Distortions in Perceived Direction of Motion Predicted by Population Response in Visual Cortex

by

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Paul Tiesinga

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

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ABSTRACT

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Abstract

The visual system is thought to represent the trajectory of moving objects in the activity of large populations of cortical neurons that respond preferentially to the direction of stimulus motion. Here I employed \textit{in vivo} voltage sensitive dye (VSD) imaging to explore how abrupt changes in the trajectory of a moving stimulus impact the population coding of motion direction in ferret primary visual cortex (V1). For motion in a constant direction, the peak of the cortical population response reliably signaled the stimulus trajectory; but for abrupt changes in motion direction, the peak of the population response departed significantly from the stimulus trajectory in a fashion that depended on the size of the direction deviation. For small direction deviation angles, the peak of the active population shifted from values consistent with the initial direction of motion to those consistent with the final direction of motion by progressing smoothly through intermediate directions not present in the stimulus. In contrast, for large direction deviation angles, peak values consistent with the initial motion direction were followed by: a small deviation away from the final motion direction, a rapid 180° jump, and a gradual shift to the final direction. These departures of the population response from the actual trajectory of the stimulus predict specific misperceptions of motion direction that were confirmed by human psychophysical experiments. I conclude that
cortical dynamics and population coding mechanisms combine to place constraints on the accuracy with which abrupt changes in direction of motion can be represented by cortical circuits.
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Chapter 1: Introduction

1.1 Overview

Encoding the trajectory of a moving stimulus that abruptly changes its direction of motion provides a particularly vivid example of the challenges inherent in using cortical circuits to represent rapidly changing stimulus features that are ubiquitous in visual scenes. Instantaneous changes in the properties of a visual stimulus are accompanied by alterations in the activity of cortical circuits that begin with some delay and continue beyond the stimulus event for 100’s of milliseconds (Sharon and Grinvald, 2002; Jancke et al., 2004). As a consequence, the cortical response to a stimulus that abruptly changes its direction of motion must involve a transition period during which the pattern of activity representing the initial direction of motion is replaced by the pattern of activity representing the new direction of motion. Given that the direction of stimulus motion is thought to be represented in visual cortex by the relative activity of a distributed population of neurons that are broadly tuned to direction of motion (Treue et al., 2000; Abbott, 1994; Pouget et al., 2003; Webb et al., 2007), this raises the question: Does the population response accurately track a stimulus that changes its direction of motion, or do the circuit dynamics that accompany changes in stimulus properties yield population representations that depart from the actual direction of stimulus motion, and, if so, how?
1.2 The realm of adaptation

The question of how prevailing stimulus conditions impact response to a new stimulus has traditionally been considered within the realm of adaptation—a temporary alteration in neuronal response that is induced by and outlasts a stimulus, and is thought to be the basis for distortions in visual perception such as the orientation tilt effect and the direction repulsion effect (Clifford, 2002). These effects typically have been studied with single unit recordings, which have revealed significant changes in response magnitude and shifts in tuning curves for stimulus features such as orientation and direction of motion (Muller et al., 1999; Dragoi et al., 2000; Dragoi et al., 2002; Felsen et al., 2002; Kohn and Movshon, 2004; Kohn, 2007). The magnitude and direction of these changes have been shown to vary systematically as a function of stimulus conditions, and these observations suggest that the population response to stimulus transitions involves significant non-linearities thus would lead to distortions in perception as a stimulus changes its direction of motion.

1.2.1 Tilt aftereffect (TAE) and direction aftereffect (DAE)

Prolonged adaptation to an oriented pattern affects the perceived orientation of a subsequently observed pattern (Gibson and Radner, 1937), a phenomenon known as the tilt aftereffect (TAE). When the angular difference between adapting and test orientation is small, the test stimulus appears to be repelled away from the adapting stimulus.
When the angular difference is large, the test stimulus will appear to be slightly attracted towards the adapting stimulus (Clifford, 2002). The direction aftereffect (DAE) is a motion analogue of the TAE. Prolonged exposure to a moving pattern affects the perceived direction of subsequent motion (Levinson and Sekuler, 1976; Patterson and Becker, 1996; Phinney, 1997; Schrater and Simoncelli, 1998; Clifford, 2002). For angles up to around 100 degrees between the directions of motion of the adapting and test patterns, the perceived direction of the test pattern tends to be repelled away from the adapting direction. For angles larger than 100 degrees between adapting and test directions, the perceived direction of the test tends to be attracted towards that of the adapter (Schrater and Simoncelli, 1998; Clifford, 2002).

1.2.2 Orientation adaptation

Compared to direction adaptation, the neural basis of orientation adaptation is more extensively studied and better understood. Since direction aftereffect shares many similarities with tilt aftereffect, understanding the neural basis of orientation adaptation might provide some insights into mechanisms of direction adaptation.

Orientation adaptation first occurs in the primary visual cortex. It is essentially absent in subcortical neurons (Ohzawa et al., 1985; Shou et al., 1996). The most prominent consequence of orientation adaptation is the suppression of cortical neural response. Adaptation to an orientation pattern has been shown to decrease the
responsiveness of cortical neurons to their preferred orientations (Movshon and Lennie, 1979). This reduction shows orientation specificity, being strongest when the adapting orientation and test orientation are identical. (Maffei et al., 1973; Carandini et al., 1998)

However, the reduction of neuronal activity is not the whole story. It has been shown that orientation adaptation can shift the peak tuning position of orientation selective neurons. Using a rapid adaptation paradigm, Muller et al. revealed that the peak orientation tuning position of complex cells in monkey primary visual cortex was affected by the adapting stimulus (Muller et al., 1999). Adapting orientations near the preferred orientation of the neuron caused a repulsive shift of the orientation tuning curve. This phenomena was also discovered in cat striate cortex by several other groups (Figure 1a, Dragoi et al., 2000; Dragoi et al., 2002; Felson et al., 2002; but also see Ghisovan et al., 2008). The magnitude of the post-adaptation shift in the preferred orientation depended on the angular difference between the adaptor and the preferred orientation (Figure 1b, Dragoi et al., 2000). The largest repulsive shift was found with small angular difference (5° to 22.5°). Repulsive shifts in V1 tuning occur after adaptation as brief as several tens or hundreds of milliseconds (Dragoi et al., 2002; Felson et al., 2002; Muller et al., 1999) or lasting as long as 20 min (Dragoi et al., 2000, 2001). In the most systematic exploration of the role of adaptation duration to date, Dragoi et al. (Dragoi et al., 2000) found repulsive shifts in V1 orientation tuning after
adaptation ranging in duration from 10s to 10min with the latter giving rise to the strongest effects.

Besides the shift of the peak orientation, the tuning curve also undergoes other changes after adaptation. After adaption to the orientation stimulus near the preferred orientation, the responses on the flank of the tuning curve near the adapting orientation were depressed, whereas responses on the opposite flank were enhanced (Figure 1a). Moreover, the orientation selectivity was broadened (Figure 1c). In contrast, after adaption to the orthogonal orientation, neurons showed a sharpening in orientation tuning (Figure 1c), along with an increase in responsiveness (Dragoi et al., 2000; Dragoi et al., 2002).

The capacity for neurons to display orientation plasticity induced by adaptation was shown to be different across the cortex (Dragoi et al., 2001). Compared to neurons located in iso-orientation domains, neurons located at and near pinwheel centers show larger repulsive shifts in orientation preference after adaptation. A possible explanation for these phenomena is that neurons in pinwheel centers receive inputs from a population of cortical neurons with a broader range of orientations (Marino et al., 2005); thus altering the efficacy of these inputs through adaptation is likely to induce more profound changes in the orientation preference of neurons at or near pinwheel centers (Dragoi et al., 2001).
1.2.3 Direction adaptation

The impact of direction adaptation has been studied in two visual cortical areas: primary visual cortex (V1) and middle temporal visual area (MT). Orderly distributed direction maps have been shown in primary visual cortex of the ferret (Weliky et al., 1996). Responsiveness of neurons in primary visual cortex is modulated by motion adaptation. This modulation is direction-specific. Prolonged adaptation with gratings drifting continuously in the preferred directions suppressed the responsiveness of cortical neurons significantly (Vautin and Berkley, 1977; von der Heydt et al., 1978; Hammond et al., 1985). Gratings drifting in directions nearby the preferred directions reduced the neuronal responsiveness to a lesser extent (Hammond et al., 1989) while gratings drifting in the null directions had no effect or slightly enhanced neuronal responsiveness (von der Heydet et al., 1978; Marlin et al., 1988; Giaschi et al., 1993).

Does motion adaptation shift the peak of the tuning curve of direction selective neurons? Kohn and Movshon recorded 40 neurons from V1. After flank adaptation (i.e., the adaptor’s direction is on the flank of the neuron’s preferred direction), no significant shifts were detected. However, they found direction tuning curves in MT were shifted by motion adaptation systematically (Kohn and Movshon, 2004). MT is an extrastriate area containing a high proportion of direction-selective cells (Zeki, 1974; Maunsell and Van Essen, 1983) and has a clearly established role in the perception of visual motion.
(Newsome et al., 1989). Experiments have shown that motion adaptation can modulate the responsiveness of MT neurons. Responses of MT neurons to motion in their preferred direction were reduced by adaptation to motion in the preferred direction and enhanced by prolonged adaptation in the opposite direction (Petersen et al., 1985; Priebe et al., 2002).

Kohn and Movshon found that adaptation to a prolonged drifting grating moving in near-preferred directions caused an attractive shift of the tuning curves, which is in the opposite direction to the shift effect induced by orientation adaptation (Figure 2a and Figure 2b, Kohn and Movshon, 2004). Response amplitude and cellular tuning width were also changed by direction adaptation. Response to test direction stimuli well-matched to the adapter were maintained best, but other test stimuli evoked much weaker responses after adaptation. Meanwhile, the direction tuning after adaptation became significantly narrower (Figure 2c). Interestingly, both changes were in the opposite direction to what had been shown by the orientation adaptation studies. The factors that account for the differences between these two lines of studies is still unknown.

1.3 Population response

As mentioned previously, orientation adaptation and direction adaptation change neuronal tuning curves in a systematic fashion. How do these changes in tuning
curves affect perception? In order to address this question, I need to introduce the concept of population response, which is believed to be the bridge between single neuron behavior and perception.

1.3.1 Sparse coding and population coding

The sensory system receives huge amount of information from the environment constantly. How does the brain encode this flood of information in order to form useful internal representations to mediate behavior? Scientists have proposed and found evidence for two encoding strategies: sparse coding and population coding (Barlow, 1972; Gross et al., 1969; Konorski, 1967; Logothetis and Sheinberg, 1996; Young and Yamane, 1992).

Sparse coding is a neural encoding strategy in which information is represented by a relatively small fraction of simultaneously active neurons out of a large population. A famous example of sparse coding is the response of neurons in visual areas of the temporal lobe to one particular object, and to that object alone. The neurons with such a high specificity are referred to as grandmother cells. Support for the grandmother cell theory comes from early and replicated studies that found visual neurons in the inferior temporal cortex of the monkey that fired selectively to hands and faces (Gross 1998; Perrett et al., 1982; Rolls, 1984; Yamane et al., 1988). Inferior temporal cells can also be trained to show great specificity for arbitrary visual objects (Logothetis and Sheinberg, 1996).
1996; Tanaka, 1996). Recently, Quiroga et al. have shown that there are cells in the human hippocampus that have highly selective responses to the presentation of images of particular individuals such as Jennifer Aniston or Bill Clinton (Quiroga et al., 2005).

A more common form of neuronal representation is population coding, in which information is encoded not by single cells, but rather by the spiking activity of a large group of more broadly tuned cells. One famous example of population coding is the representation of location in space by place cells in rat hippocampus. Place cells exhibit a high rate of firing whenever an animal is in a specific location in an environment corresponding to the cell’s “place field” (Bair, 1999; Borst and Theunissen, 1999). Place fields within the hippocampus are usually distributed to cover all locations in the environment, such as a small maze. There is considerable spatial overlap between the fields. Thus, a distinct population of neurons will respond to any given location. Population coding has been found to encode direction of motion as well. The cercal system of the cricket, which senses the direction of air current, is a vivid example. The wind direction is encoded by four low-velocity interneurons, whose preferred directions are separated by 90° from each other in direction space (Theunissen and Miller, 1991a and b). Each neuron responds with a firing rate that is closely approximated by a half-wave rectified cosine function. The response pattern of all four neurons as a whole is the internal representation of the wind direction. In mammalian visual system, it has been
shown direction of motion is encoded by a population of direction selective neurons in primary visual cortex and the area of MT. For example, in the middle temporal (MT) area of primates, many motion-sensitive neurons with a wide range of preferred directions respond to a stimulus moving in a single direction. Besides direction of motion, population coding strategies are thought to be used in early visual system to encode other features, such as orientation, color, depth etc. (Usrey and Reid, 1999; Zemel et al., 1998). Similarly, motor commands in the motor cortex are also thought to rely on population coding (Tolhurst et al., 1982).

1.3.2 Advantage of population coding

Compared to sparse coding, population coding has several important advantages. Pouget et al. have investigated this issue systematically and their views are summarized as following (Pouget et al., 2000; Averbeck et al., 2006; Pouget and Latham, 2003; Knill and Pouget, 2004):

1. Population coding is more robust. Damage to a single cell does not generate a catastrophic effect of the encoded representation because the information is distributed across many cells.

2. The overlap among the tuning curves allows precise encoding of values that fall between the peaks of two adjacent tuning curves.
3. Population coding allows simultaneous interpretation of stimulus strength and quality. For example, in primary visual system, the orientation tuning curves contain information for both stimulus contrast (amplitude) and the orientation (peak position).

4. Bell-shaped tuning curves provide basis functions that can be combined to approximate a wide variety of nonlinear mappings. This means that many cortical functions, such as sensorimotor transformations, can be easily modeled with population codes.

