Chapter 21

Motion Physiology

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We next turn to single unit physiology. Given the fact that different motion cues can serve different perceptual purposes, it seems likely that there will be a hierarchy of motion processing areas, with neurons at different levels of the visual system being selective for different aspects of retinal image motion. That is, some anatomical areas could house neurons selective for the direction of motion, others for the motions of rigid objects, and others for the motion of non-rigid biological objects.

In the following sections of the chapter, we examine in detail an important paradigm for exploring the relationships between physiological activity and perception. This paradigm is simultaneous recording of both single units and psychophysical judgments in awake, behaving monkeys. It turns out that for carefully chosen neurons, in the context of carefully designed models, there are remarkably close correlations between psychophysical and neural levels of analysis. Moreover, manipulating the activity of these neurons (with microstimulation) changes the monkey’s reports of the direction of motion! This finding strongly suggests that the affected neurons are on the causal chain between the retinal image and the monkey’s perceptions. This paradigm, and the models developed within it, are particularly exciting because they provide new and more stringent criteria for judging Causal Stories.
21.1 Visual areas selective for motion

We turn now to the neurophysiology of motion processing. Let’s begin with some guesses about what we might expect to find. We start with a bumblebees-can-fly argument. Since we can perceive the direction and speed of motion, and see the three dimensional shapes and motions of objects, there must be populations of neurons that carry this information at every relevant level of the visual system.

Moreover, the Neuron Doctrine leads us to hypothesize that at some level(s) we will encounter individual neurons that are tuned for the speed and direction of motion. If we are true believers in the Neuron Doctrine, we might also expect that at higher levels of the visual system, individual neurons will be tuned to more complex motion patterns, such as expansion patterns, deformations typical of rigid rotation, or deformations typical of biological motion. Are there neurons that are tuned to these variables? Where do they occur? And how do motion codes change from one processing level to another?

21.1.1 M cells: Responses to temporal change

We ended Chapter 13 with a summary of the properties of primate retinal M, P, and K cells. Of these three major cell types, M (parasol) cells respond most transiently to stimuli, and have the highest high temporal frequency cut-off. Also, M cells provide the major input to the dorsal stream, which has a well-deserved reputation for motion processing. Thus, in all probability the population of M cells provides the signals that will later be recoded to support motion processing. And in fact, the motion of a spatial pattern across the receptive field of a retinal M cell does yield a burst of firing.

However, just as individual cones do not code the wavelength of light, individual M cells do not carry information about motion nor about the direction of motion. That is, a prototypical M cell would respond equally well to a stimulus that moved across its receptive field in any direction; and even more importantly, it would also respond to a light that flickered on and off but did not move. Information about the speed and direction of motion is doubtless carried by the population of M cells, but not by individual primate M cells.

21.1.2 V1 cells: The appearance of direction selectivity

Direction selectivity in individual neurons arises within area V1. We have already recounted (Chapter 16, Figure 16.9) how the vigorous response of a V1 neurons to the moving edge of a slide provided the clue that allowed Hubel and Wiesel (1968) to begin to crack the V1 visual code. More recent studies have shown that about 1/4 of V1 neurons are selective for the direction of motion in 2D images. There is a concentration of directionally selective neurons in layer 4B – the layer that receives input from M cells and projects to area MT. Presumably this direction selectivity is built

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1For at least some species, motion processing begins in the retina. In particular, beginning with Barlow and Hill (1963), studies of single-unit physiology have shown directionally-selective ganglion cells in the retinas of rabbits and mice (reviewed in Vaney, Sivyer, and Taylor, 2012). Recent anatomical studies suggests similar directionally-selective cells are present in low density in the primate retina (Dacey, 2004; Yamada, Bordt, and Marshak, 2005). Because this issue awaits physiological study in primates, we will stick to the current understanding that for primates the first appearance of direction selectivity is V1.
by the elegant neurons shown in Figure 20.7 of Chapter 20, but the circuits that do the building remain a matter of controversy.

