, one that started from the spike triggered average and one that started from a random vector. For all calculations of MI in the Hybrid code, equally sized bins where used, i.e. ranked based binning, such that each bin contained approximately $L^{1/2}$ data points and there were approximately $L^{1/2}$ bins,
where $L$ is the number of frames. Constructing the bins in this way was much faster in Matlab, and also ensured that an equal number of data points fell within each bin.

![Graphs of Mild, Even, and Sigmoid nonlinearity](image)

**Figure 5.4:** Model nonlinearities. Three different nonlinearities were used in the spiking model used to test the different variants of MID and Hybrid. The 3 different nonlinearities are shown for the Rand distribution; their exact shape changes some depending upon the stimulus distribution but are similar to the ones shown.

### 5.3.7 2D Search

Unfortunately, at the time writing, MID code to find 2 or more kernels was not available. However, to test the performance of the 4 Hybrid variants a model with 2 kernels was used. For all calculations of MI in the Hybrid code, equally sized bins where used, i.e. ranked based binning, such that each bin contained approximately $L^{1/3}$ data points and the ranked-response matrix was approximately $L^{1/3} \times L^{1/3}$, where $L$ is the number of frames. The first kernel (RF1) was a 2D Gaussian and the second (RF2) was the same Gabor used in the 1 kernel case. 40,000 frames (responses) were used. The nonlinearity for the first kernel was constructed to be approximately linear.
and the second to have a divisive modulation on the first. The following Matlab code was used:

\[ p1_i = RF1 \ast (S_i - \text{mean}(S)) \]
\[ p2_i = RF2 \ast (S_i - \text{mean}(S)) \]
\[ t_i = \frac{\text{rank}(p1_i)}{40000/10 + \text{rank}(p2_i)} \]
\[ p(\text{spike} | S_i) = p(\text{rank}(t_i) + \text{Rand}(\text{-scale}, \text{scale}) > 3000) \]

For the mild nonlinearity, power=1 and scale = 80,000, the even nonlinearity power=2 and scale = 40,000 and the sigmoid nonlinearity power=1 and scale=20,000. In order to make the search as comparable to the 1 kernel case, the search was started with RF1 already being known and only the 2\textsuperscript{nd} kernel was being optimized. The execution time and mean correlation coefficient of the second kernel to the found kernel were measured.

### 5.3.8 Significant Kernels

A large issue with finding more than one kernel is determining whether the found kernel is significant or just noise. This is a hard problem with no agreed upon solution. The Hybrid method suffers from a similar problem however; a crude significance prerequisite test can be constructed using a chi2 distribution. In other words, if the found kernel does not exceed the prerequisite, it can not be significant; however exceeding this threshold does not guarantee significance. The fact that the AMI (before a threshold is subtracted) follows approximately a chi2 distribution, allows us to calculate a significance of the information gain for any found kernel compared to an uninformative kernel. The number of degrees of freedom for the chi2
test is twice the number of the low frequencies (for 1 dimension). Since the power is maximized during the search process, this can not be used as a true significance, however, a significance threshold can be used as a prerequisite for considering any found kernel as significant. Furthermore, we can calculate the proportion of the largest wavelet weight relative to the sum of all wavelet weights (absolute value) and use this as a further criterion for significance. Specifically, when there are no significant (or informative) kernels the Hybrid search tends to be biased towards finding one large wavelet weight with all other values being small. As a rule of thumb, to be considered significant, the information gain achieved by a found kernel must exceed a chi2 significance of 0.999 and the ratio of largest wavelet weight to total must be less than 0.95. This is not a true test of significance; the false positive rate is related the length of the kernel being found; data not shown.

5.4 Results

This new method was compared to the original MID method proposed by Sharpee et al. (2004). The results for the 3 nonlinearities and 3 stimulus distributions are shown in tables 5.I and 5.II for finding one linear kernel.
Table 5.I: Accuracy (mean correlation coefficient)