5. Population coding strategy allows implementation of optimal estimators such as maximal likelihood estimation and Bayesian decoding thus efficiently reducing the noise (uncertainty) in the neuronal signal. One such example is illustrated in Figure 3 (adapted from Pouget et al., 2000).

1.4 From tuning curves to population response

How do the changes in the responses of single neurons induced by adaptation affect the overall pattern of population response? For example, we know that orientation adaptation causes a repulsive shift of tuning curves in V1. But what happens in population response? Let’s work through the following example. Assume there is an array of neurons with preferred orientation ranging from 0° to 180°. Before adaptation, a
90° orientation stimulus maximally activates a neuron whose preferred orientation is 90°. After adapted to a 70° adaptor, assume that the neuronal tuning curve will be shifted by 5° (i.e. it now peaks at 95 degrees) repulsively. This means after adaptation, the stimulus that elicits the maximal response for the neuron will now be 95°. If neurons always carry the unadapted perceptual 'label', then the 95° test stimuli will be perceived as 90°. Thus, repulsive shifts of neuronal tuning curves predict attractive perceptual effects. Following the same argument, attractive shifts in tuning curves should predict repulsive perceptual effects.

### 1.4.1 Gap between tuning curves and population response

Three major obstacles prevent us from predicting the population response after adaptation based on changes in tuning curves measured in electrophysiological experiments.

First, there is a lack of agreement on the nature of the tuning curve shifts that are induced by adaptation. In cat primary visual cortex, Dragoi and his colleagues showed that orientation adaptation led to a reduction in activity for stimuli whose orientation was nearest to that of the adapting stimulus and thus resulted in an apparent repulsive shift in tuning properties (Dragoi et al., 2000). However, another group has observed the exact opposite. Ghisovan et al. have recently reported that orientation adaptation
produced an increase in activity for stimuli whose orientation was close to that of the adapting stimulus and thus generated attractive shifts (Ghisovan et al., 2008). The difference between these experimental results might be explained by the difference in the adaptation paradigm. However, currently, researchers have not reached a consensus about the tuning curve shift effect induced by adaptation.

Second, the variability across neurons creates a challenge for predicting the population response. The variability for the shift of the tuning curves are large even under the same adaptation paradigm. Part of this large amount of variability could be explained by the map structure. Neurons near the pinwheels were reported to show larger repulsive shift, whereas neurons inside the orientation domains showed significantly smaller repulsive shift. The existence of the large amount of variability makes it difficult to sum up all the neurons' contribution and predict the population response after adaptation.

Third, the complexity of the changes in single unit responses, involving simultaneous alterations in multiple response parameters, has made it difficult to specify how these effects would combine in the population response. For a typical orientation or direction tuning curve, there are four basis parameters: baseline offset, peak position, peak amplitude and tuning width. As introduced previously, adaptation
affects at least three parameters: peak position, peak amplitude and tuning width. Much attention has been focused on the impact of the tuning curve shift (i.e., changes of peak position). However, could peak amplitude and tuning width also impact the population response? Kohn and Movshon have explored the contribution of peak amplitude to population response using computation modelling approach. They found that reduction of neuronal responsivity alone could cause a repulsive shift in population response (Kohn and Movshon, 2004). Thus, a shift in tuning curves is not required to induce a shift in population response. Their findings were further verified by Gardner and his colleagues (Gardner et al., 2004). Gardner et al. built a model that contained 10,000 model neurons and systematically tested the influence of peak amplitude, peak position and tuning width on the population response (Figure 4a). Consistent with Kohn and Movshon, they found that a decrease in response gain alone would generate a repulsive shift in the population response (Figure 4b). They also found that a decrease in tuning width alone could also shift the population response repulsively, with a very similar pattern to the effect caused by gain reduction (Figure 4b). Thus, at least three parameters (peak amplitude, peak position and tuning width) need to be taken into consideration in order to predict the impact of changes at the level of single units on the population response. This presents a challenge because in primary visual cortex, orientation adaptation has been shown to reduce neuronal response amplitude, shift the
tuning curve repulsively and increase cellular tuning width. These three changes will respectively lead to a repulsive shift, attractive shift and attractive shift in population response, thus leaving the net effect undetermined.

Given these considerations, examining the impact of adaptation on the tuning curves of single units does not provide the basis for predicting the impact of adaptation on the population response.

1.4.2 Does alteration in population response necessarily involve changes of tuning curves?

In the previous section, I have questioned the feasibility of predicting the population response based on neuronal tuning curves. An implicit assumption for the tuning curve approach is that the alteration of population response after adaptation is due to shifts in the neuronal tuning curves. However, does alteration in population response necessarily involve changes in tuning curves? The answer will be yes if the population response under investigation is the steady state response for a single stimulus. That is because in that case, the population response could be inferred from the tuning curves of all the neurons. In other words, the population response is a function of the neuronal tuning curves. Thus, any alteration in population response is a reflection of changes in tuning curves. In contrast, when there are instantaneous changes in the properties of a visual stimulus, the population response is an interaction between
the pattern of activity representing the initial and new visual stimulus, because the activity of cortical circuits begins with some delay and continues beyond the stimulus event for 100’s of milliseconds (Sharon and Grinvald, 2002; Jancke et al., 2004). This interaction could be linear or nonlinear. If it is linear, the alteration of population response is a summation of the influence of the two visual stimuli, thus no changes in tuning curves are required. In this situation, measuring tuning curves does not help to infer the population response at all.

1.5 Voltage-sensitive dye imaging: a direct measure of the population response

Given the difficulty in using shifts in the tuning curves of individual units to infer changes in the population response, it is natural to ask whether there is a more direct approach to assess the population response to stimulus transitions. There are three important criteria that need to be met: First, it should have the power to record the responses of a population of neurons simultaneously; Second, it needs to have temporal resolution at millisecond level in order to capture the cortical response during the stimulus transition; Third, it should have the ability to identify the preferred stimulus property (e.g. preferred orientation, preferred direction etc) of the recorded neurons. Single unit recording match the last two criteria but miss the first one. The experimental approach that matches all the three criteria and is used in my thesis research is called voltage-sensitive dye imaging (VSDI).
Voltage-sensitive dye imaging is a powerful technique to measure dynamics of cortical population response with fine time resolution. To visualize electrical activity, the preparation under study is first stained with a suitable dye. The dye molecules bind to the external surface of cell membranes and act as molecular transducers that transform changes in membrane potential into optical signals — changes in absorption or emitted fluorescence that occur in microseconds (Shoham et al., 1999; Grinvald and Hildesheim, 2004). These optical changes are monitored with light-imaging devices, positioned on the target or, more often, in the image plane of the target formed by an optical device such as a CCD camera or a photo diode array. The amplitudes of the VSD signals are linearly correlated with both changes in membrane potential (rather than changes in current) and the membrane area of the stained neuronal elements under each measuring pixel (Cohen et al., 1974; Petersen et al., 2003). Given the staining depth of the dye (up to 1.5 mm) and the fact that by utilizing conventional optics the image contains mostly neuronal elements in the upper 0 to 400-800 microns, it is believed that most of the signal comes from layer 2 and layer 3, since the cell density in layer 1 is much lower compared to layer 2/3. VSDI offers a combination of good spatial resolution and great temporal resolution. The spatial resolution of VSDI is around 30 micron per pixel for my imaging setup. The temporal resolution of VSDI is mainly limited by the sampling rate because the dye molecule’s changes in absorption or emitted fluorescence occur in
microseconds after the voltage changes. This means that signals from VSDI reflect the neuronal activity almost in real time.

**1.6 Aim and scope of present study**

The following is a brief outline of the work presented in Chapter Two to Chapter Five. In Chapter Two, I quantify the dynamic patterns of population activity that accompany abrupt changes in the direction of motion of a random dot stimulus by using voltage sensitive dye (VSD) imaging in ferret visual cortex. The presence of an orderly columnar mapping of direction preference in ferret visual cortex makes it possible to translate the spatial patterns of VSD activity into a measure of the direction tuning of the population response. My results show that the trajectory of a stimulus that moves in a constant direction is accurately encoded by the peak of the V1 population response; however, when a stimulus abruptly changes its direction of motion, the peak of the population response transiently departs from the trajectory of the stimulus. Chapter Three describes a simple linear model that explains the characteristics of the population response for different direction deviation angles. Chapter Four provides evidence that the deviations of population response from the actual directions of stimulus motion are consistent with human misperceptions of motion direction that accompany abrupt changes in the direction of stimulus motion. In Chapter Five, I consider the relation of
these results to previous studies, and their significance for understanding population coding mechanisms.
**Figure 1:** Adaptation-induced plasticity of orientation tuning in V1 neurons.

a. Orientation tuning curves of a representative cell that was successively adapted to two different orientations. Orientation tuning during four conditions is shown in the figure: control (black), adaptation to the first orientation (solid gray), adaptation to the second orientation (dashed gray), and recovery (black, dashed line). The control preferred orientation is represented as 0°, and all subsequent tuning curves (during adaptation and recovery) are represented relative to the control condition. b. Scatter plot showing the magnitude of the post-adaptation shift in preferred orientation as a function of the absolute difference between the adapting orientation and the control-preferred orientation. c. Post-adaptation changes in orientation selectivity index (OSI). This figure is adapted from Dragoi et al., 2000.
Figure 1: Adaptation-induced plasticity of orientation tuning in V1 neurons.

Adapted from Dragoi et al., 2000
Figure 2: Direction-induced plasticity of direction tuning in MT neurons.

a. Effect of flank adaptation on the direction tuning of MT neurons. Direction tuning of an MT cell before (open circles) and after (filled circles) flank adaptation (direction indicated by arrow). Tuning is shifted towards the adapted direction, and responsivity and bandwidth are reduced. b. Direction tuning curves are shifted attractively by flank adaptation. c. Tuning bandwidth is reduced by flank adaptation. This figure is adapted from Kohn and Movshon, 2004.
Figure 2: Direction-induced plasticity of direction tuning in MT neurons.

Adapted from Kohn and Movshon, 2004
Figure 3: A neural implementation of a maximum likelihood estimator.

The input layer (bottom) consists of 64 units with bell-shaped tuning curves whose activities constitute a noisy hill. This noisy hill is transmitted to the output layer by a set of feed forward connections. The output layer forms a recurrent network with lateral connections between units (Only one representative set of connections and only nine of the 64 cells are shown). The weights in the lateral connections are determined such that, in response to a noisy hill, the activity in the output layer converges over time onto a smooth hill of activity (upper graph). In essence, the output layer fits a smooth hill through the noisy hill, just like maximum likelihood. Deneve et al. (Deneve et al., 1999) have shown that, with proper choice of weights, the network is indeed an exact implementation of, or a close approximation to, a maximum likelihood estimator. The network can also be thought of as an optimal nonlinear noise filter, as it essentially removes the noise from the noisy hill. This figure comes from Pouget et al., 2000.
Figure 3: A neural implementation of a maximum likelihood estimator.

From Pouget et al., 2000
Figure 4: Predicting the impact of tuning curve properties on population response using a population coding model.

a. Effects of different mechanisms of neural adaption on the responses of model neurons. Mechanisms of neural adaptation were: reduction of the magnitude of neural responses, narrowing of neural tuning curves, repulsion of the neural preferred direction away from the adapting direction and attraction of the neural preferred direction toward the adapting direction. Black and red curves show neural tuning curves before and after adaptation. b. Predicted population response after adaptation. This figure is adapted from Gardner et al., 2004.
Figure 4: Predicting the impact of tuning curve properties on population response using a population coding model.

Adapted from Gardner et al., 2004
Chapter 2: Capturing and decoding the dynamics of population responses to changes of motion direction

2.1 Introduction

Under natural viewing conditions, circuits in visual cortex must represent the information contained in a continuous stream of images that often contains abrupt changes in stimulus properties, such as motion direction. How are changes in the direction of stimulus motion represented in the dynamics of V1 population response? This question has been explored previously by examining the impact of neuronal tuning curves (Muller et al., 1999; Dragoi et al., 2000; Felsen et al., 2002; Kohn and Movshon, 2004). However, this approach fails to provide accurate measurement of population response (Gardner et al., 2004).

In this chapter, I describe experiments utilizing a new approach, voltage-sensitive dye imaging, to record the dynamics of population response directly. I chose ferrets as my experimental animal model, because it has been shown by optical imaging studies that direction preference is arranged in a systematic fashion in ferret V1 (Weliky et al., 1996), which allows me to identify the preferred directions for every pixel within my imaging data. By comparing the patterns of activity revealed by voltage-sensitive dye imaging with the map of preferred direction I have been able to show how the brain responds to motion transitions.
2.2 Results

2.2.1 The dynamics of the population response to motion transition in primary visual cortex vary as a function of direction deviation angle

Voltage-sensitive dye imaging of ferret visual cortex revealed strong and stable columnar activity patterns in response to random dot patterns that moved in a constant direction (Figure 5). In contrast, abrupt changes in direction of motion (see Figure 6 and Method section for visual stimulus design) were accompanied by dynamic changes in the columnar patterns whose properties varied as a function of the size of the direction deviation. Figure 7 illustrates for one experiment the typical transition patterns that were found for different direction deviation angles. In these experiments, the final direction of motion for each condition was identical—horizontal motion to the left—but was preceded by stimuli that were offset in a clockwise fashion by 45°, 90°, and 135°. As expected, the columnar patterns for different offset angle conditions were significantly different at the start of the trial interval, but were indistinguishable at the end of the trial interval (Figure 7a, b and c). For a direction deviation angle of 45°, the cortical activity shifted smoothly from the initial pattern to the final pattern without an obvious change in modulation strength (Figure 7a). For a 90° direction deviation, however, the onset of the second stimulus was accompanied by a prominent reduction in the modulation of VSD signal, which was then followed by the emergence of a new stable pattern of activity (Figure 7b). For a direction deviation angle of 135°, there was also a noticeable
reduction in the modulation of the activation pattern during the transition period (Figure 7c).