The motion tuning properties of V1 cells are relatively coarse and limited. Individual V1 neurons respond only to relatively slow speeds (e.g. $10^2$/sec), and their direction selectivity is relatively broad. Their receptive fields are small, and there is no evidence that they respond selectively to larger or more complex motion patterns such as expansion or distortion. Instead, it is as though V1 neurons signal the presence of small local motions in particular directions in the retinal image, and provide the raw materials out of which sensitivity to more complex motion patterns could be built.

21.1.3 Area MT: The classical motion area

As discussed previously, the middle temporal area, area MT or V5, is considered a central component of the dorsal processing stream, which has a well-earned reputation for processing motion. Virtually all of the neurons in MT are tuned for the direction and speed of motion, and respond with great enthusiasm to stimuli moving in their preferred direction. They also have a clear “null” direction opposite to the preferred direction of motion, and motion in the null direction often suppresses the spontaneous activity of the neuron.

A direction-of-motion tuning curve for a typical MT neuron is shown in Figure 21.1. The center of this figure shows a polar plot for the neural response as a function of the direction of motion. Around this central plot are small histograms showing example spike rate as a function of time for particular direction of motion. Interestingly, although MT neurons seem to be specialized to respond to motion, the direction-of-motion tuning of MT neurons is not particularly sharp, and a typical tuning curve might have a half-width-at-half-height of 50 to 60 degrees. Thus, MT neurons do not exhibit a sparse direction-of-motion code; information about the direction of motion must be carried in a distributed population code at this stage.

Several additional and more novel features of MT cells are interesting from the perspective of coding schemes. First, many MT neurons show the presence of silent surrounds. That is, MT neurons show classical receptive fields: any retinal location to which the neuron responds is part of the classical receptive field, and locations to which it does not respond are outside it. However, moving stimuli in regions outside the classical receptive field – within the silent surround – can strongly modulate the response of the MT neuron to stimuli within the classical receptive field. Typically, stimuli moving in the direction opposite to the cells’ preferred direction enhance the response of the neuron (other forms of interaction also occur). Such neurons seem well suited to responding to patterns of relative motion between an object and its background.

And second, there is evidence that MT neurons can be tuned for other features of motion patterns. For example, Treue and Andersen (1996) tested MT neurons with random dot stimuli containing local velocity gradients. A velocity gradient is a motion pattern within which the velocities of pattern elements vary with spatial location. For example, the dots in the top part of the display might have a different velocity than the dots in the bottom part of the display. Treue and Andersen introduced systematic variations of the speeds of dots in different locations as shown in Figure 21.2. The center of this figure is a polar plot of combinations of two velocity gradients. The surrounding ring of illustrations show the combined velocity gradients. In this example, the speed in the lower-left versus upper right part of the field varied across the horizontal axis of the figure; in addition, the speed in the upper-left versus lower-right varied across the vertical axis of the figure.
Figure 21.1: Direction-of-motion tuning in MT neurons. This polar plot shows the neural response (spikes/s) as a function of the direction of motion. The small circle around the origin represents spontaneous activity. For this cell, the response is high for directions to the up and right. Response is suppressed for the opposite direction. Individual histograms around the outside of the figure indicate activity during the period of time with the moving stimulus in the receptive field of the cell. [From Albright (1984).]
The results are for these gradients (points and solid lines) are shown relative to a constant velocity field (dashed circle). These variations did affect the responses of many MT neurons although the effects are relatively small. Since velocity gradients provide cues to complex aspects of the visual environment and the objects within it, the Neuron Doctrine suggests that we might well find visual neurons that are tuned to velocity gradients, and MT neurons seem to provide the earliest instance of this kind of tuning.

### 21.1.4 Area MSTd and the analysis of motion patterns

Beyond MT, motion signals are further processed at a number of locations, with important transformations of the motion code. For example, area MSTd (the dorsal part of the medial superior temporal region) contains neurons with very large, motion-tuned receptive fields. Many MSTd neurons respond to complex motion patterns such as rotation and/or expansion/contraction, and are tuned to, for example, the direction of rotation of a rotating pattern. Others are tuned for the orientations of planes rotating in depth (Sugahara, Korogi, Nakashima, Hamatake, Honda, and Takahashi, 2002). Similarly, MSTd neurons respond to optic flow fields: large regions of dots or other stimulus elements, moving in patterns that mimic the patterns generated in the retinal image when the subject walks around in the world. Such neurons may reveal the analysis of the shape and locomotion cues contained in complex patterns of retinal image motion.

