CHAPTER 10

Motion Perception

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INTRODUCTION

Our world is full of motion. Nearly all animals have the ability to locomote, and most use movement as the primary way to find food, potential mates, and safe shelter. Consequently, motion provides a truly fundamental source of information about the environment. Motion can provide essential clues for a predatory animal looking for its next meal, while, at the same time, the movement of the predator can sound the alarm of impending danger to potential prey. Even in our modern civilization where the food we seek is not very agile, moving objects are still critical for our survival. Accidents involving moving vehicles remain one of the top non-disease-related causes of injury and death (Centers for Disease Control and Prevention [CDC], 2013). The vital significance and ubiquitous presence of motion in our environment are reflected in our sensory apparatus. The visual system is exceptionally good at detecting and processing motion. In fact, when a classic study asked *What does the eye see best?*, the answer was "a small

moving object" (Watson, Barlow, & Robson, 1983). Motion is also remarkably effective at exogenously capturing attention; searching for Waldo in *Where's Waldo* would be trivial if Waldo waved his hands, irrespective of how many similar, but stationary, distractors are present. This remarkable sensitivity to visual motion derives from a large network of brain areas involved in motion processing. There are at least 17 distinct cortical areas or clusters of areas that respond better to moving than stationary visual stimuli (Sunaert, Van Hecke, Marchal, & Orban, 1999).

Motion perception would be an important topic of study even if its only function were to deduce the speed and direction of moving objects. Yet, sensory processing of motion accomplishes much more. At the most basic level, the presence of motion is necessary for all vision—an image stabilized such that is has no retinal motion fades away in seconds (Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). Fortunately, our eyes constantly make small involuntary eye movements, which not only refresh the retinal image but also improve our ability to see fine spatial details in stationary objects (Rucci & Poletti, 2015). In addition, motion mechanisms guide our locomotion as we move about our environment, help us predict *if* and *when* we may collide with another object, are especially potent at capturing attention (as in the Waldo

example earlier), contribute importantly to perception of object shape (structure from motion), inform us about the actions and intentions of our conspecifics (biological motion perception), and even aid our postural control.

This chapter covers these various functional roles of motion perception, along with computational challenges associated with detection and processing of motion information. These many roles of motion perception are accomplished by a network of brain areas, with each area extracting and refining a slice of information provided by moving stimuli. In fact, much of our knowledge about motion perception comes from clues derived by studying its neural mechanisms. This work, including studies of neural responses in animals and, more recently, neuroimaging in humans, has been critical for our understanding of different stages of motion processing. Accordingly, we cover the neural mechanisms of motion perception throughout this chapter.

What Is Motion?

In Newtonian physics, motion is not a fundamental property, but rather it is derived from changes in position over time. Indeed, viewing sequential snapshots of a stationary object changing position is sufficient for a vivid sensation of motion, a perceptual experience that can be metameric to viewing of continuous motion (i.e., perceptually indistinguishable despite differing in physical characteristics). This phenomenon, called *apparent motion*, occurs every time we watch video recordings and animations. We discuss apparent motion and explain why it appears as real motion later in the chapter. Here, we use it as evidence that our subjective sensation of motion can be constructed from changes of position over time. However, it is wrong to think of motion as a derived sensation. Changes in

image position on the retina do not result in motion perception when such changes are caused by eye movements. On the other hand, there are many examples of stationary stimuli that evoke the sensation of motion. This, for instance, includes the illusory motion in the motion aftereffect and motion seen in certain static images (Figure 10.1; but see Nishida & Johnston, 1999). Thus, changes in position over time are neither sufficient nor necessary for motion perception. So, rather than defining motion based on its physical characteristics, we also have to consider how our perceptual experiences of motion are created by the brain. Simply stated, perceptual motion can be defined by neural responses that result in perceived motion. This inherently circular definition highlights the importance of understanding the computational and neural mechanisms that, together with the incoming sensory information, give rise to the perceptual and functional experiences that we associate with motion.