In order to understand the relation between these columnar response patterns and the tuning of the population response to motion direction it is necessary to convolve the stimulus evoked VSD maps with the direction preference map for the same region of cortex (Basole et al., 2003; Figure 8). The resulting population response profile (PRP) represents the average activity evoked by a given stimulus across all cortical sites expressed as a function of each site’s preferred stimulus direction (Figure 8c). The PRP for each stimulus condition exhibits a single major peak that, at the beginning and the end of the trial, corresponds to the direction of stimulus motion. In addition, there is a smaller minor peak consistent with the fact that tuning for stimulus direction is not absolute: most neurons are tuned to orientation and respond less strongly to motion in the anti-preferred direction (Berman et al., 1987; Finlay et al., 1976; Moore et al., 2005). The PRP dynamics for a constant motion stimulus is shown in Figure 9. The peak direction was stabilized (Figure 9b) after the peak amplitude increased above the noise level (Figure 9c). The combined change in the peak direction and the magnitude of the population response is summarized in vector format in Figure 9d.

In the motion transition conditions, comparison of the PRP tuning dynamics for the three direction deviation angles illustrates prominent features of the population
response that differ as a function of direction deviation angle. For small direction deviation angles (45°), the peak of the population response swept smoothly and gradually from the initial direction (135°) to the final direction (180°) taking the shortest route across the intermediate direction space (Figure 10a). For somewhat larger direction deviation angles (90°), the peak of the population response also followed the shortest route across the intermediate direction space (i.e. from 90°-180°), but the transition process became compressed in time with a sharp jump in the peak of the population response that coincided with a reduction in the modulation of the VSD signal. For larger direction deviation angles (135°), the population response exhibited a distinctive triphasic pattern: an initial phase in which the peak direction turned away from the shortest route between the initial and final direction, a second phase in which the peak rapidly jumped by 180° in concert with a reduction in magnitude, and a third phase in which the peak direction gradually settled on the final direction. The combined changes in the peak direction and the magnitude of the population response for these three direction deviation angles are summarized in vector format in Figure 10b.

To confirm the systematic relation between the dynamics of the peak population response and direction deviation angle I quantified the average population response for the full range of direction deviation angles in experiments from 10 animals. The properties of the population dynamics varied continuously as a function of direction
deviation angle with an inflection point that is evident at direction deviation angles of 112.5°. For direction deviation angles of 22.5°-90°, the peak direction during the transition swept across the intermediate direction space between the initial and final direction (Figure 11a). Within this group, the rate of transition measured at the midpoint of change in peak direction (°/ms) became larger as the direction deviation angle approached 90° (Figure 11d). For direction deviation angles greater than or equal to 112.5°, the peak direction during the transition exhibited the “trihasonic” pattern (Figure 11a). Within this group, the rate of transition became smaller as the direction deviation angle approached 180° (Figure 11d). The average magnitude of the peak population response also varied systematically with direction deviation angle. For most direction deviation angles, there was a transient reduction in magnitude that reached its maximum at the midpoint of the change in peak direction (Figure 11b and c). This reduction in magnitude became greater with increasing direction deviation angle reaching its maximum at 112.5° and then becoming smaller with larger direction deviation angles (Figure 11e). For those angles where there was a prominent reduction in response, there was an equally prominent recovery which could exceed the magnitude of response to the initial direction of motion (Figure 11b and c). The magnitude at the end of the data acquisition period was lowest for the smallest angles in my sample (22.5°, 45°) and reached its highest value for the 112.5° direction deviation
angle. For a direction deviation angle of 180° (i.e., a stimulus that reverses direction), the dynamics of the population response became a simple step function with a 180° jump during the middle of the transition process and little change in magnitude (Figure 11a and d). I confirmed that the dynamics of the population response were not affected by the difference imaging strategy that I employed to enhance the VSD signal to noise ratio: analysis of the population response based on single condition images yielded similar results (Figure 12).

2.2.2 The spike discharge population response constructed from unit recording data is consistent with VSDI measurements

Voltage-sensitive dye imaging is a powerful technique for measuring the responses of large populations of neurons with fine temporal resolution. However, VSD responses are a mixture of sub-threshold and supra-threshold voltage signals, raising the possibility that the dynamics associated with changes in motion direction that I have described may not be evident in the spiking activity of V1 neurons. To address this issue, I used extracellular recordings from layer 2/3 neurons to reconstruct the dynamics of spiking activity that would be expected for the population response (Figure 13). I assume that the direction tuning function of a single neuron (i.e. the relative response of a single neuron to different directions of motion) can be used to infer the relative activity of a large population of neurons with similar tuning functions, but with different
preferred directions of motion (Treue et al., 2000). Assuming that the direction tuning curve of a single neuron is representative of a large population of single neurons, the spike discharge PRP for a stimulus moving in a single direction will be identical to the direction tuning curve of single neurons whose preferred direction of motion corresponds to the direction of stimulus motion (Figure 13a).

By similar reasoning, the spike discharge PRP for a stimulus that changes its direction of motion can be extrapolated from a single neuron’s response using a series of motion transition stimuli that (1) cover the full range of motion directions and (2) where each stimulus is composed of two successive motion stimuli with the same direction offset angle (see Methods). Figure 13b illustrates the spike discharge PRP estimated from a single unit responding to motion transition stimuli with a direction deviation angle of 90°. The pattern of activity estimated for the population response exhibits all the basic features that would be expected based on the VSD imaging (e.g., Figure 7b), notably strongly tuned responses to the first and second stimulus separated by a rapid transition in which there is a strong reduction in the tuned response. The PRPs generated with VSD imaging reflect the average activity of large numbers of neurons that have somewhat different direction tuning functions (see Li et al., 2006 Supplementary Table 1 for an analysis of the variation of single neuron direction tuning in ferret V1.). In order to better approximate the neuronal population response, I
examined the response of multiple single units (N= 18) to three direction deviation angles (45°, 90° and 135°) and then averaged the PRPs after proper alignment based on each neuron’s preferred direction (Figure 14a). The dynamics of peak direction and peak amplitude of the average spike discharge PRP varied consistently with direction deviation angle, matching the characteristic features computed from the VSD data (Figure 14b and c). For example, the peak of the population response accompanying a 45° deviation advanced smoothly and slowly through the intervening directions. In contrast, the peak of the population response associated with a 135° deviation exhibited the triphasic pattern found with VSD imaging (movement away from the intervening directions, a rapid 180° jump, and smooth decay to the second direction of motion). Difference in the magnitude of the tuned response was also consistent with the results of VSD imaging; i.e. small reductions in magnitude for small angular offsets and large reductions for larger angular offsets.

Thus, the dynamics of peak direction and peak amplitude computed for spike data are consistent with those computed from the VSD data (Figure 11), demonstrating that the population response patterns are preserved at the spike level.
2.3 Summary

In this chapter, I used voltage-sensitive dye imaging to explore how changes in the direction of stimulus motion are represented in the dynamics of V1 population response. I found that dynamics of the population response vary as a function of direction deviation angle. For direction deviation angles smaller than 90°, the peak direction sweeps smoothly from the initial direction to the final direction. For direction deviation angles larger than 112.5°, the peak direction transiently deviates away from the direction of the second stimulus, then exhibits a step function that transiently overshoots and then settles on the final direction. Dynamics of peak amplitude also vary as a function of direction deviation angle. There is often a “notch” during the transition which is largest when the direction deviation angles are near 90°. These findings were confirmed by unit recording experiments.

2.4 Materials and methods

All experimental procedures were approved by the Duke University Institutional Animal Care and Use Committee and were performed in compliance with guidelines published by the US National Institutes of Health.
2.4.1 Animal preparation

Ferrets were anesthetized with ketamine (50 mg/kg), shaved and scrubbed. The femoral vein was cannulated for delivery of 5% dextrose in lactated Ringer’s solution and paralytic, a tracheotomy performed, and the ferret placed in a stereotaxic head frame. A mixture of nitrous oxide and oxygen (2:1) with halothane or isoflurane (2-2.5%) was administered and adjusted if necessary based on EKG and expired CO₂. Body temperature was maintained at 37°C, and silicone oil was used to protect the corneas. A craniotomy was performed above primary visual cortex and the dura removed.

A stainless steel chamber was cemented (Dycal, Dentsply) to the skull. Intrinsic imaging was performed before voltage-sensitive dye imaging. For intrinsic imaging, the chamber was filled with ringer’s solution and sealed with a glass coverslip to allow viewing of the cortical surface. For voltage-sensitive dye imaging experiments, the chamber was filled with agar (0.7%) and sealed with a glass coverslip to allow viewing of the cortical surface.

After completing surgical procedures, incisions and pressure points were infiltrated with bupivacaine and anesthesia (halothane or isoflurane) was lowered to 0.75-1%. The animal was paralyzed with rocuronium bromide to prevent eye movements. Nitrous oxide and oxygen ratio was reduced to 1:1. This reduction in
anesthesia was necessary to allow visual stimulation to activate cortical circuits. Expired CO2 level was maintained at 3.5-4.5% throughout the experiment.

### 2.4.2 Intrinsic signal optical imaging

The cortical surface was visualized through a tandem lens macroscope attached to a low-noise CCD camera. The timing of stimulus presentation and collection of reference and stimulus frames were all controlled by software from Optical Imaging Inc (Rehovot, Israel). For intrinsic signal imaging I illuminated with 705 nm light. In general, I used an acquisition time of 5s following stimulus onset. The data were averaged across 25 stimulus presentations to yield the final activity map for each stimulus condition.

Visual stimuli were presented on an Apple Macintosh PowerMac G4 and a GDMF520 CRT (Sony, refresh rate 120 Hz), gamma-corrected using ColorVision Spyder (Pantone, Carlstadt, NJ). Stimulation procedures were designed using Matlab (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Visual stimuli were random dot patterns moving in 16 directions between 0° and 337.5° sampled at 22.5° increments. The dot diameter was 1° and contrast was 100% (white dots on a black background). The dot density was 0.137 dots/deg². The dot pattern moved at 10°/s with 100% coherence. Stimuli were 5s in duration with a 5s interstimulus interval.

Analysis of optical images was performed using custom designed software written in MATLAB (Mathworks, Natick, MA). Briefly, a first frame subtraction
(Bonhoeffer and Grinvald, 1996) was performed followed by a circularly symmetric spatial filter (pass band between 1.0-6.7 cycles/mm, implemented as a low-pass mean filter 5 pixels in diameter, followed by a high-pass mean filter 35 pixels in diameter). Because most neurons in ferret primary visual cortex exhibit a reduced but significant response to motion in the non-preferred direction (Moore et al., 2005), the single-pixel direction tuning curve was fitted to a double Gaussian function:

\[
M(\theta | A_0, A_1, A_2, \phi_1, \phi_2, \sigma) = A_0 + A_1 e^{-\frac{(\theta-\phi_1)^2}{2\sigma^2}} + A_2 e^{-\frac{(\theta-\phi_2)^2}{2\sigma^2}}
\]

Here M is the response of a pixel as a function of the direction of motion \(\theta\), \(A_0\) is the untuned response component, \(A_1\) and \(A_2\) are the strength of the response to the preferred and nonpreferred direction, respectively, and \(\phi_1\) is the corresponding preferred and \(\phi_2\) is the corresponding nonpreferred direction, \(\sigma\) is the tuning width. There were five parameters for 36 degrees of freedom, because \(\phi_1\) and \(\phi_2\) were constrained to be 180° apart from each other. When the fitting procedure led to a solution with \(A_2>A_1\), I exchanged \(A_1\) and \(\phi_1\) with \(A_2\) and \(\phi_2\) so that \(\phi_1\) always corresponded to highest peak in the direction tuning curve, i.e. the neuron’s preferred direction. The direction map is obtained by plotting for each pixel its preferred direction. The fitting procedure is described below in the subsection on the fits for the population response profile (PRP).
2.4.3 Voltage-sensitive dye imaging (VSDI)

I followed the protocol for VSD imaging described by Grinvald and collaborators (Grinvald and Hildesheim, 2004; Sharon and Grinvald, 2002; Shoham et al., 1999). Briefly, the cortex was stained with the VSD RH-1691 by circulating the dye in a chamber over the cortex for 2 hr and washing it out with ringer’s solution. Images were acquired with a CCD digital camera at a frame rate of 340 Hz and a spatial resolution of 30 μm per pixel. Frame acquisition was synchronized with the heartbeat. Respiration was stopped during the acquisition. The cortex was illuminated by a 100 W halogen light. The filter settings were as described previously (Shoham et al., 1999): The excitation filter was band-pass at 630 ± 10 nm, and the emission filter was high-pass, with a cutoff at 665 nm.

In the motion transition experiments, the visual stimuli started with 150 ms gray screen presentation followed by a 300 ms flickering dot pattern, which was designed to activate the cortex uniformly, without preference for any direction domain. Subsequently, two stimulus components each lasting 1 s were presented, with the direction of the second component different by an angle which varied between 22.5° to 180° with 22.5° angular increments. The parameters of the random dot pattern were the same as those in the intrinsic imaging experiments. The average luminance was the same for the two motion components as well as for the flicker stimulus. A difference
map was determined to obtain a higher signal to noise ratio, which meant that each stimulus condition was paired with another one with 90° angular offset in the direction of both its motion components (Figure 6).

2.4.4 VSDI data analysis

The evoked response to each stimulus was calculated for each pixel in three steps in order to eliminate artifacts due to heartbeat and respiration (Grinvald et al., 1984; Sharon et al., 2007). First, the response was averaged across trials. Second, the response averaged across the 150 ms prior to stimulus onset was subtracted in order to remove slow stimulus-independent fluctuations in illumination and background fluorescence levels. Finally, $\Delta F/F$ was determined by subtracting the response to a blank stimulus and dividing by it. In addition, the data were high-pass filtered (low frequency cut off 1.0 cycles/mm, implemented as a high-pass mean filter 35 pixels in diameter) to remove spatial gradients and isolate the local modulation patches.