### 21.1.5 Other areas?

Finally, as one moves even farther along the motion processing pathway, and increasingly close to the beginnings of coding for motor actions, one begins to see neurons coded in coordinates appropriate to the production of motor actions. A great deal is known, for example, about the neural codes required for the planned production of particular eye movements, and about the production of the motor movements themselves. Unfortunately, this book has to stop somewhere, and these preparations for motor action cannot be included in more detail.

### 21.2 Summarizing motion processing as a hierarchical system

In summary, and simplifying a highly complex topic, we can imagine the motion processing system as composed of several stages. V1 neurons, with their small receptive fields, are tuned to the directions of motion of small local elements in the 2-dimensional retinal image. To date there is little evidence that they take on more complex tasks, (but it is possible they have just not been asked the question in the right way). In any case, V1 neurons could provide the building blocks out of which neurons tuned to more complex aspects of motion patterns can be built. MT neurons, with their larger receptive fields, may begin the analysis of simple patterns of motion, such as responding to motion flow fields and differences in the direction of motion between objects and their backgrounds. And MSTd neurons might be specialized to respond to more complex motion patterns, perhaps including the patterns that signal the shapes of three-dimensional objects and biological motion.
Figure 21.2: MT neuron response to velocity gradients. A. Response of cell to stimuli moving in different directions. B. Response of cell to stimuli moving at different speeds. C. Response of cell to the eight velocity gradients illustrated around the outside of this polar plot. It shows the neural response (spikes/s) relative to the response to a flat velocity profile moving at the preferred speed (dashed circle). [From Treue and Andersen (1996, Figure 2, p. 801).]
21.3 Introducing causal stories for motion

Prior to the 1990s, speculations about the dependence of visual function on visual structure were based on two main sources of information. As discussed earlier, lesion studies have classically been used to argue that particular anatomical structures are necessary for the occurrence of particular behaviors and/or perceptions. And since the advent of single unit studies in the early 1960s, correlations between the tuning characteristics of individual neurons and the characteristics of perceptual and/or behavioral data, have been used to argue that particular neurons or anatomical structures are sufficient to support particular perceptions and/or behaviors. As discussed earlier, these arguments are attractive, but subject to important limitations.

During the early 1990s, a new approach to the neuron/perception question arrived on the scene: single unit recording in awake, behaving monkeys. With this technique, the activity of individual neurons and the perceptions of the animal (as indicated by their behavioral reports) are recorded simultaneously, in response to the same stimuli. With this approach, neural activity and behavior can be compared in detail, on a trial-by-trial basis. Such remarkable techniques potentially bring us closer to the goal of understanding the neural basis of perception. A particularly insightful series of experiments using this paradigm has been carried out by William Newsome and his colleagues.

We begin with a general description of the technique, many aspects of which are novel and complex. To begin with, it takes several months to prepare a monkey to become a subject in these experiments (not a good thesis project!). First, a device for stabilizing head position must be attached to the monkey’s skull, and a search coil used for recording eye movements must be implanted around one eye. If these surgeries are successful, the monkey then undergoes several months of training as a psychophysical subject. After training is complete, more surgery is undertaken: a cylinder that allows recording electrodes to be lowered into the brain is surgically implanted on the skull. If all of these initial steps are successful, the actual experiments can begin.

The stimuli used in many of the experiments from the Newsome lab are fields of moving dots: the stochastic motion stimuli that were introduced in the prior chapter (see Figure 20.1). In such a stimulus, each dot can be displaced along a different trajectory between frames. The manipulated parameter is the degree of correlation of motion between two frames: the fraction of the dots that are displaced in the same direction. In more recent papers this is often called the motion coherence.