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Rand</th>
<th>MID</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o w/ MI</th>
<th>MID random start</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>0.804</td>
<td>0.832</td>
<td>0.852</td>
<td>0.791</td>
<td>0.773</td>
<td>0.729</td>
</tr>
<tr>
<td>Even</td>
<td>0.067</td>
<td>0.982</td>
<td>0.985</td>
<td>0.535</td>
<td>0.073</td>
<td>0.193</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>0.980</td>
<td>0.977</td>
<td>0.980</td>
<td>0.970</td>
<td>0.972</td>
<td>0.970</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Sparse</th>
<th>MID</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o w/ MI</th>
<th>MID random start</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>0.828</td>
<td>0.838</td>
<td>0.851</td>
<td>0.478</td>
<td>0.718</td>
<td>0.703</td>
</tr>
<tr>
<td>Even</td>
<td>0.193</td>
<td>0.983</td>
<td>0.922</td>
<td>0.203</td>
<td>0.226</td>
<td>0.155</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>0.978</td>
<td>0.977</td>
<td>0.978</td>
<td>0.818</td>
<td>0.902</td>
<td>0.973</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Pink</th>
<th>MID</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o w/ MI</th>
<th>MID random start</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>0.699</td>
<td>0.631</td>
<td>0.758</td>
<td>0.697</td>
<td>0.695</td>
<td>0.681</td>
</tr>
<tr>
<td>Even</td>
<td>0.934</td>
<td>0.890</td>
<td>0.924</td>
<td>0.924</td>
<td>0.938</td>
<td>0.926</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>0.940</td>
<td>0.867</td>
<td>0.889</td>
<td>0.916</td>
<td>0.928</td>
<td>0.935</td>
</tr>
<tr>
<td>Nonlinearity</td>
<td>MID</td>
<td>Hybrid w/ MI</td>
<td>Hybrid w/o wavelets</td>
<td>Hybrid w/o wavelets w/ MI</td>
<td>MID random start</td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>-----</td>
<td>--------------</td>
<td>---------------------</td>
<td>--------------------------</td>
<td>------------------</td>
<td></td>
</tr>
<tr>
<td><strong>Rand</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mild</td>
<td>371</td>
<td>235</td>
<td>232</td>
<td>212</td>
<td>227</td>
<td>364</td>
</tr>
<tr>
<td>Even</td>
<td>382</td>
<td>177</td>
<td>255</td>
<td>163</td>
<td>138</td>
<td>393</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>361</td>
<td>190</td>
<td>252</td>
<td>184</td>
<td>216</td>
<td>355</td>
</tr>
<tr>
<td><strong>Sparse</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mild</td>
<td>298</td>
<td>249</td>
<td>243</td>
<td>185</td>
<td>146</td>
<td>304</td>
</tr>
<tr>
<td>Even</td>
<td>303</td>
<td>177</td>
<td>252</td>
<td>183</td>
<td>143</td>
<td>299</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>322</td>
<td>222</td>
<td>264</td>
<td>195</td>
<td>191</td>
<td>314</td>
</tr>
<tr>
<td><strong>Pink</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mild</td>
<td>371</td>
<td>143</td>
<td>174</td>
<td>137</td>
<td>162</td>
<td>366</td>
</tr>
<tr>
<td>Even</td>
<td>337</td>
<td>115</td>
<td>211</td>
<td>136</td>
<td>230</td>
<td>346</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>322</td>
<td>141</td>
<td>218</td>
<td>136</td>
<td>414</td>
<td>326</td>
</tr>
</tbody>
</table>

To test the accuracy and execution time of the various search methods for a 2 dimensional search the 4 Hybrid variants were used with the 3 stimulus distributions (Rand, Sparse and Pink) and 3 nonlinearities (Mild, Even and Sigmoid). To make the comparison as fair as possible to the 1 kernel case, the search was started with the first kernel already known and the algorithm need only find the second kernel. The accuracy and execution times are shown in tables 5.III and 5.IV.
Table 5.III: Accuracy for 2\textsuperscript{nd} Kernel (mean correlation coefficient)

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Hybrid</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o wav w/ MI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>0.821</td>
<td>0.682</td>
<td>0.793</td>
<td>0.070</td>
</tr>
<tr>
<td>Even</td>
<td>0.987</td>
<td>0.988</td>
<td>0.186</td>
<td>0.013</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>0.978</td>
<td>0.981</td>
<td>0.978</td>
<td>0.980</td>
</tr>
</tbody>
</table>

Sparse

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Hybrid</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o wav w/ MI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>0.797</td>
<td>0.585</td>
<td>0.319</td>
<td>0.027</td>
</tr>
<tr>
<td>Even</td>
<td>0.988</td>
<td>0.988</td>
<td>0.068</td>
<td>0.021</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>0.983</td>
<td>0.986</td>
<td>0.700</td>
<td>0.725</td>
</tr>
</tbody>
</table>

Pink

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Hybrid</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o wav w/ MI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>0.557</td>
<td>0.523</td>
<td>0.698</td>
<td>0.475</td>
</tr>
<tr>
<td>Even</td>
<td>0.892</td>
<td>0.903</td>
<td>0.938</td>
<td>0.811</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>0.790</td>
<td>0.793</td>
<td>0.933</td>
<td>0.937</td>
</tr>
</tbody>
</table>

Table 5.IV: Execution Times for 2\textsuperscript{nd} Kernel (Seconds)

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Hybrid</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o wav w/ MI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>467</td>
<td>912</td>
<td>504</td>
<td>788</td>
</tr>
<tr>
<td>Even</td>
<td>569</td>
<td>1218</td>
<td>453</td>
<td>753</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>521</td>
<td>1644</td>
<td>557</td>
<td>2188</td>
</tr>
</tbody>
</table>

Sparse

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Hybrid</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o wav w/ MI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>498</td>
<td>862</td>
<td>624</td>
<td>843</td>
</tr>
<tr>
<td>Even</td>
<td>532</td>
<td>1271</td>
<td>497</td>
<td>870</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>456</td>
<td>1165</td>
<td>524</td>
<td>1109</td>
</tr>
</tbody>
</table>

Pink

<table>
<thead>
<tr>
<th>Nonlinearity</th>
<th>Hybrid</th>
<th>Hybrid w/ MI</th>
<th>Hybrid w/o wavelets</th>
<th>Hybrid w/o wav w/ MI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mild</td>
<td>347</td>
<td>777</td>
<td>393</td>
<td>865</td>
</tr>
<tr>
<td>Even</td>
<td>470</td>
<td>1148</td>
<td>495</td>
<td>1044</td>
</tr>
<tr>
<td>Sigmoid</td>
<td>689</td>
<td>2133</td>
<td>571</td>
<td>2541</td>
</tr>
</tbody>
</table>
5.5 Discussion

As one can see from Table 5.1, there are 3 variants that perform well: MID, Hybrid and Hybrid with MI. Hybrid with MI consistently outperformed all other variants except for MID under some of the pink noise cases and Hybrid under the even, sparse noise case. Since the sparse noise case is the one we were most interested in, we focused on these results though we acknowledge that the MID method outperforms our approaches under 2 of the pink noise cases, which was the stimulus distribution for which MID was originally tested and optimized.