The direction preference map acquired by intrinsic imaging was aligned with the images acquired by VSD imaging using the blood vessel patterns. To interpret the patterns of activity evoked by various stimulus configurations, I calculated a population response profile (PRP), which captured the relative activation of each pixel in the region of interest (ROI) in terms of the pixel’s preferred direction (Basole et al., 2003; Figure 8c). Specifically, the pixels inside the ROI were sorted into 36 bins by the preferred direction.
The averaged values for these pixels in the patterns of activity were calculated for each direction bin. The resulting histograms were fitted with double Gaussian functions to determine the peak direction and amplitude (Figure 8d and e).

The following functions were used to analyze the PRPs obtained from difference images:

\[ M(\theta | A_0, A_1, A_2, \phi_1, \phi_2, \psi_1, \psi_2, \sigma) = A_0 + A_1 e^{-\frac{-(\theta - \phi_1)^2}{2\sigma^2}} + A_2 e^{-\frac{-(\theta - \phi_2)^2}{2\sigma^2}} - A_1 e^{-\frac{-(\theta - \psi_1)^2}{2\sigma^2}} - A_2 e^{-\frac{-(\theta - \psi_2)^2}{2\sigma^2}} \]

(2)

Here, \( M \) is the response, \( \theta \) is the preferred direction of the neurons, \( A_0 \) is the remaining untuned response component, \( A_1 \) and \( A_2 \) are the responses of pixels for which the stimulus corresponds to the preferred and nonpreferred directions, respectively, \( \phi_1, \phi_2, \psi_1 \) and \( \psi_2 \) are the corresponding peak directions and \( \sigma \) is the tuning width. In total there were 5 parameters for 36 degrees of freedom, because \( \phi_1 \) and \( \phi_2 \) were constrained to be 180° apart from each other and \( \psi_1 \) and \( \psi_2 \) were constrained to be 180° apart from each other and to be 90° apart from \( \phi_1 \) and \( \phi_2 \), respectively.

For each time frame, the squared difference between the measured response \( M_{exp}(\theta) \) and the fitting function \( M(\theta | A_0, A_1, A_2, \phi_1, \phi_2, \psi_1, \psi_2, \sigma) \) was minimized as a function of the parameters by least squares curve fitting using Optimization Toolbox in Matlab (lsqcurvefit). To avoid sub-optimal solutions corresponding to local minima, the fitting procedure was repeated 800 times and the solution with the lowest...
difference was retained. The average R square value of the fits was around 0.85. Incorporating additional parameters in the fitting function did not significantly improve the R square value.

In order to determine the robustness of the estimated fitting parameters, I first estimated the error in the binned PRP using a bootstrap procedure (Davison and Hinkley, 1997). The original PRP for the example data set was obtained using 48-50 trials per stimulus condition. I created 10 datasets by randomly drawing, with replacement, 40 trials from the original set, and determined the PRP for each of them. The standard deviation in the PRP across these sets was used as an estimate for the error in the PRP. It did not exceed 20% of the peak response. The effect of this variability on the fitting procedure was estimated by using 400 PRPs generated by adding a random noise to each bin with a standard deviation as much as (20%) or larger (30%) than the estimated PRP variability. The fits to PRPs at steady state (prior to the motion transition and after the motion transition) were not significantly affected. For instance, at a noise level of 30%, the peak direction and amplitude averaged across the 400 sample PRPs matched those determined from the fit to the data to within 1%, with a standard deviation of 2.7° and 9% of the mean, respectively. The fits remained good during the motion transition for small deviations such as 45°, but when the angle of deviation was 90° the fits were affected by the added noise due to the reduction in the modulation of the VSD signal.
For instance, for the latter I obtained at 200 ms after the change of the stimulus motion, a standard deviation of 22° and 25% of the mean, for the peak direction and amplitude, respectively.

I also performed the PRP analysis on single condition maps (Figure 12); in that case each PRP was fitted by Equation (1). Note that for the PRP analysis \( \theta \) corresponds to the preferred direction of the pixel, whereas in the original application of Equation (1) it was the stimulus direction. These two interpretations of the same formula are illustrated in Figure 12a and b.

### 2.4.5 Electrophysiology

Single unit activity was recorded extracellurally from V1 with MPI microelectrodes (impedance = 1.0 MΩ, Microprobe Inc, Gaithersburg, MD). Action potentials were recorded from the supragranular layers (<600 μm) and discriminated using Spike2 software (Cambridge Electronic Design, Cambridge, UK). The visual stimulus was the same as the one used in VSDI experiments. However, the direction deviation angle between the two components was held constant, and the direction of the first stimulus was varied instead across 16 angles with 22.5° angular increments (Figure 13b). I displayed the activation relative to the spontaneous activity, which was obtained by subtracting the response to a blank stimulus (population averages are shown in Figure 14a). The reconstructed population response profile was then fitted by Equation
(1) to identify the peak direction and amplitude (Figure 14b and c). In order to be consistent with the VSD experiments, only the modulated component is shown (the untuned component has been removed).
Figure 5: The population response to a constant motion stimulus in ferret primary visual cortex.

VSD images acquired using a visual stimulus with a constant motion direction (135°).

The signal strength becomes stronger over time while the activity pattern remains the same. Each frame of image is the averaged response of 50 msec.
Figure 5: The population response to a constant motion stimulus in ferret primary visual cortex.
Figure 6: Visual stimuli and difference image analysis.

a. A pair of visual stimuli with the same direction deviation angle of 45°. The red arrows represent the moving direction of the corresponding random dot pattern. b. Bright-field image showing the cortical surface and the region of interest (ROI) outlined in green. c. Difference image created by subtracting the cortical images corresponding to the two stimulus conditions. The red and green dots show areas of high activation corresponding to condition 1 and 2, respectively. These locations are conserved in the difference image, but the overall signal to noise level has increased.
Figure 6: Visual stimuli and difference image analysis.
Figure 7: The population response to motion transitions with different direction deviation angles in ferret primary visual cortex.

a. VSD images acquired during a 45° deviation in motion direction. The activity pattern shifts smoothly from one stable pattern to the next without a decrease in signal strength.

b. VSD images acquired during a 90° deviation in motion direction. During the transition the activity pattern decreases in magnitude.

c. VSD images acquired during a 135° deviation in motion direction. The magnitude of the activity pattern also decreases during the transition.
Figure 7: The population response to motion transitions with different direction deviation angles in ferret primary visual cortex.
Figure 8: Population response profile (PRP) analysis and decoding method for the peak direction and amplitude.

a. A single time-frame of the VSD difference image. b. The direction preference map acquired using intrinsic imaging. c. PRP analysis quantifies the mean stimulus-evoked activation of pixels with a given preferred direction. Each component in the difference image leads to a major and a minor peak and trough, respectively, each of which can be fitted by a Gaussian. d. Fit of the PRP to a combination of two upward and two downward Gaussian functions as given in Eq.2 in methods. e. The peak direction and amplitude is determined from the fitting function as the location and height of the highest peak.
Figure 8: Population response profile (PRP) analysis and decoding method for the peak direction and amplitude.
Figure 9: Dynamics of the population response to a constant motion stimulus in ferret primary visual cortex.

a. Population response profile analysis. Vertical dashed lines represent the time at which the motion stimulus was on. b. Dynamics of peak direction. c. Dynamics of peak amplitude. d. Dynamics of direction vector.
Figure 9: Dynamics of the population response to a constant motion stimulus in ferret primary visual cortex.

(a) Population Response Profile (PRP)

(b) Peak Direction (deg)

(c) Peak Amplitude ($\Delta F/F, \times 10^4$)

(d) Dynamic of Direction Vector
Figure 10: Dynamics of the population response to motion transition in ferret primary visual cortex vary as a function of direction deviation angle.

a. Population response profile analysis for direction deviation angles of 45°, 90° and 135°. Vertical dashed lines represent the time at which the motion direction changed. Grey dots represent the decoded peak directions. b. Dynamics of direction vectors. Grey arrows show the direction of time flow.
Figure 10: Dynamics of the population response to motion transition in ferret primary visual cortex vary as a function of direction deviation angle.
Figure 11: Dynamics of the population direction tuning function depend on direction deviation angle.

a. Dynamics of normalized peak direction for different direction deviation angles, as labeled in the graph (n = 3 animals for direction deviation angles of 22.5°, 45°, 67.5°, 90°, 112.5°, 135° and 157.5°; n = 2 animals for direction deviation angle of 180°). b-c. Dynamics of normalized peak amplitude for direction deviation angles ≤ 90° and angles ≥ 112.5°, respectively. d. Rate of transition (°/ms) near the midpoint of change in peak direction (results are mean ± s.e.m.). e-f. Normalized peak amplitude near the midpoint of change in peak direction and at the final steady state, respectively (results are mean ± s.e.m.).
Figure 11: Dynamics of the population direction tuning function depend on direction deviation angle.
Figure 12: Results obtained using PRP analysis on single condition images are similar to that obtained from difference images.

a. PRP analysis for direction deviation angles 45°, 90° and 135°, as labeled in the graph. Vertical dashed lines represent the time at which the motion direction changed. Grey dots represent the peak directions. b-e. Dynamics of peak direction, normalized peak direction, peak amplitude and normalized peak amplitude, respectively.
Figure 12: Results obtained using PRP analysis on single condition images are similar to that obtained from difference images.
Figure 13: Dynamics of the population response to changes of motion direction can be extrapolated from unit recording experiments.

a. The spike discharge PRP for a stimulus moving in a single direction could be inferred from direction tuning curve of single neurons. b. Population response profile for motion transition is computed by varying the direction of the first movement component between 0° and 360°, while maintaining a constant direction deviation with the second component. An example spike discharge PRP so constructed for a direction deviation angle of 90° is shown here.
Figure 13: Dynamics of the population response to changes of motion direction can be extrapolated from unit recording experiments.
Figure 14: The population response constructed from electrophysiological data is consistent with VSDI measurements.

a. Average of constructed PRPs for, from left to right, a direction deviation angle of 45° ($n = 7$ sites), 90° ($n = 7$ sites) and 135° ($n = 4$ sites). b-c. The corresponding dynamics of normalized peak direction and amplitude for direction deviation angles 45°, 90° and 135° (results are mean ± s.e.m.).
Figure 14: The population response constructed from electrophysiological data is consistent with VSDI measurements.
Chapter 3: Mechanism of population response to changes in motion direction: linearity vs non-linearity

3.1 Introduction

The experiments described in Chapter Two have shown that the dynamics of the population response to motion transitions in primary visual cortex vary as a function of direction deviation angle. What are the mechanisms that underlie the dynamics? Many previous studies have shown changes in tuning curves after orientation adaptation or direction adaptation, suggesting that the population response to stimulus transitions involves significant non-linearities (Muller et al., 1999; Dragoi et al., 2000; Felsen et al., 2002; Kohn and Movshon, 2004). However, the dynamics of population response might also be explained by the linear summation of the cortical response elicited by the two stimulus components. Ben-Yishai et al. investigated the process of stimulus transition using computational modeling approaches. They found the population response in V1 during the stimulus transition could follow a static wave pattern (linear) or a travelling wave pattern (nonlinear) depending on the properties of feed forward inputs and recurrent connections (Ben-Yishai et al., 1995). If the recurrent connections are non-orientation selective and the LGN inputs are highly orientation selective, the brain activation follows static wave pattern during the orientation transition. During the
transition, the activity profile that peaks at the initial orientation decays in magnitude while another activity profile peaks at the new orientation grows. In contrast, if the recurrent connections are highly orientation selective and the LGN inputs are non-orientation selective, the brain activation follows a traveling wave pattern. During the transition, the population activity travels across the intermediate orientation space without significant change in its shape.

In this chapter, I construct a simple linear combination model and compare the predicted dynamics of the population response to those that are observed in Chapter two. I also conduct voltage-sensitive dye imaging experiments that allow me to compare the response to the motion transition with that expected from the linear sum of the response to the component directions of motion.

### 3.2 Results

#### 3.2.1 A linear combination model explains certain aspects of the population response to rapid changes in motion direction

What accounts for these systematic departures of the population response from the trajectory of the moving stimulus? At least some of these effects might be explained by a simple linear summation of the gradual reduction in response to the first direction of motion combined with the gradual increase in response to the second direction of motion. Smooth shifts in the peak of the population response with little decline in
magnitude might be expected when the populations of neurons most activated by the two individual stimuli (‘the major peaks’) are partially overlapping. Significant reductions in magnitude accompanied by abrupt jumps in the population peak would be expected when the major peaks for the two stimuli are largely complementary (~90° offset), and the triphasic transition pattern might result when the angular offsets are so great that the major peak associated with the first stimulus partially overlaps the minor peak of the second stimulus. To test this possibility, I have constructed a simple linear combination model in which the cortical response to motion transition was modeled as a weighted sum of responses to the components (Figure 15a). The PRPs of two motion components were obtained from a fit to the VSD data shown in Fig.1 (Figure 15b), while the dynamics of the weighting factors were assumed to be simple linear processes (Figure 15c). The dynamics of population response to motion transitions with different direction deviation angles predicted by the model were shown in Figure 16a-d. I found that the linear combination model was sufficient to account qualitatively for many of the features associated with the dynamics of the population response during the transition. For example, the linear model predicts the smooth progression through intermediate directions for small direction deviations and the triphasic pattern for larger direction deviation angles. It also accounts for the systematic relation between direction deviation angle and the transient reduction in response during the transition. I performed a
sensitivity test for two parameters in the model: direction selectivity and tuning width. Enhancement of direction selectivity or increase of tuning width will shift the dynamics of peak direction towards the smooth progression (S Shape) mode while away from the triphasic pattern mode (Figure 17).

Note, however, that the linear summation model failed to account for the changes in magnitude that follow the motion transition (Figure 11f). The magnitude at the end of the data acquisition period was lowest for the smallest angles in my sample (22.5°, 45°) and reached its highest value for the 112.5° direction deviation angle. These changes are likely to reflect longer lasting adaptation mechanisms that have been the subject of numerous previous studies (Dragoi et al., 2002; Vautin et al., 1977; Priebe and Lisberger, 2002; Carandini et al., 1998).