As already introduced, stochastic motion stimuli are theoretically attractive for several reasons. Since none of the dots move continuously, these stimuli do not promote tracking eye movements as edges and gratings do, so the subject can hold his eye relatively still during the experiment. Moreover, to perceive the predominant direction of motion in a stochastic motion stimulus requires combining information across broad retinal regions, and separating one direction of motion from all of the others. Thus, these stimuli are custom designed to isolate a higher level of motion processing than are the edges and gratings initially used to test V1 neurons.

The response measure used by the Newsome group is also novel from our perspective. Rather than pushing levers or buttons to indicate the perceived direction of motion (as we would tend to do in human psychophysics), the monkeys are trained to use eye movements. As shown in Figure 21.3A, the monkey’s task is to fixate a fixation point during the stimulus presentation, and then shift fixation to one of two target lights, depending on which direction of motion he wishes to report (e.g. the upper dot for upward motion or the lower dot for downward motion).

In a typical experiment, the percent coherence among the dots is varied from trial to trial. The monkey’s task is to report the direction of motion on each trial. Since this is an externally referenced
Figure 21.3: Illustration of the spatial and temporal characteristics of a typical experiment from the Newsome laboratory. Panel A shows the spatial configuration. The monkey fixates the cross at FP. The electrode is advanced into area MT to isolate a neuron that is tuned to a particular speed and direction of motion. Its receptive field is located, and a stochastic motion stimulus is presented within a stimulus aperture centered on the receptive field. Two target lights (LEDs in the figure) are illuminated in line with the preferred and null directions of motion for the neuron. Panel B shows the timing of a trial. The fixation point comes on, and the monkey shifts gaze to fixate it (shown in the eye position trace). The stochastic motion stimulus is then presented for 2 sec. As the stimulus goes off, the target lights come on, and the monkey shifts her gaze to one or the other target light to indicate her judgment of the direction of stochastic motion on that trial. The activity of the neuron is also recorded throughout the trial. [Modified from Britten et al. (1992, Fig. 2, p. 4748).]
task, there is a right answer, and the monkey is rewarded with a few drops of water or juice after each correct response. The behavioral data, then, take a familiar form: psychometric functions showing the monkey’s percent correct as a function of the percent coherence in the stochastic motion stimulus.

To begin an experimental run, the monkey is seated in a primate chair, and the experimenter prepares to record both the eye movements and the responses of single cells. The experimenter then advances the microelectrode to locate a single neuron that is responsive to motion, in the vicinity of area MT. Once a neuron has been found, its classical receptive field, direction selectivity, and speed selectivity are determined.

Finally, the experiment proper can begin. The monkey fixates the fixation point. He is presented with a field of stochastic motion stimuli matched to the size and location of the receptive field of the particular neuron under study, moving in either the preferred or the null direction of motion, at the preferred speed (the ultimate custom-designed stimulus!). The experimenter varies the percent coherence within the stimulus and measures the response of the neuron, while the monkey uses eye movements to the target lights to make judgments concerning the direction of motion of the stimulus. The monkey’s behavior can then be compared to the neuron’s behavior, either as a statistical average or on a trial-by-trial basis.

The work of Newsome and his colleagues is marked by particularly elegant choices of experiments, logic, models, and data analyses, to exploit the full value of the joint physiological and behavioral data. Since the most fundamental concern of this book is the logic of relating system properties to neural activity, these experiments are of special interest. We here review three experiments and critically examine the conclusions that can be drawn from them.

21.4 Do neurons have sufficient reliability to predict behavior?

Consider first a study by Britten, Shadlen, Newsome, and Movshon (1992) that addressed the question: Do the signals in individual neurons in MT have sufficient reliability to provide the neural basis for the behavioral data?

The behavioral data produced by the awake, behaving monkeys are straightforward: psychometric functions. Similarly, the physiological data show the responses of MT neurons to stochastic motion stimuli of various coherences, in the preferred and null directions of the neuron. To allow direct comparisons of the neural to the behavioral data, the data from individual neurons were processed through a signal-detection-based model to yield what Britten and colleagues call a neurometric function. The model (which is too complex to recount here, but which involves only the recorded neuron and a postulated identical neuron tuned to the opposite direction) provides an estimate of how well the monkey could perform if he based his responses solely on the activity of two neurons like the particular neuron recorded simultaneously with the behavioral data.