For the Rand and Sparse stimulus distributions with the even nonlinearity the MID algorithm fails quite dramatically. The main issue is that the optimization is quite sensitive to the starting position in the search space. Since for an even nonlinearity, the spike triggered average (STA) was entirely noise, therefore, the MID search was consistently being started from an uninformative point. For the Rand stimulus case, the STA actually seems to be a local maxima for which the original MID fails to escape. For comparison, see the MID with a random start point, and the accuracy is improved such that the correct answer is found approximately 20% of the time.

For the sparse noise case, the benefit of wavelets is most demonstrated. For the Mild and Even cases, the Hybrid approach substantially outperforms the MID approach (Table 5.1) and this has to do with the spatial smoothness assumption being imposed by the wavelets. The issue being that the relative sign of two pixels is determined by the co-occurrence of two events at both pixels at the same time; for the
sparse binary noise case, this is very rare. Therefore, the signal determining the
relative sign of two pixels to one another is very weak and without a smoothness
assumption is virtually impossible to find for the even nonlinearity or more than 1
kernel. For the Mild and Sigmoid cases the relative sign for each pixel is known
because the STA is reasonably close to the correct answer. MID never found the
correct answer for the sparse even case, therefore the mean correlation coefficient of
0.193 is not indicating a 20% failure rate but in fact that the found kernel was always
far from the correct answer. Further, there seems to be a benefit of using AMI for the
search method for the even case; about 5% of the time the Hybrid with MI search did
not find the correct answer. This is obviously a small percentage; however, the
Hybrid approach with AMI seems to consistently outperform the case with MI when
the search is noisy or particularly hard (Table 5.III mild nonlinearities). This
advantage is most likely due to the fact that AMI is smoother than MI and therefore
small beneficial steps toward the optimal solution are not lost, which would have been
obscured by the binning noise of MI. Another issue with using a binned version of MI
is that the number of bins must be chosen. This in theory should increase the
computational time associated to the MI methods because other bin sizes must be
tested in order to find the optimal size. The bin sizes use for MI were automatically
calculated to be as close as possible to \( L^{1/(N+1)} \) where \( L \) is the number of frames and \( N \)
is the number of kernels being found; this results in a very reasonable compromise
between the number of bins and the number of data points per bin, however, other bin
sizes were not tested.
To test the idea that AMI may perform best for very weak or small datasets, we tested much smaller dataset sizes (1,000 and 4,000) and used Hybrid and Hybrid with MI for comparison. Hybrid had fewer failures than MI, though MI was slightly more accurate when a failure did not occur; consistent with the other results here. However, it can not be ruled out that the failures were not due to the choice of bin size since that was not varied. One might also argue that AMI may be more sensitive to an even nonlinearity due to the fact that the lowest frequency, depending upon the phase, can be an even function; this may be the case, however, it does not explain the advantage AMI had over MI for the Mild nonlinearities in Table 5.III.

The use of wavelets is not always beneficial. For the pink noise distribution, which is already spatially smooth, using wavelets under 2 of the three cases is detrimental (compare with and without wavelet conditions in Table 5.I and 3.III for pink noise). However, for the mild nonlinearity, which is also the nosier and therefore harder to find, wavelets exhibit a benefit, see Table 5.I Pink noise for Hybrid with MI. Another issue is that the use of wavelets also introduces a dependence of the accuracy of the result on the choice of analysis window. Specifically, including extra pixels around the receptive field in the analysis will reduce the assumption that receptive fields are predominantly composed of low spatial frequencies by shifting the low spatial frequencies to higher ones. Therefore, the benefit of using wavelets can be lost; however, in simulation there does not seem to be a loss of accuracy below that of MID, except in the pink noise case, already mentioned.
It is also interesting to note how much the start condition affects the MID results. When the MID search is not started from the STA, it performs significantly worse (Table 5.I, MID vs. MID random start). This suggests that MID may not be as optimal for searching for 2 or more kernels, since the STA can not be used as a starting point for more than 1 kernel. At the time of writing, the MID code for 2 or more kernels was not publically available and therefore could not be tested.

In Table 5.II the computational time associated to the different algorithms for all 9 stimulus and nonlinearity combinations is shown. In general, the MID analysis ran in approximately twice the time of the Hybrid, however this is largely due to the fact that the Hybrid approach used single floating point precision math while the MID code used double (a 2 times speedup). In Table 5.IV one can see a substantial computational cost difference between MI and the Hybrid method. Even though there is a small benefit in accuracy with the highest signal cases for using MI there is a substantial computational cost associated to this small gain, though the magnitude of this gain depends upon the exact nonlinearity and therefore can be larger in some cases.

It should also be noted that there is a significant computational cost for performing the inverse wavelet transform, which is used many times during the course of the search. What is interesting though is that often there is no net loss in computational time as compared to the other methods not using wavelets (Table 5.I and 5.III, Hybrid vs. Hybrid w/o wavelets). This is most likely due to the fact that searching in the wavelet domain is easier and therefore converges to the optimal
solution in a smaller number of iterations. However, as the kernel size is increased, the wavelet transform becomes significantly more computationally expensive. Therefore, the balance of computational time may not be maintained thus for larger sizes other methods may run faster.