In my linear model, I assumed that the onset response latency for the second motion component was the same as the offset response latency for the first motion component. Some studies showed that the onset latency is longer than offset latency (Bair et al., 2002). Modification of the weighting factor dynamics based on these studies does not impact the overall pattern of the model predictions. In fact, the key features that appear to account for these population effects are: (1) the non-instantaneous nature of circuit dynamics, (2) the presence of single neuron responses to both the preferred
and anti-preferred directions of motion, and (3) the broad tuning of individual neurons for motion around the preferred and anti-preferred directions.

**3.2.2 Additional nonlinear mechanisms shape the dynamics of population response**

In the previous section, I have shown that a simple linear combination model could explain many features associated with the dynamics of the population response during the transition. However, one might argue that the inputs (Fig. 4b and c) that were fed into the model do not necessarily represent biological conditions. To address this concern, I have conducted VSDI experiments that captured the cortical responses to motion transitions and the corresponding individual motion components. These experiments allowed me to directly compare the response to the change in motion direction with that expected from the linear sum of the response to the component direction of motion (Figure 18). For large deviation angles (135°) the linear sum of the components is a close match for the peak direction and peak amplitude time course. But for smaller deviation angles, the linear sum differed from the transition condition, especially in the magnitude of the response during the transition: the linear sum condition exhibits a prominent reduction in response magnitude that was not evident in the experimental condition (Figure 19a). Linear regression analysis of the linear summation and experimental conditions from 3 experiments (Figure 20) confirmed that
the linear summation of the component responses accurately predicted the dynamics of population response in the experimental conditions prior to the transition (correlation coefficient equals to $0.97 \pm 0.01$, $0.99 \pm 0.01$ and $1.00 \pm 0.01$ for $45^\circ$, $90^\circ$ and $135^\circ$ respectively), and for values taken during the motion transition (100 ms to 300 ms) for the $135^\circ$ direction deviation angle, but not for the $45^\circ$ and $90^\circ$ conditions (correlation coefficient equals to $1.97 \pm 0.05$, $1.26 \pm 0.03$ and $0.98 \pm 0.02$ for $45^\circ$, $90^\circ$ and $135^\circ$ respectively). As shown by the vector plots (Figure 19b), the transition between the initial state and final state in the experimental conditions is smoother compared to the linear summation conditions for the smaller direction deviation angles ($45^\circ$ and $90^\circ$). Thus, while the basic qualities of the population response to motion transitions are consistent with linear summation, additional nonlinear mechanisms shape the dynamics of population response both during and after motion transitions.

### 3.3 Summary

In this chapter, I showed that a linear combination model could explain many aspects of the population response to motion transitions, such as the S-shape pattern and triphasic pattern for the dynamics of peak direction and the reduction of peak amplitude in the middle of motion transition. However, additional nonlinear mechanisms also involved to shape the dynamics of population response. For example, the response amplitude after motion transition is modulated in a systematical fashion that is
consistent with previous adaptation studies. The magnitude of tuning strength for small motion transition, such as 45°, is larger compared to the linear sum condition, which makes the transition process even smoother than what is predicted by linear combination model.

3.4 Materials and methods

3.4.1 Linear combination model

The dynamics of cortical activation was studied by determining the PRP as a function of time \( M_{\exp}(\theta, t) \). To evaluate to what extent the cortical response to a motion transition could be understood in terms of a linear combination of responses to component stimuli, it was compared to the following linear combination model (Figure 15a):

\[
M_{\text{lin}}(\theta, t) = \alpha(t)N_1(\theta) + \beta(t)N_2(\theta) \tag{3}
\]

Here, \( M_{\text{lin}} \) is the model response to the motion transition, \( \theta \) is the preferred direction of the neurons, and \( t \) is time. \( N_1 \) and \( N_2 \) is the steady state PRP corresponding to the direction of the first and second component, respectively. \( \alpha \) and \( \beta \) are the weighting factors for the two motion components. The functions \( N_1 \) and \( N_2 \) were given by the functional form of Equation (2), which was interpreted as the population activity for the stimulus direction in each of two component stimuli (Figure 15b). The parameter
values \((A_0 = 0.039, A_1 = 0.698, A_2 = 0.441\) and \(\sigma = 38.3\) were obtained from a fit to a typical VSDI dataset and \(\phi_1\) was set to the direction of the first and second component for \(N_1\) and \(N_2\), respectively. For the first 50 ms after the motion transition, \(\alpha(t) = 1\) and \(\beta(t) = 0\), whereas during the 500 ms long transition period \(\alpha(t)\) linearly decayed to zero and \(\beta(t)\) linearly increased to one (Figure 15c). After reaching these values \(\alpha(t)\) and \(\beta(t)\) remained constant. To determine the population dynamics, I fitted for each \(t\) value, \(M_{lin}(\theta,t)\) to Equation (2). This yielded the peak direction \((\phi_1)\) and amplitude \((A_1)\) as a function of time (Figure 16).

### 3.4.2 VSDI experiment to test the linearity

The visual stimuli used in the motion transition condition were similar to those described in Chapter Three. Briefly, the visual stimuli started with a 150 ms gray screen presentation followed by a 300 ms flickering dot pattern. Subsequently, two stimulus components were presented with the direction of the second component different by an angle of 45°, 90° and 135°. The duration of the first motion component was reduced to 500 ms in order to shorten the imaging time, while the duration of the second motion component was kept as 1 s. The parameters of the random dot pattern were the same as those given in Chapter Three. To test for linearity, the response was also obtained to two control conditions for which either the first or second motion component was replaced by a flickering dot pattern, respectively.
Figure 15: A linear combination model explains certain aspects of the population response to motion transition.

a. The response to a transition is modelled as a weighted sum of responses to the components.  
b. Example steady state PRP for two motion components with a direction deviation angle of 90° obtained from a fit to the VSD data shown in Figure 1.  
c. Dynamics of the weighting factors for two motion components with a direction deviation angle of 90°. The (red) weight $\alpha$ of the first component decays linearly from a value of 1 before the transition to 0 during a 500 ms interval, whereas the (green) weight $\beta$ of the second component increases from 0 to 1 during that time interval.
Figure 15: A linear combination model explains certain aspects of the population response to motion transition.
Figure 16: Dynamics of population response predicted by the linear combination model.

a. The resulting model PRPs are shown for direction deviation angles 45°, 90° and 135°, as labeled. b. Dynamics of normalized peak direction for different direction deviation angles, as labeled in the graph, obtained from a linear combination model. c-d. Dynamics of the normalized peak amplitude for direction deviation angles ≤ 90° and angles ≥ 112.5°, respectively, obtained from a linear combination model.
Figure 16: Dynamics of population response predicted by the linear combination model.
Figure 17: Sensitivity test for two parameters in the linear combination model.

a. Relationship between direction selectivity and break point. The break point is defined as the direction deviation angle upon which the dynamic of peak direction shifts from S-shape pattern to triphasic pattern. Enhancement of direction selectivity (decrease minor/major peak amplitude ratio) predicts a larger break point. The parameter of neuronal tuning width, Sigma, is set to be 38.3° in this panel. Grey triangle indicates the parameters used in the model shown in Figure 15 and Figure 16 (minor/major peak amplitude ratio = 0.632, Sigma = 38.3°).

b. Relationship between tuning width and break point. Broader tuning width predicts a larger break point. The minor/major peak amplitude ratio is set to be 0.632 in this panel.
Figure 17: Sensitivity test for two parameters in the linear combination model.
Figure 18: A direct test for linearity of the population response.

a. Responses to motion transition with direction deviation angles of 45°, 90° and 135°. b. The predicted responses based on linear superposition of the transition from stimulus component 1 to flickering dot pattern and that from flickering dot pattern to stimulus component 2. c. The difference between the two. Grey dots represent the decoded peak directions.
Figure 18: A direct test for linearity of the population response.
Figure 19: Population responses demonstrate a nonlinearity that depends on direction deviation angles.

a. The corresponding dynamics of peak direction and amplitude for (red) transition conditions and (blue) linear sum conditions. b. Dynamics of direction vectors for transition conditions and linear sum conditions. Grey arrows show the direction of time flow.
Figure 19: Population responses demonstrate a nonlinearity that depends on direction deviation angles.
Figure 20: Evidence for nonlinear dynamics during the transition period.

I show scatter plots of the PRP for the transition condition versus the sum of PRPs corresponding to the motion component 1 to flickering dot pattern and the flickering dot pattern to motion component 2 conditions. I show data from before the transition (−200 ms to 0 ms) in blue and during the transition (100 ms to 300 ms) in red for direction deviation angles 45°, 90° and 135°, as labeled. The linear summation of the component responses accurately predicted the dynamics of population response in the experimental conditions prior to the transition (correlation coefficient equals to 0.97 ± 0.01, 0.99 ± 0.01 and 1.00 ± 0.01 for 45°, 90° and 135° respectively), and for values taken during the motion transition (100 ms to 300 ms) for the 135° offset condition, but not for the 45° and 90° offsets (correlation coefficient equals to 1.97 ± 0.05, 1.26 ± 0.03 and 0.98 ± 0.02 for 45°, 90° and 135° respectively).
Figure 20: Evidence for nonlinear dynamics during the transition period.
Chapter 4: Perceptual distortions in motion trajectory

4.1 Introduction

The question of how prevailing motion stimulus conditions impact perception to a new motion stimulus has been studied within the realm of direction adaptation. Prolonged adaptation to direction stimulus has been shown to cause a direction aftereffect (DAE) (Levinson and Sekuler, 1976; Patterson and Becker, 1996; Phinney, 1997; Schrater and Simoncelli, 1998; Clifford, 2002). For angles up to around 100 degrees between the directions of motion of the adapting and test patterns, the perceived direction of the test pattern tends to be repelled away from the adapting direction. For angles larger than 100 degrees between adapting and test directions, the perceived direction of the test tends to be attracted towards that of the adapter (Schrater and Simoncelli, 1998; Clifford, 2002). However, there are two major differences between the stimuli used in the typical DAE experiments and natural visual stimuli. First, the adapting stimuli in DAE experiments usually lasts for a long time, often for 1 min or longer. Such prolonged adaptation rarely happens under natural viewing conditions. Second, there are often intervals between the adapting stimuli and testing stimuli, which are absent in natural environment. Thus, the DAE effects reflect the perception of test
stimuli on steady state responses rather than the perception of a stimulus that changes its direction of motion per se.

In Chapter Two, I showed that dynamics of the population response to motion transition vary as a function of direction deviation angle. How do these dynamics of population response impact motion perception? I address this question in this chapter. I first predict the distortions of perceived motion trajectories based on the dynamics of population response and then verify my predictions by conducting psychophysical experiments.

4.2 Results

4.2.1 Distortions in perceived motion trajectory accord with the dynamics of the population response

Given the evidence that the neural representation of motion direction departs from the actual direction of stimulus motion, I asked what impact this departure might have on the perceived trajectory of objects that change their direction of motion. I estimated the perceived trajectories for bilinear motion transitions with different deviation angles by assuming (1) the perceived motion direction at any given time point is determined by the dynamic of peak direction obtained from the population response (2) the moving distance within a time frame is a constant (i.e., constant speed is assumed) (Figure 21). For direction deviation angles less than 90° (22.5°, 45° and 67.5°), the perceived motion trajectories predicted by the model were more gradual (smoother)
than the actual stimulus trajectories; the degree of smoothing was greatest for the 22.5° stimulus and least for the 67.5° stimulus. In contrast, for direction deviation angles of 112.5° and 135°, the perceived motion trajectories predicted by the model were more acute (sharper) than the actual stimulus trajectories. No perceptional distortions were predicted for direction deviation angles of 157.5° and 180° (Figure 22).

These predictions were tested in a human psychophysical experiment that measured the perceived trajectory of a moving dot stimulus. The first phase of the dot motion was always along a straight line, followed by a second phase in which the dot assumed one of 9 different trajectories: either a straight line or a curved path on either side of the straight line (Figure 23). The curved trajectories could be convex (i.e., smoother than the line) or concave (sharper than the line). Subjects indicated the perceived trajectory of the second phase of dot motion by choosing between two alternatives: motion trajectories smoother than the line or motion trajectories sharper than the line. Instead of a random dots pattern, a single dot motion was chosen as the visual stimulus because it provided the best comparison to the results with the ferrets; it was critical for the humans to maintain fixation and this was nontrivially easier for a single dot motion display compared to a full motion display. I set the transition point from the first to the second motion component to be 4.9° below and 1° to the right of a
central fixation point so that the change of motion direction happened at the peripheral visual region (5° eccentricity).

The psychometric functions for small direction deviation angles, such as 22.5°, 45° and 67.5°, were shifted leftwards systematically (Figure 24a) as indicated by negative RC50 values (Figure 25a and b), hence the subjects’ perception of the motion trajectories was smoother than the actual stimulus trajectories. In contrast, the psychometric functions for direction deviation angles of 112.5° and 135° were shifted rightwards (Figure 24b) with positive RC50 values (Figure 25a and b), indicating that the subjects’ perception of the motion trajectories was sharper than the actual stimulus trajectories. These observations were further confirmed by examining the subjects’ reports for the bilinear stimulus trajectories. The probability of reporting smoothing trajectory was significantly larger than chance level (50%) for direction deviation angles at 22.5°, 45° and 67.5°, and significantly smaller than chance (50%) for direction deviation angles at 112.5°, 135° (Figure 25c and d).

4.2.2 The perception distortion for motion trajectory could not be explained by positional information

Interestingly, the distortions of motion transition perception depend on eccentricity. The bias gets significantly weaker in fovea visual region (Figure 26a). I hypothesize this effect is related to the position acuity. Ultimately, both positional
information and directional information must be integrated in judgements of motion trajectory. In the foveal visual region, the position acuity is so high that it provides perceived trajectories with high fidelity thus precludes any distortions predicted by the direction perception. In contrast, when eccentricity increases, the position acuity gets worse (Figure 26b and c) and thus the distortion of direction perception becomes more evident.