A set of psychometric functions and their corresponding neurometric functions are shown in Figure 21.4. Of course, the results vary from one neuron to the next. Panels A and B show two cases of nearly exact correspondence between simultaneously recorded psychometric and neurometric functions. About half of the neurons conformed to this pattern. Panels C and D show cases in which the monkey was more sensitive than the neuron (panel C) or vice versa (panel D).

Now, what do we make of these data? Britten and his colleagues argue that the close match between psychometric and neurometric functions supports the argument that, under the conditions tested, the information carried by a single MT neuron and its oppositely-tuned twin is sufficient
Figure 21.4: Psychometric and neurometric functions. The open symbols are psychometric functions derived from the monkey’s behavioral responses. The solid symbols are neurometric functions derived from the responses of the individual neuron. Psychometric and neurometric functions often coincided closely (panels A and B). In other cases, the animal could be more sensitive than the individual neuron (Panel C) or vice versa (Panel D). [Modified from Britten et al. (1992, Fig. 6, p. 4752).]
to control the monkey’s judgments of the direction of motion of the stochastic motion stimuli. To quantify this relation, they describe a model of neural pooling that combines information from some number of similarly-tuned neurons to yield the behavior. Given assumptions about number of neurons and the degree of correlation in the noise, they can predict behavioral sensitivity from the sensitivity on single neurons. In particular, given weak correlations among similar neurons, only a handful on neurons were necessary to yield the behavior. The experiment, then, provides a very sophisticated sufficiency argument for the dependence of behavior on neural activity.

Some have criticized this experiment as showing neural performance that was too good. Afterall, it seems very likely that one pools information over more than just few neurons. This issue was revisited and probably resolved by Cohen and Newsome (2009). They wondered whether the monkey used the entire time the stimulus was displayed to make their response. If the monkey used only information from the first part of the trial, then averaging the neural data over the entire 2 second display would give it an unfair advantage. To address this, they taught the monkey to make speeded responses and measured the response time. This motivated the monkey to use only the minimum time to view the stimulus and now one can compare the monkeys performance to the neuron for just the relevant amount of time. This refinement allowed for a more precise comparison between behavior and neural sensitivity. The result of this study is that the neurons were typically about a factor of two less sensitive than behavior. This difference in sensitivity is consistent with a neural pooling of perhaps 100 similarly-tuned and weakly correlated neurons. Thus we now have a plausible story how for a given motion stimulus, a set of 100 neurons for a can yield behavior with the right amount of sensitivity.

21.5 Correlations between neural activity and behavior

A second question – trial-by-trial correlations between single unit activity and behavior – was addressed by Britten, Newsome, Shadlen, Celebrini, and Movshon (1996). The essence of the study stems from the fact that with repeated presentations of the same stimulus, the response of the individual neuron will vary from trial to trial. The question is, keeping the stimulus fixed, will the monkey’s behavioral response vary in correlation with the neuron’s response? Specifically, will the monkey tend to report motion in the neuron’s preferred direction on trials on which the neuron happens to fire at a higher rate, and the neuron’s null direction on trials on which the neuron happens to fire at a lower rate? This correlation has been called choice probability.

Such an analysis is shown in Figure 21.5. In this particular example, a stimulus with 0% correlation was presented repeatedly within a sequence of trials of other correlations. For 0% correlation, of course, there is no net motion signal created by the stimulus. Yet the neuron produced a variable number of spikes from one trial to the next; and the data show a small but clear tendency for the the monkey’s response to vary in correlation with the firing rate of the neuron! Since the correlation is not introduced by the stimulus, it must arise within the monkey’s visual system, and is consistent with the activity of these neurons plays a causal role in generating the monkey’s perceptual report.

Interpreting causality from correlation is always difficult. In this case, a key assumption is that the noise in neurons relevant to the monkey’s perceptual report is independent of the noise in neurons that are irrelevant to the monkey’s report. Cohen and Newsome (2008) measured the

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2For more on the use of response time in psychophysics, see Palmer, Huk, and Shadlen (2005).
correlation between MT neurons that were sensitive to a variety of motion directions. This data was then analyzed by Cohen and Newsome (2009) with respect to choice probability. They found that noise in neurons is correlated even if they are selective to very different directions. This correlation was not anticipated in the early studies of choice probability. Given such noise correlations, even directionally selective neurons that are believed to have little to do with the decision about direction of motion will show a choice probability. Thus, this analysis of choice probability is probably less useful than originally suggested. If only one could avoid the problems of interpreting a correlation and directly manipulate neurons.