There is also an interesting possibility of combining AMI and MI so that a course estimate can be found early in the search using AMI and then switch to MI for the later stage so as to achieve the optimal accuracy possible. It would further be interesting for the possibility of switching to the pixel domain for the final stage optimization so as to maximize performance even for the pink noise case.

One could criticize the choice of spiking model; the model turns out to be a half rectified linear function in rank-space, where more of a sigmoidal function in projection-space. To address this concern we implemented a converse spiking model, one that was half rectified in projection-space and more complicated in rank-space. All results were qualitatively the same. MID was still the best for most pink noise cases and Hybrid was still the best for the Sparse Even case. The small differences were that the accuracy differences between MID and Hybrid with MI were gone for the non-pink noise cases. Also, the accuracy while using AMI was a little lower but still within the range seen between MID and Hybrid from Table 5.1, in particular the Mild cases, just reversed; data not shown. Most importantly, the Hybrid method consistently found the correct answer, while the MI based methods had a similar failure rate using this more linear model as that shown in Table 5.1 for the Even
nonlinearity. Furthermore, this criticism can only be applied to the results in Table 5.I since MI in Table 5.III was calculated based upon ranks and MID was not tested.

5.6 Conclusion

A new approach to the maximally informative dimension algorithm proposed by Sharpee et al. (2004) was presented, that uses a new, approximate mutual information measure and a Hybrid search method. This new Hybrid method was found to perform similarly or better than the original MID method for two stimulus distributions. The accuracy of the Hybrid method was substantially better than MID for Sparse noise and for Even nonlinearities. The computational time for the new method is about half of the original, but that is most likely due to a change from double to single floating point math. For finding 2 or more linear kernels the Hybrid method using AMI and wavelets consistently performed similarly or better than all of the other variants and was consistently the fastest variant as well. A method now exists that allows one to use sparse binary noise stimuli and still recover 2 or more linear kernels. This new method is a general solution; however, it can still be improved upon.

5.7 Acknowledgements

This chapter was co-authored with Bart Krekelberg, Tom Albright and the dissertation author; it is being prepared for publication.
5.8 References


Chapter 6: A non-parametric circular test for differences in mean direction with low circular concentrations.

6.1 Abstract

A new circular test (circular Kruskal-Wallis, abbreviated as cKW) is proposed to test whether two or more mean directions are significantly different from one another. The advance compared to the traditional Watson-Williams test is that it can be used with non unit-length data vectors and even when circular concentrations are low. We compare the cKW test to the Watson-Williams’ test for power and false positive rate. The cKW test performs similarly to the Watson-Williams’ test for high circular concentrations and functions as desired for low circular concentrations when datasets are sufficiently large. This non-parametric test provides a new tool to assess the significance of differences in orientation tuning and/or direction tuning properties of early visual cells.

6.2 Introduction

Two of the stimulus features studied most by visual neurophysiology are orientation and direction. It is well known that many neurons in early visual areas are tuned for these stimulus features and that the neurons are often arranged in orderly
maps of feature preference. To quantify these response properties one often needs to compare preferred features across neurons, or across stimuli. For instance, a quantification of whether two neurons prefer significantly different orientations provides insight into the layout or resolution of a cortical map of orientation. Similarly, a test that determines whether different stimuli elicit different direction preferences in the same neuron allows one to discuss the invariance of a cortical representation. Because orientation and direction are circular variables, however, traditional statistical techniques cannot be applied to them.

The accepted test for determining if two (or more) circular mean directions are significantly different from one another is the Watson-Williams’ test (Watson and Williams, 1956). For the purposes described above, however, the Watson-Williams’ test has two significant shortcomings. First, it fails for low circular concentrations (concentration values >1 or 2, or equivalently the length of the resultant (\( \bar{R} \)) greater than approximately 0.45: Batschelet (1981) and Jammalamadaka (2001); for a circular normal distribution this would correspond to a standard deviation of less than 75 degrees), even for an infinite amount of data. This means that the test cannot be applied to neurons that are either inherently weakly selective (which is the case in many visual areas) or are stimulated by weak stimuli (such as with a very low coherence motion stimulus). The second shortcoming is that the Watson-Williams’ test is only concerned with whether a neuron responded to a direction or not; by ignoring the level of response, much information on the properties of the neuron could be lost. To address these issues we propose a new test that is applicable for extremely
low circular concentrations and uses weighted vectors (directions or orientations weighted by the response of the neuron). In this chapter we present the test and compare its performance to the Watson-Williams’ test for both power and false-positive rates over a range of circular concentrations, angular differences and dataset sizes.