Stimulus motion has been shown to impact human perception of position (Whitney & Cavanagh, 2000; Whitney, 2002). For example, the initial (Frohlich, 1929) or final position (Freyd & Finke, 1987) of a moving object can appear shifted in the direction of motion. Could the distortions in perceived trajectory shown in the periphery visual region be explained by position perception, even under a low visual acuity? To address this question, I have designed an experiment to reconstruct the motion trajectory solely based on position information (Figure 27). My experimental results demonstrated that the reconstructed motion trajectory based on position information showed no systematic curvature bias. Therefore, position cue information did not contribute to the distortion of the perceived trajectory measured in my experiments.
4.3 Summary

In this chapter, I implemented a simple model to predict perception of motion trajectory based on dynamics of population response to motion transition. For direction deviation angles less than 90° (22.5°, 45° and 67.5°), the perceived motion trajectories were predicted to be more gradual (smoother) than the actual stimulus trajectories. In contrast, for direction deviation angles of 112.5° and 135°, the perceived motion trajectories were predicted to be more acute (sharper) than the actual stimulus trajectories. No perceptional distortions were predicted for direction deviation angles of 157.5° and 180°. These predictions were verified by psychophysical experiments. I also demonstrated the perceptual distortion for motion trajectory could not be explained by position perception.

4.4 Materials and methods

4.4.1 Experiment 1: Measure the distortion of motion transition perception.

Subjects. Subjects were four students (3 male and 1 female; average age was 27.8 years; standard deviation was 2.5 years) at Duke University, all with normal or corrected-to-normal vision. One subject was the first author (WW) and the remaining three subjects were naïve observers. All experimental procedures were approved by the Duke University Institutional Review Board.
Apparatus. Visual stimuli were presented on a PowerMac G4 and a GDMF520 CRT (Sony, refresh rate 120 Hz), gamma-corrected using ColorVision Spyder (Pantone, Carlstadt, NJ). Stimulation procedures were designed using Matlab (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The experiments were conducted in a dimly lit room. The subjects were seated 100 cm from the monitor, although they were permitted slight movement.

Stimuli. The visual stimulus was a white dot (0.1° diameter, 100% contrast) presented on a black background. The dot moved at 10°/s in two distinct motion components. In the first motion component, the dot moved from left to right along a straight line for 0.3s. In the second motion component, the dot moved towards a new direction along either a straight line or along a curve slightly bent on either side of an imaginary straight line for 0.3s. The transition from the first to the second motion component occurred 4.9° below and 1° to the right of a central fixation point so that the change of motion direction happened at the peripheral visual region (5° eccentricity). There were 8 different direction deviation angles in the experiment, ranging from 22.5° to 180° with 22.5° angular increments. I also varied stimuli eccentricity systematically (1°, 5° and 10°) in order to test the relationship between eccentricity and the distortion of motion transition.
perception. The direction deviation angle was set to be 45° in these experiments. The stimulus differences between this psychophysics component (a single dot on a uniform background) and the physiology component (a random dot pattern) were introduced for several reasons, with the most critical being practical – whereas the ferrets were anesthetized and paralyzed, the human were awake and free to make eye movements. Pilot studies determined that subjects were better able to maintain fixation with a single moving dot than with a full fields of motion.

Procedure. The experimental task followed a two-alternative forced choice (TAFC) paradigm (Green and Swets, 1966). Observers maintained fixation on the central point and observed the presentation of a moving dot, after which they indicated the perceived dot motion trajectory by choosing between two alternatives: a motion trajectory smoother than a bilinear line and a motion trajectory sharper than a bilinear line. To test how the perceived motion deviated from the veridical straight line trajectory (for instance, making an angle of 45° with the horizontal), I constructed comparison trajectories characterized in terms of the parameter RC (relative curvature, Figure 23). For RC=0, the trajectory is a straight line; for RC<0, it is convex, with a direction of motion just after the transition larger than 45°; for RC>0, it is concave and the direction of motion just after the transition is less than 45°. The trajectory is described by
(x(t), y(t)) (t is time), which can be characterized by two differential equations:

\[
\frac{dx}{dt} = v_x(t) \quad \text{and} \quad \frac{dy}{dt} = v_y(t),
\]

where \(v_x\) and \(v_y\) denote the velocity components of the dot.

This can be simplified by eliminating time \(t\) in favor of \(x\), yielding \(\frac{dy}{dx} = \frac{v_y(x)}{v_x(x)}\). For \(RC > 0\), the following choice leads to curves satisfying my requirements: \(\frac{dy}{dx} = \frac{100(x - \hat{y})}{RC}\), where \(RC\) is a parameter and the reason for the hat on \(y\) is given below. This leads to a trajectory \((x, y)\) that goes from \((0, 0)\) to \((1, \hat{y}(1))\). When I define \(y(x) = \hat{y}(x)/\hat{y}(1)\), the trajectory ends at \((1, 1)\) as desired. The explicit form is then as follows:

\[
y(x) = \frac{-RC + 100x + RC \exp(-100x/RC)}{-RC + 100 + RC \exp(-100/RC)}.
\]

For \(RC < 0\), I exchanged the \(y\) and \(x\) coordinates to obtain:

\[
x(y) = \frac{RC + 100y - RC \exp(100y/RC)}{RC + 100 - RC \exp(100/RC)}.
\]

Subjects received 10 minutes of training before the data collection for each block. During the training, I set the RC value to be -20, -10, 10 and 20. These parameters generated obvious smoothing trajectory and sharpening trajectory, allowing the subjects to understand the experimental paradigm. Feedback was provided by the experimenter during the training period if necessary or if questions were raised. During the data collection, 9 curvatures were assigned for the trajectories of the second motion.
component in each block (1 straight line and 4 curvatures on either side, RC value was set to be -8, -6, -4, -2, 0, 2, 4, 6, 8). The subjects were asked to judge the trajectory solely based on their perception. No feedback was given during the data collection. The task was presented in multiple blocks (8 different direction deviations, ranging from 22.5° to 180° with 22.5° angular increments). To minimize subject bias, I randomized the number (from 40 to 60) and sequence of different RC presentation in each block. To reduce chances of fatigue, rest periods were included within each block and only a limited numbers of blocks were performed on a given day.

Data analysis. The psychometric functions relating the probability P to the convexity/concavity parameter RC were fitted to a Boltzmann sigmoidal function using Origin (OriginLab, Northampton, MA):

\[ P(RC) = 1 - \frac{1}{1 + \exp\left(\frac{(RC - RC_{50})}{\sigma_{RC}}\right)} \]  

(4)

Here, the parameters are the RC value for which the probability is 50%, RC_{50}, and the steepness \(\sigma_{RC}\). Student t test was used to determine the significance level (* \(p<0.05\), ** \(p<0.01\), *** \(p<0.001\)).

4.4.2 Experiment 2: Measure the noise of position judgment at different eccentricities and reconstruct motion trajectory using positional information.

Subjects. Same as Experiment 1.
Apparatus. Same as Experiment 1.

Stimuli. The visual stimuli were identical to Experiment 1 except where noted here. In this experiment, the dot moved rightwards along a straight line for 0.3 s and then changed its direction of motion for 45° or 135°. After the motion transition, the dot traveled a certain distance and disappeared. For each direction deviation angle, the dot could disappear from five different positions (the position was randomly chosen each trial and they are depicted by the colored dots in Figure 27a). The eccentricity was tested at 1°, 5° and 10°.

Procedure. Observers maintained fixation on the central point and observed the presentation of a moving dot, after which they were asked to indicate the position where the dot disappeared by clicking on the position with a computer mouse. Subjects were allowed to break the fixation while clicking the mouse in order to minimize motion errors. To prevent the subject from memorizing the positions, I jittered the starting point of the moving dot and aligned the data by the starting point for each trial. Subjects were informed that the positions where the dot disappeared were randomized, so that they would need to make their mouseclick solely based on their perception in the current trial. Subjects received 2 minutes of training before data collection and no feedback was
given during the training. There were 600 trials and for the whole task, the direction of
the deviation angle (45° or 135°) and the position where the dot disappeared were
randomly determined. The task was broken into 5 blocks and rest periods were included
within each block.

Data analysis. I computed the average point of the mouseclicks averaged across trials. To
measure the noise of position judgment, I aligned the mouseclicks for all the positions to
their corresponding central mass and estimated the radius of noise spread (shown by
Figure 26b, the circles covered 80% of the mouseclicks). To reconstruct the motion
trajectory, I estimated the radius of the noise spread for each position individually and
drew circles with respect to the corresponding central mass (shown by Figure 27b).
Figure 21: A simple model to predict perceived trajectory.

(top) The perceived trajectory for the direction deviation angle of 45° is predicted to be smoother than the actual stimulus trajectory while (bottom) the perceived trajectory for the direction deviation angle of 135° is predicted to be sharper than the actual stimulus trajectory. From left to right, I show the actual stimulus, the simulated dynamics of peak direction and the trajectory reconstructed based on the simulated peak direction.
Figure 21: A simple model to predict perceived trajectory.
Figure 22: The perceived trajectory predicted by VSD data.

Grey icons on the right corners of each panel represent the veridical stimulus trajectory. For each time frame (2.92 msec), the motion trajectory advances an arbitrary unit in 2-D space.
Figure 22: The perceived trajectory predicted by VSD data.
Figure 23: Experimental paradigm to measure the distortion of human perception of changes in stimulus motion.

Please refer to the method section for details. Briefly, the visual stimulus was a moving dot with two motion components. In the first motion component, the dot moved from left to right along a straight line for 0.5s. In the second motion component, the dot moved towards a new direction along either a straight line or a curve slightly bent on either side of the straight line with certain amount of curvature for 0.5s. Observers maintained fixation on the central point and observed the presentation of a moving dot, after which they indicated the perceived dot motion trajectory by choosing between two alternatives: a motion trajectory smoother than a bilinear line and a motion trajectory sharper than a bilinear line.
Figure 23: Experimental paradigm to measure the distortion of human perception of changes in stimulus motion.
Figure 24: Experimental results from an example subject.

a. Smoothing effects for direction deviations smaller than 90°. Black line represents the information of the visual stimuli (ideal observer’s experimental results) b. Sharpening effects for direction deviations of 112.5° and 135°.
Figure 24: Experimental results from an example subject.
Figure 25: Summary of the data from all subjects (n=4).

a. RC₅₀ value for different direction deviation angles. b. Mean RC₅₀ value for different direction deviation angles (results are mean ± s.e.m.). c. Probability to choose a smoothing trajectory when RC = 0 as a function of direction deviation angles for individual subjects d. the corresponding mean ± s.e.m.
Figure 25: Summary of the data from all subjects (n=4).
Figure 26: The distortion of motion transition perception and perception of positional information at different eccentricities.

a. The distortion of motion transition perception gets larger as eccentricity increases. b. Position acuity decays as eccentricity increases. Please refer to Supplementary method for detailed experimental design (Psychophysics, Experiment 2). c. The radius of noise spread at different eccentricities.
Figure 26: The distortion of motion transition perception and perception of positional information at different eccentricities.
Figure 27: Reconstructed motion trajectories based on positional information exhibit no curvature bias that is consistent with the distortion of motion transition perception (data acquired at 5° eccentricity).

a. Experimental paradigm to reconstruct motion trajectory based on position perception. In this experiment, a dot moved rightwards along a straight line for 0.3 s and then changed its direction of motion for 45° or 135°. After the motion transition, the dot traveled a certain distance and disappeared. For each direction deviation angle, the dot could disappear from five different positions (depicted by the five colored dots). Subjects maintained fixation with 5° eccentricity and observed the presentation of a moving dot, after which they were asked to indicate the position where the dot disappeared by clicking on the position with a computer mouse. The dashed lines represent the reconstructed motion trajectories that would be consistent with the distortion of motion perception I observed. b. Mouseclicks for two direction deviation angles (45° and 135°) in two subjects. Large filled colored dots represent the actual positions where the moving dot disappears. Empty colored dots represent the positions the subjects chose. c. Reconstructed motion trajectory for two direction deviation angles (45° and 135°) in two subjects. Filled colored dots represent the actual positions where the moving dot disappears. Colored circles cover 80% of the mouseclicks for each corresponding position. Note the perceived dot positions are shifted in the direction of motion for both 45° and 135°. However, the reconstructed motion trajectories show no sign of curvature bias that are consistent with the distortion of motion transition perception I observed.
Figure 27: Reconstructed motion trajectories based on positional information exhibit no curvature bias that is consistent with the distortion of motion transition perception (data acquired at 5° eccentricity).

**a**

Figure 27: Reconstructed motion trajectories based on positional information exhibit no curvature bias that is consistent with the distortion of motion transition perception (data acquired at 5° eccentricity).

**b**

**c**

Distance in 2D space (deg)
Chapter 5: Discussion

The results presented in my thesis provide the first direct assessment of the population response of V1 neurons to changes in direction of motion. I showed that when a stimulus changes direction abruptly, the population response deviates significantly from the direction of stimulus motion. These changes can largely be explained by a simple linear combination model. The dynamics of population response are consistent with perceptual distortions that accompany instantaneous changes in motion direction. In this chapter, I first discuss the relationship between these results and earlier studies. Then I summarize the key components that account for the distortions in direction perception and generalize my results to other visual attributes and other sensory systems. Finally, I point out some limitations of the current study and discuss future directions.