21.6 Microstimulation biases the reported direction of motion

In a third and most striking experiment, Newsome and his colleagues (Salzman, Murasugi, Britten, and Newsome, 1992) investigated the effects of cortical microstimulation on the monkey’s psychophysical performance. Fortunately, like area V1, area MT has a columnar organization. That is, groups of neurons that respond to the same direction of motion lie near each other in columnar compartments. This anatomical arrangement makes it possible to place a stimulating electrode in one location within MT and stimulate mostly or entirely neurons that respond to a single direction of motion. In principle, this experiment has the potential to avoid the issues of interpreting correlations between neural activity and behavior because the neural activity is manipulated rather than simply measured.

To begin their experiment, Saltzman et al. first recorded the direction preferences of MT neurons within a local region, and selected regions of MT in which neurons encountered over at least 200 micrometers had similar preferred directions. Electrical stimulation consisted of a series of tiny
electrical pulses to this chosen region. Such electrical pulses probably increase the firing rates of neurons in their immediate vicinity. As before, the monkey’s task was to view a stochastic motion display and judge the direction of motion. Stimulation and no-stimulation trials – trials on which the monkey’s cortex received electrical stimulation, and trials on which it did not – were interleaved in the experiment. The hypothesis was that electrical stimulation should increase the probability that the monkey will report motion in the preferred direction of the stimulated MT neurons.

Results from four different stimulation sites are shown in Figure 21.6. In each case, the addition of electrical stimulation shifted the psychometric function leftward. In other words, for each level of coherence in the stimulus, microstimulation influenced the monkey to report the cell’s preferred direction of motion on an increased fraction of trials! (Variations in the size of the effect are attributed to variations in the success with which the electrical stimulation was confined to a single compartment, as well as other factors).

What are we to make of these data. Unlike all of the earlier experiments, which are more correlational in nature, microstimulation constitutes an experimental manipulation of the activity of the neurons in area MT. The results show that externally caused changes in the firing rates of neurons in MT cause changes in the behavior of the animal. Thus, this experiment adds particularly compelling evidence supporting the causal role of directionally selective MT neurons in determining the perceptual reports of the animal.

An important remaining question is, what is the mechanism of action of the electrical signals? In particular, do they influence the sensory signal (and thus the animal’s perception), or a post-perceptual decision process, or just the motor responses of the animal? To explore the decision process explanation, monkeys were tested with electrical stimulation applied in a different region of the visual field than the region in which the stochastic motion stimuli were presented. Distant microstimulation did not affect the monkeys’ psychophysical reports, ruling out a major influence of the stimulation solely on a decision process. To explore the motor explanation, microstimulation was applied out of synchrony – just before the presentation of the stochastic motion stimulus, rather than simultaneously with it. The electrical stimulation was also ineffective in this condition, and no extraneous eye movements correlated with the delivery of the electrical stimulation were seen. Finally, Ditterich, Mazurek, and Shadlen (2003) used microstimulation in a response time version of this task. They showed systematic effects on the speed of the response that were as expected if the microstimulation was acting like an additional motion stimulus. Newsome and his colleagues therefore argue that the electrical stimulation had its influence early rather than late: on the animal’s perceptions; rather than just on the decision process or the motor response.

## 21.7 Consciousness or just behavior?

In Chapter 18 we used the deleterious effects of dorsal stream lesions, and the speed and directional tuning of dorsal stream neurons, to argue that area MT is an important location on the causal chain for neural signals that underlie the perception of motion. We also argued, however, that tuning curves and lesion experiments are rather blunt tools for defining causal relations between perception and behavior.