6.3 Methods

The premise of the new circular test (circular Kruskal-Wallis, or cKW) is to reduce the dimensionality of the data to be 1 dimensional so that linear statistics can be applied on two 1 dimensional datasets. The null hypothesis is that the circular distributions have the same mean direction irrespective of differences in their mean vector length. If the null hypothesis is true then the grand mean vector across all j groups, is the best estimate of the common mean direction. Therefore, any deviations in the projection of the data values along the axis perpendicular to the common mean direction would suggest that the mean directions are different. The procedure is as follows:

We make use of complex numbers to represent two-dimensional circular data points. In the example of direction tuning cures, the real component of the complex number represents the horizontal direction of the stimulus, and the imaginary component represents the vertical direction of the stimulus. Let \( X_j \) be a collection of complex data vectors of length \( n_j \), each complex number represents one circular data point. Thus \( n_j \) is the number of data points for group j. Define \( V_j = \sum_{n_j} X_j \), the vector
sum of the data points per group; \( V = \sum_j V_j \), the grand vector sum; and \( L_j = \sum_n |X_j| \),

the total vector length per group, where \( | \cdot | \) denotes the magnitude of the complex number. To begin the test, rotate all points by the angle of the grand vector sum, \( V \), and normalize by \( L_j \). This leads to the collection \( Y_j = \frac{X_j V^*}{L_j |V|} \), where \( V^* \) is the complex conjugate (this rotates \( X_j \) by the grand mean direction). Define \( R_j \) and \( I_j \) as the real and imaginary part of \( Y_j \); these values will be used by two separate parts of the significance test. The first part of the significance test uses a Kruskal-Wallis test (Kruskal and Wallis 1962) on the \( I_j \)'s; this will test the null hypothesis that all \( j \) groups have the same median (specifically 0). If the \( I_j \)'s have significantly different means then the corresponding circular distributions are unlikely to have the same mean direction.

\[
p_{kw} = KruskalWallis(I_j's)
\]

Because this test is concerned only with the direction perpendicular to the common mean direction (imaginary dimension), this test loses power for angular differences on the order of 180 degrees. To compensate for this loss of power, a secondary test needs to be performed to test whether the angular difference is near 180 degrees, or equivalently of opposite sign. Using a same-sign test (definition to follow) on the \( R_j \)'s allows one to test for this. The reasoning is that, if we can reject the hypothesis that the data vectors in all \( R_j \) have the same sign, then the mean directions
must be different. However, if we cannot reject the same-sign null hypothesis, then the
KruskalWallis test will not suffer from a loss of power.

To estimate the probability associated with the null hypothesis that the $R_j$’s
(real dimensions) have the same sign, we use the standard error of the mean
approximation. Specifically, we assume that $p(\mu_j, \bar{R}_j) \sim N(\bar{R}_j, s_{R_j}/\sqrt{n_j})$, where $\mu_j$ is
the true mean for $R_j$, $\bar{R}_j$ is the observed mean and $s_{R_j}$ is the observed standard
deviation of $R_j$. In other words, we want to know the significance of the sign of $\bar{R}_j$.

Using this approximation, $p_j = \phi\left(-\frac{\bar{R}_j}{s_{R_j}/\sqrt{n_j}}\right)$, where $\phi(\cdot)$ is the cumulative normal
distribution. The closer $p_j$ is to 1 the more confident we are that the sign is positive
and the closer to 0 the more negative.

A simple way to progress would be to calculate the product of all $p_j$’s and $1-p_j$’s and add them together. However, this test would be highly biased for a dataset
where all $\mu_j$’s were 0 (thus the $\bar{R}_j$’s would have an equal probability of being
positive or negative since the true mean is 0). In other words, this test would only be
applicable when means are much larger or smaller than 0. Instead, a test is needed
that takes into account how different the means are from 0. To do this, first separate
the $p_j$’s into two groups, ones that are less than 0.5 ($p_l$’s) and those that are greater
($p_g$’s). Then to calculate the significance of the means being different from 0 combine
them using Fisher’s method (Fisher 1928): $q_l = \text{cum} \chi^2(-2 \ln(\prod p_l), 2n_l)$,
$q_g = \text{cum} \chi^2(-2 \ln(\prod (1-p_g), 2n_g)$, where $n_l$, $n_g$ are the number of $p_j$’s which are
less than and greater than 0.5, respectively. $\text{cum}\chi^2(\ )$ is the cumulative $\chi^2$ distribution, and for the special case where the degrees of freedom are zero ($n_l$ or $n_g$ are 0) $\text{cum}\chi^2(\ )$ is 0. The absolute difference between $q_l$ and $q_g$ is an indication that all means have the same sign; the further from 0 the more likely. The absolute value of the difference of two flat distributions results in a triangular distribution, which can be transformed back into a flat distribution with the following (the same-sign test):

$$p_{ss} = 1 - \left( 1 - |q_l - q_g| \right)^2$$

The full circular Kruskal-Wallis test we propose is to take the minimum of the Kruskal-Wallis test on the imaginary dimension and the same-sign test on the real dimension.

$$p_{ckw} = \min(p_{kw}, p_{ss})$$

It should be noted that this test is intended for datasets where all groups are predetermined to be significantly tuned using a Rayleigh test (or equivalent). While this test has reasonably good properties for datasets with flat circular distributions (Table 6.I and Table 6.II last rows), the concept of a mean direction for an untuned circular distribution is undefined.

### 6.3.1 Example

In Figure 6.1 a sample circular distribution is shown for two groups: black and gray dots. The mean directions for both the gray and black distributions are shown, and the grand mean direction is shown in thick black. Visually, the black and gray distributions appear to have significantly different mean directions. In (b) the
distributions have been rotated by the grand mean direction (thick black line), and a histogram of the imaginary (vertical) dimension is shown; the Kruskal-Wallis test along this dimension results in $p_{kw} \ll 0.001$. The difference in mean direction results in a very large difference in mean as exemplified by the large shift between black and gray in the histogram. In (c) The histogram of the real (horizontal) dimension is shown, which corresponds to $p_{ss} = 1$; both of these distributions have the same sign (positive). Given these $p_{kw}$ and $p_{ss}$, the cKW test allows us to reject the null hypothesis that these distributions have the same mean at a significance level of 0.001.