A Brief History of Motion Perception Research

Some of the earliest documented insights into motion perception can be traced to ancient Greek philosophers. Descriptions of apparent motion, induced motion and the motion aftereffect are found in the writings of Euclid, Lucretius, and Aristotle (Wade, 1996, 2006). Such observations continued over the centuries, often by prominent thinkers, including Ibn Al-Haytham, Leonardo da Vinci, and John Locke (Wade, 1996). However, systematic empirical study of motion perception remained undeveloped until the 20th century. At the beginning of the century, Gestalt psychologists focused on motion grouping and the phi phenomenon—a form of long-range apparent motion (Wertheimer, 1912). Several decades later, neurophysiological recordings demonstrated that visual neurons are very
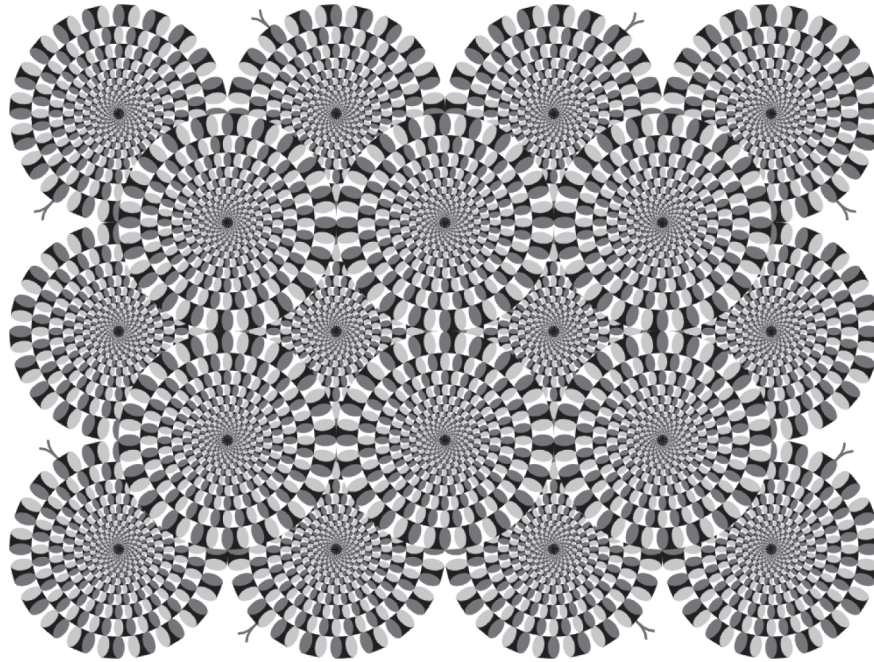
Figure 10.1 Rotating snakes illusion created by Akiyoshi Kitaoka (http://www.ritsumei.ac.jp/ ~akitaoka/index-e.html). In this static image, observers typically perceive illusory rotating motion in their visual periphery. The illusion is negligible in foveal vision, so shifting of one's gaze to the center of a rotating snake stops its illusory rotation. Color version of this figure is available at http://onlinelibrary.wiley .com/book/10.1002/9781119170174.
SOURCE: Copyright A. Kitaoka 2003 (September 2, 2003). Reprinted by permission.

sensitive to moving stimuli and that many exhibit high selectivity for motion direction (Barlow, 1953; Hubel & Wiesel, 1962; Lettvin, Maturana, Mcculloch, & Pitts, 1959).

Psychophysical work on motion perception picked up in the 1970s, with a strong focus on establishing the limits of motion perception. This is also when, thanks to the rise of computers, researchers started using a range of specialized stimuli to probe visual motion processing, many of which are still in use today. The use of sinusoidal gratings was inspired by the emerging Fourier theory of visual perception. Random-dot-kinematograms were developed to study motion perception while minimizing the contribution of explicit position cues. Johansson (1973) introduced point-light animations that remain the main stimulus for

studying biological motion. These early years of modern motion psychophysics are nicely summarized in a review by Nakayama (1985). 1985 was also an important year in motion perception research. *The Journal of the Optical Society* published a special issue on motion that included papers describing three computational models of motion perception (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). As detailed later in the chapter, these papers still remain very influential in our understanding of motion processing. Thirty years later, they continue to be highly cited, together accumulating more than 5,000 citations.

During the 1980s and 1990s, there was a significant expansion of motion perception research, both because of new questions raised by previous work and an increasing

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availability of computers, which allowed unprecedented opportunities in advancing experimental designs. Around that time, motion research became less constrained by available technology, with the experimenter's insight becoming the main limiting factor. Researchers largely focused on questions about different types of motion perception (short-range vs. long-range, first-order vs. second-order vs. third-order), speed perception, interactions between motion perception and other visual domains (e.g., color and depth), and rules governing integration and segregation of local motion signals (e.g., aperture problem, work with plaids, motion transparency). Although more recent motion perception research has expanded to include other research topics, many of these questions are still relevant and are covered in this chapter. The reader can find more details from excellent reviews of this work by Sekuler, Watamaniuk, and Blake (2002) and Burr and Thompson (2011). Nishida (2011) also covers this research, with a remarkably comprehensive review of work between 2001 and 2010.