5.1 Relationship to earlier studies

5.1.1 Dynamics of population response to motion transition

The question of how prevailing motion stimuli the impact the response to a new stimulus has traditionally been studied using unit recordings in V1 and MT within an adaptation experimental paradigm.
In primary visual cortex, motion adaptation has been shown to change the responsiveness of neurons systematically. Adaptation with drifting gratings in the preferred direction significantly suppressed the neuronal response (Vautin and Berkley, 1977; von der Heydet et al., 1978; Hammond et al., 1985). Drifting gratings in directions nearby the preferred directions reduced the neuronal responsiveness to a lesser extent (Hammond et al., 1989) while drifting gratings in the null directions had no effect or slightly enhanced neuronal responsiveness (von der Heydt et al., 1978; Marlin et al., 1988; Giaschi et al., 1993). Kohn and Movshon suggested that motion adaptation in primary visual cortex does not shift the peak positions of direction tuning curves (Kohn and Movshon, 2004). However, as they pointed out in the paper, their sample size of V1 neurons was relatively small (40 neurons) and thus “could easily have failed to detect a small shift at the population level” (Kohn and Movshon, 2004).

In area MT, motion adaptation modulates the responsiveness of neurons in a very similar fashion to V1. Responsiveness of MT neurons was reduced by adaptation to motion in the preferred direction and enhanced by prolonged adaptation in the opposite direction (Petersen et al., 1985; Priebe et al., 2002). However, motion adaptation causes more profound consequences for MT neurons besides gain modulation. Kohn and Movshon found that adaptation to a prolonged drifting grating moving in near-
preferred direction caused an attractive shift of the tuning curves (Kohn and Movshon, 2004). In addition, the direction tuning after adaptation became significantly narrower.

Although a wealth of information has been gathered about the influence of motion adaptation on neuronal response, it is difficult to use this information to infer the dynamics of population response to motion transition for several reasons. First, inferring how changes in single unit tuning curves impact the population response is not straightforward. Single unit tuning curves undergo changes in multiple parameters including peak position, tuning width and response amplitude and each of these parameters would be expected to have an impact on the population response profile, often in different directions, leaving the population response profile undetermined. Second, the non-instantaneous nature of circuit dynamics alone might cause changes in population response during the transition even without any alteration of neuronal tuning curves. Thus, I have adopted an alternative approach, namely the voltage sensitive dye imaging technique, to investigate the population response directly. My experimental results show that the population response deviates significantly from the direction of stimulus motion and does so in a direction deviation angle dependent fashion.

One of the striking aspects of my results is that the dynamic behaviour of the peak of the population response—specifically, the shifts in the peak to different motion
directions following changes in stimulus direction—can largely be accounted for on the basis of the linear sum of the response to the component directions. The fact that the linear sum dominates the behaviour of the peak direction is surprising given the evidence from single unit recordings indicating that short stimulus presentations can induce adaptive ‘attractive shifts’ in the tuning curves of single units which might be expected to impact the peak of the population response in a non-linear fashion. I have not assessed the direction tuning curves of individual neurons using my stimulus configuration; I note, however, the impact of the non-instantaneous nature of circuit dynamics could not be revealed by examining the direction tuning curves. It is also the case that many (most) studies of adaptation employ paradigms in which the adapting stimulus is presented for a much greater period of time, and non-linear effects on the peak of the population response might be more evident under these conditions. Nevertheless, my results indicate that for rapid changes in direction that are a common occurrence in natural vision, the behaviour of the peak direction of the population response is well accounted for by a linear combination model. Recent studies using VSD imaging to examine the population response to rapid shifts in grating orientation have also found that the peak of the population response is well predicted by the linear sum of the response to the component stimuli (Benucci et al., 2006).
In contrast to the linear behaviour of the peak direction of the population response, the peak amplitude of the population response exhibited significant departures from a linear sum. In particular, the peak amplitude during the motion transition for small angular offsets was significantly greater than that predicted from the component responses (Figure 18). In addition, the peak amplitude of the population response following the motion transition could be less than or greater than the initial response, and this varied depending on the direction deviation angle (Figure 11f). The transient non-linear enhancement for small angular deviations during the transition has no clear counterpart in single unit recordings, but the longer lasting changes in peak amplitude following the motion transition are consistent with adaptation-induced alterations in the responses of single units following changes in stimulus grating orientation (Vautin et al., 1977; Priebe et al., 2002; Carandini et al., 1998). Changes in stimulus orientation are accompanied by a suppression of neuronal response to the units preferred orientation, which is greatest for small angular offsets and is replaced by facilitation at 90 degree offsets, matching the effects that are seen in the population response (Dragoi et al., 2002; Carandini et al., 1998). How these transient and longer lasting changes in the magnitude of the population responses are reflected in perception remains unclear, although the longer lasting changes are likely to account for the
stimulus specific reduction (and enhancement) in contrast sensitivity that accompanies adaptation of a grating stimulus (Dragoi et al., 2002; Clifford et al., 2001).

5.1.2 Distortions of motion direction perception induced by stimulus context

The impact of stimulus context on motion direction perception has been extensively studied. Prolonged exposure to a unidirectional moving pattern alters the perceived direction of subsequent motion (Levinson and Sekuler, 1976; Patterson and Becker, 1996; Phinney, 1997; Schrater and Simoncelli, 1998; Clifford, 2002), this phenomena is referred as direction aftereffect (DAE). For angles up to around 100 degrees between the directions of motion of the adapting and test patterns, the perceived direction of the test pattern tends to be repelled away from the adapting direction. For angles larger than 100 degrees between adapting and test directions, the perceived direction of the test tends to be attracted towards that of the adapter (Schrater and Simoncelli, 1998; Clifford, 2002).

In my thesis study, I find distortions in direction perception induced by motion transitions. My analysis of the perception of single dots reveals that observers’ perceptions of instantaneous changes in motion direction exhibit smoothing and sharpening distortions that vary with the angle of deviation in a fashion that accords with the behaviour of the population response, whose peak directions show significant
departures from the actual direction of stimulus motion. However, the perceptual distortions that I observed are very different from DAE. For small direction deviation angle, the perceived direction during the motion transition in my study lies between the initial direction and the final direction; while it is repulsively shifted (larger than the final direction) in DAE. For large direction deviation angle, the perceived direction during the motion transition overshoots for a brief period (larger than the final direction) before it settles down at the final direction; while it is attractively shifted (smaller than the final direction) in DAE. The discrepancy between my observations and DAE could be explained by the difference in the experimental paradigm. Compared to the motion transition stimuli that I used in my experiments, the adapting stimuli in DAE experiments usually last for a much longer duration, such as 1 minute (Kohn, 2007; Clifford, 2002). Moreover, there are often intervals between the adapting stimuli and testing stimuli in DAE experiments. Thus, the DAE reflects a long-lasting impact of motion adaption on the perception of test stimuli in steady state, while the perceptual distortions that I reported reflect the “real time” perception for motion transition per se.

There are a few studies that have investigated motion transition using experimental paradigms similar to mine. Several studies examined the reaction time that is required to detect a motion direction change (Dzhafarov et al., 1993; Hohnsbein and Mateeff, 1998; Mateeff et al., 1999; Genova et al., 2000; Mateeff et al., 2005). For example,
Hohnsbein and Mateeff found that the reaction time to change in direction of visual motion decreases as the direction deviation angle increases (Hohnsbein and Mateeff, 1998). These results are consistent with the dynamics of population response revealed in my experiments. I have shown that the rate of the transition for the peak of the population response increases when the direction deviation angle gets larger (Figure 11). Thus, naturally, the latency to reach a detection threshold of change in motion direction will decrease as the direction deviation angle increases. There are also several studies that examined the perceived trajectories during the motion transition (Tripathy and Barrett, 2003; Tripathy and Barrett, 2004; Tripathy and Barrett, 2006). Tripathy and Barret reported qualitatively that the perceived shape of the deviating trajectory was very different from the bilinear trajectory that was actually presented: the perceived trajectories tend to be temporally continuous and spatially smooth (Tripathy and Barrett, 2003). The distortions in the perceived trajectories persist even when eye movements are eliminated (Tripathy and Barrett, 2006). Moreover, the distortions were more apparent when the number of distractors was increased (Tripathy and Barrett, 2004). The direction deviation angle used in Tripathy and Barrett’s experiments were always less than 90 degree, thus the smooth trajectory that they reported is consistent with my observations. Their findings about influence of distractors also support my hypothesis about the interaction between positional signal and directional signal. Ultimately, the
perceived motion trajectory is a product of the interaction between positional information and directional information. The distortions of motion trajectory are mainly contributed by the directional information due to the departure of the population response from the actual stimulus. The directional information, on the other hand, comes in from a separate channel. When the acuity of positional information is high, the position information dominates the perception and thus effectively prevents the distortions brought by the directional information channel. In contrast, when the acuity of positional information is low, the distortions coming from the directional information channel leaks through and thus dominates the perception. The above hypothesis is supported by my experiments that measure the perceptual distortions at different eccentricities. The influence of distracters reported by Tripathy and Barrett provides another piece of evidence supporting my hypothesis. When there are more distractors in the task, the position acuity gets worse and then the distortions will thus become more apparent.

A number of studies have shown that motion can impact human perception of position (Whitney & Cavanagh, 2000; Whitney, 2002). For example, the initial (Frohlich, 1929) or final position (Freyd & Finke, 1987) of a moving object can appear shifted in the direction of motion. Could the distortions in perceived trajectory be explained by position perception that is altered by the motion experience rather than the directional
information itself? I think this is unlikely to be the case, because the reconstructed motion trajectory based on positional information showed no systematic curvature bias, although the perceived dots positions were indeed shifted along the direction of motion (Figure 27).

To summarize, I find that observers’ perceptions of instantaneous changes in motion direction exhibit smoothing and sharpening distortions that vary with the angle of deviation in a fashion that accords with the behaviour of the population response. The smoothing distortion for small angular changes has been noted in a previous study of dot motion (Tripathy and Barrett, 2003; Tripathy and Barrett, 2004; Tripathy and Barrett, 2006), but this is the first study to report a systematic relation between smoothing and deviation angle and the inversion of the effects for large angular offsets. The attribution of these misperceptions in trajectory to the dynamics of the population response of V1 direction selective neurons is strengthened by the fact that they are not predictable from the observers’ judgement of stimulus position along the trajectory (Figure 27). Ultimately, both positional information and directional information must be integrated in judgements of motion trajectory; under the conditions of these experiments, the weighting of directional information appears to exceed that of the positional information.
5.2 The combination of the cortical dynamics and population coding mechanisms places constraints on stimulus representation

5.2.1 Key components that accounts for the distortions in motion direction representation

I have shown that during motion transition, the population response of primary visual cortex deviates significantly from the direction of stimulus motion. What factors contribute to these deviations? The nonlinear changes in neuronal tuning curves do not play a major role here because the deviations are well predicted by a simple combination model. Instead, the three factors that appear to account for these population effects are:

(1) The non-instantaneous nature of circuit dynamics. The non-instantaneous nature of circuit dynamics provides a time window in which the population responses activated by the prevailing stimulus and the new stimulus coexists.

(2) The presence of single neuron responses to both the preferred and anti-preferred directions of motion. The double-peak feature of the direction tuning curve accounts for the triphasic pattern that is found for the dynamics of peak direction with a large direction deviation angle. During the transition, the major peak of the population response elicited by the prevailing motion stimuli interacts with the minor peak of the population response elicited by the new stimuli (Figure 16). Thus, the peak direction follows the trend of the minor peak of the new stimuli until the major peak of the new stimuli becomes dominant, exhibiting seemingly counterintuitive triphasic pattern.
The broad tuning of individual neurons for motion around the preferred and anti-preferred directions. The tuning width accounts for the smooth progression pattern that is found for the dynamics of peak direction with a small direction deviation angle. During the transition, the major peak of the population elicited by the prevailing motion stimuli now interacts with the major peak of the population response elicited by the new stimuli (Figure 16). Thus, the peak direction follows the trend of the major peak of the new stimuli, sweeping across the direction space between the initial direction and the final direction.

A bell shape tuning curve is a basic feature of the population coding strategy. There are many advantages with bell shape functions as introduced in Chapter 1. For example, it is robust. Damage of a single neuron will not have a catastrophic impact on the encoded representation. The overlap among the tuning curves also allows precise encoding of values that fall between the peaks of two adjacent tuning curves. Moreover, a bell shape tuning curve provides a set of basis functions that can be combined to approximate a wide variety of nonlinear mappings. However, as shown previously, the population coding mechanism does bring a side effect when combined with cortical dynamics, namely it places constraints on the accuracy with which abrupt changes in direction of motion can be represented by cortical circuits.
5.2.2 Interaction between population coding and cortical dynamics in other visual attributes

I have demonstrated that the combination of the cortical dynamics and population coding mechanisms places constraints on motion direction representation. Could this finding be generalized? In this and the next section, I discuss the interaction between population coding and cortical dynamics in other visual attributes and other sensory modalities respectively.

**Orientation.** Transition of orientation stimulus causes “apparent rotation”. When two perspective views of an object with different orientations are repeatedly shown, the observer will experience the object rotating from one view to the other, such that intermediate views are subjectively experienced (e.g., Shepard & Judd, 1976). This effect is reminiscent of the smoothing effect of the perceived direction during motion transition. Since orientation is encoding in a very similar fashion as direction, following the same logic in my thesis study, the apparent rotation effects could be explained by the overlap of the population response elicited by the two orientation stimuli during the transition. Indeed, Benucci et al. have examined the population response to rapid shifts in grating orientation using VSDI (Benucci et al., 2006). They found that the peak orientation of the population response during the transition swept through the intermediate orientation space between the initial orientation and the final orientation. They also demonstrated that the cortical response pattern is well predicted by the linear
sum of the response to the component stimuli. The triphasic pattern did not show up in the orientation transition because orientation tuning curves are always a single peak Gauss function.