The Newsome group experiments have gone further. They have shown that individual MT neurons are sensitive enough – and are sufficient – to control the monkey’s perceptual reports of the direction of motion. And most importantly, microstimulation of MT neurons influences the monkey’s perceptual reports in orderly ways. These experiments clearly probe the question of the
Figure 21.6: Effects of cortical microstimulation on behaviorally measured psychometric functions. The horizontal axis (labeled “correlation”) shows the percent coherence in the stochastic motion stimulus. The vertical axis, labelled “proportion PD”, shows the proportion of trials on which the monkey’s report of the direction of motion coincides with the preferred direction of motion of the neurons in the column in which the microelectrode is situated. The four panels show four different microstimulation sites. The open and closed circles show psychometric functions on no-stimulation and stimulation trials respectively. In each case microstimulation shifts the psychometric function to the left. That is, at each percent correlation of the stimulus, microstimulation increases the percent of trials in which the monkey reports motion in the preferred direction of the stimulated neurons, as though the microstimulation increased the magnitude of the motion signal in the preferred direction. [From Salzman et al. (1992, Fig. 4, p. 2336).]
21.8. CONCLUSION: AS GOOD AS IT GETS!

neural basis of motion perception more deeply than did earlier lesion studies and tuning studies. Moreover, they greatly strengthen the argument that neurons in MT are important elements along a causal chain leading from moving stimuli to the monkey’s behavioral reports of his perception of such stimuli.

But can we make a stronger claim? On the basis of all of these experiments, one might wish to argue that the activities of MT neurons mediate the conscious perception of motion. Alternatively, it is possible that microstimulation provides a cue for the direction of motion but is not equivalent in appearance to a visual stimulus. One cannot ask the monkey what the motion “looked like” in the microstimulation condition. This distinction bears careful examination, but for the moment, we will content ourselves with the weaker conclusion: that MT neurons are a major processing stage along the causal chain that leads to the monkey’s perceptual reports of motion and its direction. We will return to the question of the neural correlates of consciousness, and how they might be studied, in Chapter 26.

21.8 Conclusion: As good as it gets!

In summary, the perception of motion is a classic area of perceptual science. Our description of some of the most historically puzzling aspects of motion perception has barely scratched the surface of this interesting and complex topic.

A unique feature of the topic of motion processing is the progress computational neuroscientists have made on characterizing the patterns of motion that different kinds of physical motion produce in the retinal image. The translation, rotation and distortion of objects lead to different, complex patterns of retinal image motion, and these patterns can therefore serve as cues to the properties and motions of physical objects.

Some possible neural bases for motion analysis are remarkably well known. There are indeed neurons, early in the dorsal stream, that are selective for the direction of motion; and later in the dorsal stream, for more complex motion patterns. Moreover, the use of awake, behaving animals has led to a series of studies that provide particularly compelling evidence that these directionally tuned neurons play a major causal role in determining a monkey’s reports and perceptions of the direction of motion.

A cautionary note: given the experiments reviewed above, you might be tempted to believe that MT neurons and other dorsal stream neurons are specialized for the analysis and perception of motion. But remember that it’s impossible to test a single neuron on all of the possible stimulus dimensions. In many of the studies cited above, neurons were tested systematically with moving stimuli of various kinds. But there have been fewer studies with stimuli varying in color, or contrast, or distance or depth, and it turns out that MT neurons are also selective within several of these domains. In particular, many MT neurons are selective among stimuli that vary in stereoscopic depth (Chapter 24). If we overgeneralize our characterizations of the roles of particular neurons or structures too early, we may have to eat our words.

Finally, how do we compare the causal story for MT mediating motion discrimination to other examples? In particular, recall the case of cone spectral sensitivities mediating color matching. That prior case was much simpler to approach because variations in light intensity and wavelength affect the cones directly. In contrast, it requires a clever microstimulation experiment to make that case in MT. What else might we want? Regarding the anatomy and physiology, the relevant cell types in MT are not yet established. Regarding the psychophysical tasks, it is not yet clear what
kind of motion is critical to MT activity. Is it specific to translational retinal motion? Or is it more
general? Putting these ideas together, one can imagine discriminating alternative hypotheses that
specify particular cell types in particular areas mediating particular kinds of motion. This example
is very good, but it can become even better.