In the past 15 years, we have seen great progress on many longstanding topics in motion research, including biological motion, interactions between motion and position, motion adaptation, and optic flow. We have also seen the emergence of (largely) new areas of research such as multisensory motion perception and Bayesian models of motion processing. General information about the Bayesian approach can be found in Chapter 2 in Volume 5 of this series.

LOCAL MOTION ANALYSIS

Motion Detectors

Motion, in physical terms, can be defined as changes in space over time. Imagine an object located at a position x_1 at a time t_1. Now, at
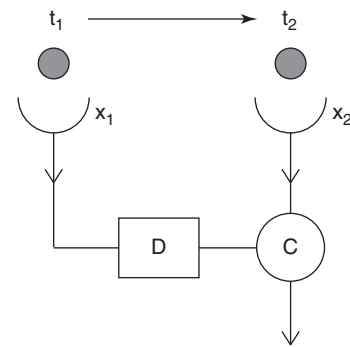
Figure 10.2   An illustration of a Reichardt detector sensitive to rightward motion. As an object (gray circle) moves from position x_1 to position x_2 over time (t_1, t_2), its presence at locations x_1 and x_2 is captured by detector subunits (shown as semicircles). Critically, the output from the left detector subunit is delayed (D) and then compared (C) with the output from the right detector subunit. The presence of this delay gives rise to the motion direction selectivity of the Reichardt detector.
SOURCE: From Perrone and Thiele (2001). Copyright 2001. Reproduced with permission of Macmillan Publishers Ltd.

a later time point (t_2), let us say the object's position has changed to x_2 (Figure 10.2). In this simple scenario, one can easily conclude that the object has moved from x_1 to x_2. The direction of motion is given by the relative positions of x_2 and x_1, while its speed is given by both the time it took the object to move from x_1 to x_2 and the distance between x_1 and x_2 (assuming linear trajectory and constant velocity). Thus, to perceive motion of this object, the visual system should be able to reliably monitor changes both in space and in time. This is necessary to detect local motion signals, which, as detailed later in the chapter, are building blocks of a wide range of global and higher-order motion perception abilities.

One of the earliest and the simplest models of local motion detection, built based on the observation of beetles' behavior, is known as the Reichardt detector (Borst, 2000; Hassenstein & Reichardt, 1956; Figure 10.2).

The Reichardt motion detector elegantly implements a mechanism that is sensitive to changes in space and in time—a key requirement for local motion detection. The first stage of the Reichardt detector consists of two simple subunits that monitor two spatially offset locations. These subunits will fire if a luminance change is detected at their receptive field locations. The outputs from the two subunits are then compared, but only after the output from one of the locations is delayed before reaching the comparison stage. This asymmetrical delay in the sampling of two neighboring locations gives rise to the detector's direction selectivity; a motion detector that has a delay unit connected to the left subunit (as in Figure 10.2) will be sensitive to rightward motion, and vice versa for a detector that has a mirror-symmetrical structure. Simple modifications in the model can also give rise to speed selectivity. For example, the detector can be made more sensitive to slower speeds by prolonging the delay duration and/or increasing the spatial separation of the subunits. We cover the mechanisms of speed perception in more detail later in the chapter.

The Reichardt motion detector has had a considerable influence on how researchers formalized and studied motion detection in humans as well as other animals. Barlow and Levick (1965) were able to evoke responses from rabbits' direction selective retinal ganglion cells with two discrete *stationary* flashes at different locations. As predicted by the Reichardt model, a smooth motion trajectory is not required for evoking motion selective responses (this property—also known as apparent motion—are further discussed in this section). While the simplicity of the Reichardt motion detector makes it intuitive, it does require elaboration to better accommodate the complexity in motion analysis. For example, a single Reichardt detector can be "tricked" to responding by a stationary

flicker whose period matches the detector's delay time. This problem can be solved by pairs of mirror-symmetrical Reichardt detectors (e.g., rightward and leftward selective) connected such that their responses can cancel each other. Here, any flicker driven response will be identical in each direction-selective detector, and thus, will not evoke responses in the whole circuit. Other elaborations of the Reichardt motion detector include the orientation- and gradient-based models (Adelson & Bergen, 1985; Clifford & Ibbotson, 2002; van Santen & Sperling, 1985; Watson & Ahumada, 1985; for reviews see: Borst & Egelhaaf, 1989; Borst, 2000; Krekelberg, 2008), which still form the basis of more recent models that incorporate neural findings (e.g., Simoncelli & Heeger, 1998).