In the next sections we will evaluate the performance of the cKW test in terms of false-positive rates and power, and compare the performance with alternative tests.

Figure 6.1: Visual representation of the circular Kruskal-Wallis test. A sample circular distribution is shown for two groups: black and gray dots, with corresponding mean vectors shown as arrows; the thick black line is the grand mean direction. In (b) the distributions have been rotated by the grand mean direction, and a histogram of the imaginary (vertical) dimension is shown; the Kruskal-Wallis test along this dimension results in $p_{kw} \ll 0.001$. In (c) the same-sign test is illustrated. The histogram of the real (horizontal) dimension is shown, which corresponds to $p_{ss} = 1$ (both have the same sign).
6.3.2 Unit Vectors

We first compare the cKW test with the Watson-Williams test. Since the Watson-Williams test is only intended for unit length vectors, the input distributions in this section are limited to be circular normal distributions.

6.3.3 False Positives

To determine and compare false positive rates, we generated datasets $X_j$'s of the form $x \sim N(m, s), X_j = \text{complex}(\cos(x), \sin(x))$, where $m$ is the mean and $s$ is the standard deviation of the Gaussian distribution. Both groups are drawn from this distribution to construct datasets for which a rejection of the null hypothesis represents a false positive; the mean directions were the same. For numerical simulations 100,000 iterations were performed with 2 groups of 1,000 observations per group. Results are shown in Table 6.1. The Watson-Williams’ (WW) test began to fail for $\bar{R}$ values below 0.3. The WW test performed considerably better than expected, considering that previous reports have recommended that the test should not be used for $\bar{R}$ values of less than 0.45 (Jammalamadaka, Batschelet), this may be a consequence of the particular circular distribution we used. The proposed test (cKW), however, clearly outperforms the Watson-Williams test and maintains correct false-positive levels for all values of $\sigma$ tested.
Table 6.1: Comparing false-positive rates between WW and cKW.

<table>
<thead>
<tr>
<th>σ</th>
<th>$\bar{R}$</th>
<th>WW $\alpha=0.01$</th>
<th>WW $\alpha=0.05$</th>
<th>WW $\alpha=0.1$</th>
<th>cKW $\alpha=0.01$</th>
<th>cKW $\alpha=0.05$</th>
<th>cKW $\alpha=0.1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.2</td>
<td>0.98</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>1.0</td>
<td>0.60</td>
<td>0.01</td>
<td>0.04</td>
<td>0.08</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>1.6</td>
<td>0.28</td>
<td>0.02</td>
<td>0.08</td>
<td>0.14</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>2.2</td>
<td>0.09</td>
<td>0.15</td>
<td>0.27</td>
<td>0.36</td>
<td>0.01</td>
<td>0.04</td>
<td>0.09</td>
</tr>
<tr>
<td>3.0</td>
<td>0.030</td>
<td>0.59</td>
<td>0.69</td>
<td>0.74</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>Infinite</td>
<td>0.000</td>
<td>0.62</td>
<td>0.72</td>
<td>0.77</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
</tbody>
</table>

6.3.4 Power

This section investigates the power of the cKW test for unit vectors and compares it with the power of the Watson-Williams test. Since power is a function of angular difference between two circular distributions, many angular differences between 0 and 180 degrees were tested. A unit vector distribution was used, once again with 2 groups, and 1,000 observations per group, 1,000 tests were performed per angle. Several different $\sigma$’s were tested, 0.6, 1.6 and 2.4 with corresponding $\bar{R}$ values of 0.84, 0.28, 0.06. The results are shown in Figure 6.2.

Figure 6.2: Power for different circular concentrations. The radius corresponds to the proportion of iterations for which $p < 0.01$ and the angle is the introduced angular difference between the two datasets. The cKW test performed similarly to the WW test for narrow distributions (‘circle’). For ‘plus’ the plot suggested that WW test had slightly higher power than cKW, however this was caused by an increased false-positive rate for $\sigma=1.6$ (Table 6.1). There is no corresponding plot with WW for black ‘triangle’ because this is substantially out of the valid range for WW, which dominated entirely by false-positives.
The black curves correspond to the cKW test and the gray curves correspond to the WW test. The radius corresponds to the proportion of iterations for which \( p < 0.01 \) and the angle is the angular difference between the two datasets. In other words, the data point at 90 degrees and radius is 0.4 represents the outcome that the cKW test rejects the null hypothesis approximately 40% of the time at the 0.01 level when the angular difference is 90 degrees for \( \sigma = 2.4 \). The figure shows that the cKW test performed similarly to the WW test for narrow distributions (‘circle’). For ‘plus’ the plot suggested that WW test had slightly higher power than cKW, however this was caused by an increased false-positive rate for \( \sigma = 1.6 \) (Table 6.1). The WW test is not shown for \( \sigma = 2.4 \) because the circular concentration of the dataset is too low and the false-positive rate was not maintained (Table 6.1). While the cKW test maintained its false-positive rates, the power was reduced for such low circular concentrations. Increasing the number of observations per group improved the power of the cKW test even for very diffuse distributions (Section 8).