**Position.** Position transitions also generate perceptual distortions. For instance, a stationary square briefly preceding a long stationary bar presentation elicits the so-called line-motion illusion. Subjects perceive the bar drawn from the side of the square (Wertheimer, 1912; Kenkel, 1913). Could this illusion be explained by the combination of the cortical dynamics and population coding? Position is encoded in visual cortex in the form of retinotopic map. Adjacent neurons in visual cortex have receptive fields that include slightly different, but overlapping portions of the visual field. The position tuning width might provide the explanation for the perceptual distortions in position transition. This hypothesis is supported by Jancke et al., who captured the population response elicited by line-motion stimulus using VSDI (Jancke et al., 2004). They found that the line-motion stimuli induced the dynamic activity pattern resembling that evoked by fast movement stimuli. This response pattern was partially explained by the linear summation of the activity profile elicited by the two individual stimuli. Moreover, when there was an interval of 350 ms between the square and bar, no line-motion effect was perceived and the brain activity pattern no longer resembled that evoked by movement stimuli, suggesting that a time window in which the population responses
activated by the prevailing stimulus and the new stimulus coexist is required to generate the line-motion effect.

**Speed.** Schlack et al., have recently found that speed transitions can alter the perception of speed (Schlack et al., 2008). They measured the perceived speed for a dot pattern moving at 24°/s for 500 ms preceded by several stimuli that last for 1 sec with different moving speed: 1°/s, 12°/s, 24°/s, 36°/s and 48°/s. They found the perceived speed for the test stimulus is positively correlated with the speed of the preceding stimuli. A preceding stimulus with a higher speed leads to a higher perceived speed for the test stimulus. Schlack et al. tried to explain these results by changes of speed tuning curves after speed adaptation (Schlack et al., 2007; Schlack et al., 2008). However, it is possible that their experimental results could be simply explained by the combination of cortical dynamics and the population coding of speed. Speed is encoded in MT by speed tuned neurons. Similar to orientation and direction tuning curves, speed tuning curves generally have a broad tuning width. During speed transitions, the cortical response is an interaction between the population responses elicited by the two stimuli with different speeds, which is likely to resemble the population response induced by a stimulus with an intermediate speed. Theoretically, an imaging experiment that examines the dynamics of population response during the speed transition would test my hypothesis directly. VSDI might not be the ideal approach here because it
requires a map of speed preference due to the limit of spatial resolution. Unfortunately, the existence of speed map is still under debate.

5.2.3 Interaction between population coding and cortical dynamics in other sensory modalities

**Somatosensory system.** Transition of somatosensory stimuli could generate tactile illusions. The most famous example is the cutaneous rabbit illusion, in which a sequence of three or more taps to two skin sites evokes the perception of an object hopping along the skin from the first site to the second, landing in the process on intervening skin that was never touched. The illusion was first described by Geldard and Sherrick (Geldard & Sherrick, 1972). Recently, Blankenburg et al. examined brain activity in human somatosensory cortex associate to cutaneous rabbit illusion using fMRI. They found the illusory tap sequence activated contralateral primary somatosensory cortex, at a somatotopic location corresponding to the filled-in illusory perception on the forearm (Blankenburg et al., 2006). Moreover, the amplitude of this somatosensory activation was comparable to that for veridical stimulation including the intervening position on the arm. Due to the low temporal resolution of fMRI, Blankenburg et al.’s study could not test the hypothesis that the filled-in activities can be explained by the combination of the cortical dynamics and the population coding of somatosensory system. However, this hypothesis is likely to be true given the large
receptive field size in the forearm region. Again, animal studies using VSDI could
address this question directly.

**Auditory system.** Transition of auditory stimuli with different frequencies has
been extensively studied (Carlyon, 2004). If a tone sequence, consisting of two tones with
frequencies A and B, is presented in a pattern of repeating triplets, the sound perception
will be different depending on the frequency difference between A and B. When the
frequency difference is small (<10%), listeners hear a galloping rhythm, corresponding to
the repeating triplets. When the frequency difference is large, however, the alternating
sequence perceptually splits into two parallel auditory streams, one with a frequency
“A”, and the other with a frequency “B” (Miller and Heise, 1950; Bregman and
Campbell, 1971; Van Noorden, 1975; Anstis and Saida, 1985). The perceptual
organization of sequential sound components is referred to as “auditory stream
segregation”, which is an important function of the auditory system, because we often
need to track one sound source (e.g., one speaker) in a background of competing sounds.
The neurophysiological basis of auditory stream segregation is still unknown. Since
frequency is considered to be encoded by the tonotopic maps in the auditory system, a
population response model has been proposed to explain auditory stream segregation
which depends on the frequency difference (Fishman et al., 2001; Carlyon, 2004). When
the frequency difference between A and B is small, the population response patterns
activated by A and B are only slightly separated, thus the cortical activities during the transition resemble both of them, generating a coherent perception (galloping rhythm) for the sound sequence. While when the frequency difference between A and B is large, there is virtually no overlap between in the population response generated by the tones, which might provide a neural basis for the effects of frequency separation on streaming. If the above hypothesis is true, listeners should hear a illusory tone with an intermediate frequency during the tone transition when the frequency difference between A and B is small. This experiment has not yet been done presumably due to technical difficulty to quantitatively measure the perceived frequency during the short transition period.

**Olfactory system and Gustatory system.** From the existing literatures, I didn’t find many interesting perceptual distortions generated by the transition of olfactory or gustatory stimuli. This might because the stimulus features that are encoded by olfactory system and gustatory system are better described by a discrete distribution rather than a continuous distribution, which is different from other stimuli features discussed previously. For instance, unlike orientation/direction/speed/sound frequency, there are no continuously distributed tastes between two tastes, such as salty and sweet. Thus, even though the population response elicited by both stimuli interact with each
other during the stimulus transition, the resulting cortical activities are not labeled by
the olfactory or gustatory system as a new smell or taste respectively.

To summarize, I have shown the combination of the cortical dynamics and
population coding mechanisms places constraints on motion direction representation.
This finding could be generalized to many other visual attributes and other sensory
modalities. The perceptual distortions might be beneficial, for example, the smoothing of
small direction deviations and the sharpening of larger deviations could serve to
enhance the discrimination of continuous and discontinuous motion trajectories. But
even if these perceptual distortions are not beneficial, their existence must represent an
acceptable tradeoff that balances the need for accuracy with the innumerable advantages
that are afforded by distributed coding mechanisms (Pouget et al., 2000; Averbeck et al.,
2006; Pouget and Latham, 2003; Knill and Pouget, 2004; Dayan and Abbott, 2001; Rieke
et al., 1997).

5.3 Limitations and future directions

In this section, I consider some general limitations of the present study as well as
possible future directions.

5.3.1 Sources of VSD signals

As I introduced in Chapter 1, VSDI is an innovative method to measure the
cortical population response directly. However, the exact sources of the VSD signals are
still under debate. VSDs can bind to various neuronal compartments — including the dendrites, axons and cell bodies (Grinvald and Hildesheim, 2004). It can also bind to glial membranes and reflect slow changes in the membrane potential of activated glia (Konnerth and Orkand, 1986; Lev-Ram and Grinvald, 1986). Thus, in the VSDI data, a single pixel contains signals that come from all the above sources rather than a single cell. Since the membrane areas of dendrites and axons are much larger than that of cell bodies, it is believed that most of the VSD signal originates from cortical dendrites and axons. Moreover, because the cortical dendrites are often far more spatially confined than the axons, the VSD signals that show spatial patterns (such as those in my thesis study) mainly reflects dendritic activity. This dendritic origin of the signal can affect the spatial resolution of VSDI, because the dendrites of cells spread in 3D space. Nevertheless, it has been shown by many studies that VSD signals are highly correlated with changes in membrane potential measured by intracellular recordings (Sterkin et al., 1998; Grinvald et al., 1999; Petersen et al., 2003). This similarity also indicates that the contribution of slow glial depolarization to the VSDI signal is minimal. In my thesis study, I have applied a differential imaging analysis approach, which helps to improve the spatial resolution. More importantly, I also did extracellular recording experiments to verify the VSD data. The dynamics of the spike discharge population response
constructed from unit recording data are consistent with VSDI measurements, which alleviates the concern about the sources of VSD signals.

5.3.2 Contribution of different neurons to the population response

In my thesis study, I used a population response profile (PRP) analysis method to quantify the imaging data (Figure 8). This approach treats every pixel in the data set equally. However, this might not be the most appropriate way to analyze the data. Previous studies on orientation adaptation effects have indicated that orientation plasticity shows some map region specificity (Dragoi et al., 2001). Neurons located at and near pinwheel centers show larger orientation plasticity (Dragoi et al., 2001), probably because they receive broader inputs from nearby neurons (Marino et al., 2005). One question arising from this is whether direction plasticity shares the same feature or not. The direction map in primary visual cortex consists of regions within which direction preference changes in a slow, continuous fashion. These regions are separated by winding boundaries (fractures) across which direction preference shifts abruptly (Weliky et al., 1996). Recent evidence has shown that neurons near the fractures have lower direction selectivity strength compared to neurons in the direction domains (Ohki et al., 2005). It is possible that neurons near the fractures receive broader inputs from other directional cells, which might endow them with more adaptation-induced direction plasticity. If this is true, these neurons might behave differently during motion
transitions. To test this hypothesis, I could perform data analysis for the population responses of neurons near the direction fractures and inside the direction domains separately and compare the results. If these two groups of neurons do respond differently during the motion transitions, then how they contribute to motion perception respectively? Since the accuracy of direction information is much higher for the neurons in the direction domains, it seems like those neurons should play a more important role in perception. However, one can also argue for exactly the opposite: the cortex might be sensitive to changes of tuning curve properties, thus the neurons near the fractures should be assigned a larger weight. To address this question, I could use different combinations of the weighting factors to generate the population response profile and then compare their predictions of direction perception to the perceptual distortions we measured psychophysically.

5.3.3 Methods to decode the population response profile

There are at least three approaches to decode the population response: vector average, winner-take-all and maximum-likelihood approach. Many physiological studies have attempted to distinguish between vector average and winner-take-all for reading out population response in MT. Vector average approach calculates the peak direction and magnitude using weighted average of the direction vectors, while winner-take-all approach determines the peak direction and magnitude by the most active
directionally tuned column of MT neurons. As demonstrated by Newsome and his colleagues, the method utilized by cortical networks to decode the population response in MT depends on two factors: task demands and the behavioral objective of the monkey (Groh et al., 1997; Salzman and Newsome, 1994; Nichols and Newsome, 2002). When discriminating very different visual motion directions, the perceptual system employs a winner-take-all algorithm (Salzman and Newsome, 1994), whereas the saccadic and smooth-pursuit eye movement systems read off the vector average of competing velocity signals in MT (Groh et al., 1997; Lisberger and Ferrera, 1997). However, winner-take-all and vector average are not the optimal decoding method in every situation. Purushothaman and Bradley showed that a monkey’s performance on a fine direction-discrimination task is better explained by an algorithm that selectively emphasizes the activities of the high-precision neurons (Purushothaman and Bradley, 2005). Moreover, recent work suggests that the likelihood function is an optimal estimator of performance on a wider range of perceptual tasks (Paradiso, 1988; Seung andSompolinsky, 1993; Sanger, 1996; Deneve et al., 1999). Maximum-likelihood method have been successfully applied to many sensory domains, such as orientation (Regan and Beverley, 1985), motion (Weiss et al., 2002; Webb et al., 2007), and multisensory integration (Ernst and Banks, 2002).
In my thesis study, I fitted the population response profile with double Gaussian functions in order to identify the peak direction and response amplitude. This approach is essentially a class of maximum-likelihood algorithms. The dynamics of the decoded peak direction predict perceptual distortions in motion trajectory that accord with human perception, suggesting that maximum-likelihood method does a good job to decode peak direction during the motion transition. It will be interesting to decode the population response using vector average and winner-take-all approach, and then compare those results with my current results. This comparison will provide more insight about the decoding mechanism that the brain employs for motion direction.

5.3.4 Interpretation of the human psychophysical data

In my thesis study, I found perceptual distortions in motion trajectory that depends on direction deviation angle. These distortions are consistent with predictions based on the dynamics of population response measured in VSDI experiments. I also ruled out the contribution of positional information to the perceptual distortions in the psychophysical experiments. However, one might still argue that the motion trajectory distortions are not related to direction perception and the linkage between these two is an epiphenomenon. Admittedly there are weaknesses in a correlative argument especially when comparisons are being drawn between the responses in ferret visual cortex and human perception. Nevertheless, the population effects in the ferret are likely
to generalize to any population coding mechanism, and fMRI and perceptual studies have provided evidence that neurons in human visual cortex have bell shaped tuning functions that lie at the heart of the effects that I have described. There is one experiment that might potentially pin down the causality between the motion trajectory distortions and dynamics of the population response. If the direction tuning curves in human visual cortex can be measured accurately, one can test the relationship between the tuning width (and directionality) and the amplitude of perceived motion trajectory distortions across subjects (Please refer to Figure 17). The prediction is the subjects that have direction tuning curves with a broader tuning width or larger directionality index will have a larger smoothing bias of the perceived motion trajectory in the psychophysical experiments.

5.4 Conclusion

I conclude that cortical dynamics and population coding mechanisms combine to place constraints on the accuracy with which abrupt changes in direction of motion can be represented by cortical circuits. This previously unrecognized correlation between V1 responses and perception has become evident because I have been able to extract the dynamics of the population tuning function, a property that cannot be assessed by more traditional approaches that have focused on the direction tuning curves of individual neurons. Instead, the three factors that appear to account for these population effects
are: (1) the non-instantaneous nature of circuit dynamics, (2) the presence of single neuron responses to both the preferred and anti-preferred directions of motion, and (3) the broad tuning of individual neurons for motion around the preferred and anti-preferred directions. The smoothing of small direction deviations and the sharpening of larger deviations could serve to enhance the discrimination of continuous and discontinuous motion trajectories. But even if these perceptual distortions are not beneficial, their existence must represent an acceptable trade-off that balances the need for accuracy with the innumerable advantages that are afforded by distributed coding mechanisms (Pouget et al., 2000; Averbeck et al., 2006; Pouget and Latham, 2003; Knill and Pouget, 2004; Dayan and Abbott, 2001; Rieke et al., 1997).
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