Among more elaborated models, Adelson and Bergen (1985) conceptualized that any motion signal can be expressed as an orientation in space-time plane. For example, as illustrated in Figure 10.3A, a stimulus moving horizontally to the right can be represented as a slanted line on a space-time plot where the steepness of the orientation is determined by the stimulus speed. Consequently, a detector that can detect the *orientation* in space-time effectively detects motion direction and speed. This was an appealing idea as the first cortical site that has motion detectors in primates—the primary visual cortex (V1)—is also notable for the abundance of neurons that detect orientation of static stimuli. Adelson and Bergen (1985) formalized their idea in a model that implements spatiotemporal energy filters. Each filter is oriented in space and time, and performs weighted sum of its inputs, yielding filter selectivity to moving stimuli of certain direction and speed. To make the filters phase-independent and insensitive to contrast polarity, the responses from a quadrature pair of these linear filters (i.e., sine and cosine phases) are combined (namely, squared and summed). Then, the

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Space (x)

Time (t)

(A)   (B)   (C)   (D)   (E)
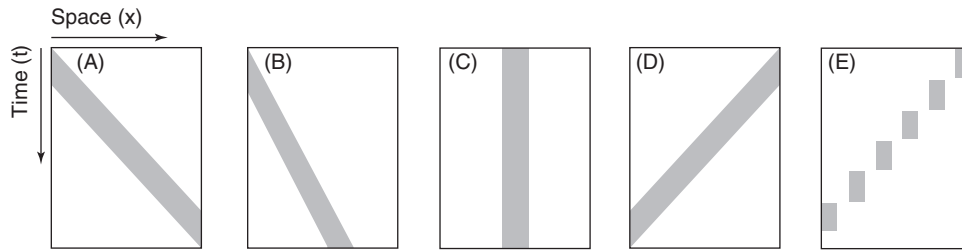
Figure 10.3   Illustrations of space-time plots. Time is shown on the y-axis and horizontal position is shown on the x-axis. For simplicity, it is assumed that all position changes happen in the horizontal direction. Different panels show various constant velocity motions: (A) rightward motion, (B) rightward motion as in panel A but at higher speed, (C) a stationary object, (D) leftward motion at speed identical to panel A and (E) abrupt changes in location that do not contain smooth physical motion but still evoke a sensation of object motion (the apparent motion phenomenon).

response from this unit is subtracted from that of another quadrature pair tuned to the opposite direction. This component of the model implements motion opponency. Here, the perceived motion direction is dependent not only on the detected motion direction, but also on whether the opposite direction signal is present. For example, if a moving grating is superimposed with another grating moving in the opposition direction, those motions cancel each other out, typically resulting in a perception of counterphase flicker. Other studies that were published in the same year (van Santen & Sperling, 1985; Watson & Ahumada, 1985) use slightly different approaches, but are similar in that they also make use of the space-time filters to analyze motion signals. Around the same time, Burr and Ross (1986) provided empirical support for a key role of spatiotemporal filters in motion detection. They psychophysically measured human visual sensitivity to moving gratings for a range of spatial and temporal frequencies and employed a masking paradigm to probe the spatiotemporal selectivity of stimulated motion detectors. The resulting sensitivity map revealed a spatiotemporal tuning function of the motion detector consistent with receptive field structures oriented in space and time.

Perception of Apparent Motion

While being seemingly simple, the Reichardt-style models can explain a number of perceptual phenomena, including the reverse-phi illusion (Anstis, 1970) and fluted-square-wave illusion (Adelson, 1982; Adelson & Bergen, 1985). One of the key predictions that the models make is that people should be able to see continuous motion, not only from an object that smoothly moves on a trajectory, but also from a static image that abruptly changes its position (Figure 10.3E). The latter—perception of continuous motion from static stimuli—is called apparent motion. Examples of apparent motion can be easily found in everyday life, such as neon marquee signs of old theaters, flip book animation, and *all* moving video viewed on TVs, computer screens, smartphones, and movie theater screens. Key properties and limitations of apparent motion are nicely illustrated in the wagon-wheel illusion (e.g., Finlay & Dodwell, 1987). This illusion was named after the depiction of wagons in Western movies, where the perceived direction of the rotating spokes of the wagon wheel reverses time-to-time. The phenomenon depends on the sampling rate of the video camera and the rotating speed of the wheel. If the sampling rate of the camera is sufficiently slow

relative to the rate at which spokes of the wheel rotate, the resulting rotating motion can be in the opposite direction from the real motion. Interestingly, a qualitatively similar illusion can also be experienced during natural viewing (e.g., when directly observing a rotating wheel of a car; Purves, Paydarfar, & Andrews, 1996). Several mechanisms have been proposed to account for such illusory motion reversals under continuous light, including the limitations in discrete sampling by the visual system (Andrews & Purves, 2005; VanRullen, Reddy, & Koch, 2006), rivalry between motion detectors encoding opposite directions (Kline, Holcombe, & Eagleman, 2004), and attentional tracking (Arnold, Pearce, & Marinovic, 2014). However, a convincing explanation of this phenomenon has been elusive.