### 6.3.5 2D Vectors

The previous section tested only unit-vectors to allow a direct comparison with the standard Watson-Williams test. The cKW test was, however, developed to allow testing of two-dimensional circular data. In this section we investigate the false-positive rates for the cKW test using vectors that vary both in direction and length.
Distributions were constructed from a 2 dimensional Gaussian with the mean in the real dimension shifted by different amounts to achieve different $\bar{R}$ values.

### 6.3.6 False Positives

To test the false positive rates, we generated $X_j$'s of the form $X_j = \text{complex}(N(shift,1), N(0,1))$, i.e. distributions with the same mean direction, but varying mean vector lengths. For numerical simulations, we performed 10,000 iterations with 2 groups of 1,000 observations per group and several $\bar{R}$ values. The results are shown in Table 6.II. The results are very similar to Table 6.I; the cKW test maintains the desired false-positive levels even for small $\bar{R}$ values.

<table>
<thead>
<tr>
<th>Shift</th>
<th>$\bar{R}$</th>
<th>wWW $\alpha$=0.01</th>
<th>wWW $\alpha$=0.05</th>
<th>wWW $\alpha$=0.1</th>
<th>cKW $\alpha$=0.01</th>
<th>cKW $\alpha$=0.05</th>
<th>cKW $\alpha$=0.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.0</td>
<td>0.97</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>1.0</td>
<td>0.65</td>
<td>0.01</td>
<td>0.04</td>
<td>0.08</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>0.4</td>
<td>0.31</td>
<td>0.03</td>
<td>0.09</td>
<td>0.15</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>0.05</td>
<td>0.049</td>
<td>0.42</td>
<td>0.54</td>
<td>0.61</td>
<td>0.01</td>
<td>0.05</td>
<td>0.10</td>
</tr>
<tr>
<td>0</td>
<td>0.000</td>
<td>0.65</td>
<td>0.74</td>
<td>0.78</td>
<td>0.01</td>
<td>0.05</td>
<td>0.11</td>
</tr>
</tbody>
</table>

### 6.3.7 Power

To test the power of the cKW test for two-dimensional vectors, we generated two-dimensional distributions with parameter values that resulted in circular concentrations similar to Section 5. Shifts of 1.6, 0.3, and 0.07, were tested, which have similar $\bar{R}$ values to the $\sigma$’s tested before Figure 6.2. The results are shown in Figure 6.3. The styling is the same as Figure 6.2, with similar results; the cKW test’s power for 2D vectors with differing lengths is comparable to the WW test’s power for
unit length vectors. For instance, angular differences of \(~30\) degrees are detected with 80\% power for distributions with \(R=0.24\), and nearly 100\% for \(R=0.92\).

Figure 6.3: Power for different circular concentrations for 2D distributions. The styling is the same as Figure 6.2, with similar results; the cKW test’s power for 2D vectors with differing lengths is comparable to the WW test’s power for unit length vectors.

6.3.8 Sample Sizes

We tested the influence on samples size on the cKW test.

6.3.9 Large Sample Sizes

Larger datasets were tested to confirm that increasing the number of observations per group increases the power of the cKW test. The same parameters were used as section 4.2, \(\sigma=2.4\) or \(\bar{R}=0.06\). Four different sizes of observations per group were used: 1,000, 2,000, 5,000 and 10,000. The results are shown in Figure 6.4. Note that ‘triangle’ is the same as Figure 6.2 ‘triangle’. Power did in fact increase as \(N\) increased; showing that considerable power can be obtained even for data sets with very low circular concentrations as long as the data set is large enough.
Figure 6.4: Power as a function of N. The styling is the same as Figure 6.2. Note that ‘triangle’ is the same as Figure 6.2 ‘triangle’. Power did in fact increase as N increased; showing that considerable power can be obtained even for data sets with very low circular concentrations.

6.3.10 Small Sample Sizes

All results thus far have been for datasets with relatively large N. Many biological research questions involve datasets with smaller N’s. To assess the validity of the cKW test for such datasets, we compared the power of the cKW to the WW test for small N, shown in Figure 6.5. It was found that for high circular concentrations ($\bar{R} > 0.6$) with 2 groups the power of the cKW breaks down in comparison to the WW test for when there are less than 10 to 20 observations per group (solid and large dash lines). For intermediate concentrations ($0.45 < \bar{R} < 0.6$) an N of up to 50 may be required for two tests to have similar power (small dashed lines). For datasets with more than 2 groups, larger N’s are required for the two tests to perform similarly.
Figure 6.5: Power as a function of small N. The power for both WW and cKW are shown for two different mean direction differences (120 and 180) as a function of N. The vertical axis is the proportion $p<0.01$, or equivalently the power. For small N, cKW has significantly less power than WW however this difference disappears quickly as N increases.

6.4 Discussion

The non-parametric circular test proposed here maintained false-positive levels for situations where the Watson-Williams’ test failed. The test performed similarly in both power and false-positive rate for situations where the Watson-Williams’ test can be applied ($\bar{R}$ values greater than 0.45) for datasets with large N. The cKW test functions for weighted vector distributions for which the traditional Watson-Williams’ test was not intended. However, some power is lost compared to the Watson-William’s test, which may limit the usefulness of this test for some biological datasets with small numbers of samples.

Of course, the cKW analysis can be applied to any circular dataset, not just orientation or direction. Furthermore, there is the possibility that a 3 or even N dimensional version of this test could be derived. We, however, are not actively pursuing this.
Finally, Fisher (1953) proposed a test that does function correctly for low circular concentrations; however, it is restricted to unit length vectors drawn from a von Mises distribution. Many real-world datasets do not fit this restriction, and the non-parametric test we propose here has the advantage that it can be applied to sets of 2D vectors drawn from arbitrary distributions.

6.5 Acknowledgements

This chapter was co-authored with Bart Krekelberg, Tom Albright and the dissertation author; it is being prepared for publication.

6.6 References


Chapter 7: Conclusions

7.1 Classical Receptive Fields

In Chapters 2, 3 we studied the receptive field structure of area MT cells using a sparse motion stimulus. We used this stimulus in conjunction with reverse correlation in order to estimate what features of the motion stimulus modulated the response of the cell.

In Chapter 2, we tested assumptions about MT receptive field properties using the Spike Triggered Average (STA) as an estimate of the Classical Receptive Field. Contrary to a common assumption, we found that half of the cells studied preferred more than one direction of motion. This changing preference was most often a subtle change, on the order of 45 degrees across the receptive field, however a certain subset of cells preferred two distinct directions of motion. More traditional stimuli were used to confirm these receptive field properties implied by the STA. For the large change in direction preference, this change was confirmed by the simpler stimuli results. However, the more subtle change in preference was not conclusively confirmed using the more traditional stimuli; this was later addressed in Chapter 3.

An interesting possibility is that these changing direction preference cells may be precursors to area MST, which is selective to more complex motion, such as expansion, contraction, or rotation. MST is believed to require subunits selective to more complex motion than simple translation, and this subtle change may be the required building block.
Finally, many receptive fields were found to be entirely disjoint in space; meaning they were composed of highly direction selective subregions separated by non-, or less selective regions. These results have strong implications for the construction of receptive fields and the underlying physiology; however, it is not obvious what benefit to area MT this structure may have. Some implications are that wiring within area MT may not be as selective as originally believed or may be more error prone.

7.2 Surround Structure

In Chapter 3, the surround structure of MT receptive fields was studied using Maximally Informative Dimensions. Three types of structures were found: surround suppression, off preferred direction suppression, and omni-modulation. The fact that the surround was found using this technique is not surprising; however, the fact that it was found provides credibility to the technique. Furthermore, we believe this study provided the first physiological data from area MT in support of a divisive nonlinearity of the form originally proposed by Simoncelli and Heeger.

The off preferred direction suppression structure was unexpected. This structure had a nonlinearity similar to the surround, but the spatial extent was limited to the classical receptive field and the structure was selective for a direction of motion different than that preferred by the CRF. These off direction preference structures were consistent with explaining the subtle change in direction preference observed in Chapter 2. The data is consistent with a model where the feed forward input to MT
prefers one direction of motion; however, there can be suppressive mechanisms that are modulated by different directions (RF2). When the feed forward and suppressive mechanisms interact as they would for the stimulus used, the estimate of direction preference (STA) will be a combination of these two influences. This could explain why the uniform flow fields generated the same level of response as the locally optimized stimulus based upon the STA (FlowField_global vs. FlowField_local; Chapter 2).

Simoncelli et al. (1998) proposed population normalization as a technique to improve direction tuning in their model of area MT. In the model, units selective to all directions of motions were pooled to normalize responses; therefore, the pooled response should not be direction selective. Furthermore, the model assumed a divisive normalization. The omni-modulation is not direction selective and therefore consistent with this model. However, the nonlinearity observed for the omni-modulation is not consistent with a simple divisive normalization.

### 7.3 Object Motion

In Chapter 4, we studied a novel motion capture stimulus. The stimulus exhibited very strong psychophysical effects where a local region was perceived as moving in a global direction even when true motion was injected that was counter to this global direction. This stimulus setup was then adapted to be used to study area MT. One can think of motion capture as possibly being mediated by an extreme surround, one dictated by context. However, once color and motion directions and
location were taken into account, we did not find any responses in area MT that were consistent with the strong human perceptual effect. We did not confirm that the monkey perceived this illusion, however, Majaj et al. (2007) demonstrated that area MT seems to only encode for local motion and not global motion, even when the global motion is the only motion perceived. The results in Majaj et al. (2007) are consistent with the results here, indicating that area MT may naturally only encode local motion.

### 7.4 Maximally Informative Dimensions

In Chapter 5 a heuristic approach to Maximally Informative Dimensions was presented. We demonstrated that an approach using wavelets and Approximate Mutual Information demonstrated a significant benefit in accuracy, in particular for sparse binary stimulus distributions, over the method originally developed by Sharpee et al. (2004). Since the stimulus used in Chapters 2, 3 was sparse and essentially binary it was necessary to develop this heuristic approach.

### 7.5 Circular Statistics

In Chapter 6 a new circular statistic test was proposed. This test was necessary in order to determine the significance of the change in direction preference across the receptive field reported in Chapter 2. We demonstrated why the Watson-Williams (WW) test was not appropriate for our data; specifically the WW test requires circular distributions that are far more concentrated than those measured in Chapter 2. We
demonstrated that the new test had stable false positive rates for all circular concentrations and therefore it is a useful statistical test.

7.6 References