Direction Selectivity

Early evidence for direction-selective channels comes from the work by Levinson and Sekuler (1975). To test the existence of independent direction-selective channels, the researchers used a summation technique, in which the contrast threshold for detecting the test moving grating was measured while a background grating moving in the opposite direction was presented at a subthreshold level. They hypothesized that, if a single channel encoded motion signals, then the presence of the subthreshold moving grating should help the detection of the test grating by adding the signals. The results, however, showed that the thresholds for detecting the test grating were not affected by the contrast of the background grating, supporting the hypothesis that independent channels in the brain encode opposite direction signals. Note that these results are not inconsistent with earlier described motion opponency, which describes interactions between suprathreshold motion signals (Stromeyer, Kronauer, Madsen, & Klein, 1984).

In primates and many other mammal species, direction selective cells can be first found in the primary visual cortex (V1). The pioneering work of Hubel and Wiesel in cats (Hubel & Wiesel, 1959) and monkeys (Hubel & Wiesel, 1968) showed that V1 neurons respond best to oriented lines, but also that a substantial portion of neurons in V1 is tuned to motion directions. These neurons respond best if an oriented bar moves across the receptive field in their preferred directions, while exhibiting a weak or no response for opposite, antipreferred, direction. Computational work has shown that the V1 neurons are well suited to analyze local motion information, which is subsequently fed into later stages of motion processing where more complex analyses take place (Emerson, Bergen, & Adelson, 1992; Heeger, Simoncelli, & Movshon, 1996; Simoncelli & Heeger, 1998).

Speed Perception

Successful perception of object motion requires the estimation of both direction and speed, which together define object velocity. However, relative to our understanding of motion direction perception, there is more uncertainty about the exact mechanisms underlying perception and encoding of speed. As noted earlier, Reichardt-type models can encode speed through adjustments in the delay unit and/or spacing of subunit detectors, while in motion energy models, speed is represented by spatiotemporal energy orientation. Speed perception, however, is more complex than just detecting local speed signals.

Our ability to discriminate speed is known to have constant Weber fraction (McKee, 1981; Orban, De Wolf, & Maes, 1984; Pasternak, 1987; Watamaniuk & Duchon, 1992), meaning that the minimum detectable speed difference increases in proportion to the base

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speed being compared. Yet, at the same time, perceived speed can vary depending on various factors. This includes luminance levels (slower perceived speed at lower luminance levels; e.g., Gegenfurtner, Mayser, & Sharpe, 2000), stimulus size (faster perceived speed for smaller stimuli; e.g., Ryan & Zanker, 2001), eccentricity (slower perceived speed at periphery than fovea; e.g., Johnston & Wright, 1986; Kwon, Tadin, & Knill, 2015), type of motion (radial motions appear faster than translations or rotations; e.g., Clifford, Beardsley, & Vaina, 1999; Geesaman & Qian, 1998), pursuit eye movement (slower perceived speed during pursuit; e.g., T. C. A. Freeman, Champion, & Warren, 2010), and past exposure to different speed distributions (Kwon & Knill, 2013). Of the factors that influence speed perception, the most widely studied is the effect of contrast on perceived speed. Everything else being equal, a lower contrast object will be perceived as moving more slowly than otherwise identical high contrast object (Stone & Thompson, 1992; P. G. Thompson, 1982). This effect is also known as the Thompson effect.

A key requirement for models of speed perception is to explain such biases in speed estimates under various test conditions. Currently, the leading model relies on a Bayesian framework to explain how deviations in speed perception arise (Stocker & Simoncelli, 2006; Weiss, Simoncelli, & Adelson, 2002). The critical aspect of this class of models is that it incorporates our prior knowledge of the speed statistics in the environment. Namely, a belief that objects in nature, while able to move fast, usually tend to be stationary or move at slower speeds. In the Bayesian framework, the perceptual inference of speed will be biased toward this *slow speed prior* in conditions where there is high stimulus uncertainty. This framework intuitively explains the Thompson effect. When the uncertainty is high because of

lower stimulus contrast, motion processing tends to rely more on the prior, biasing speed perception toward slower speeds (Weiss et al., 2002). A study shows that the slow speed prior, combined with optimal integration of signals from spatiotemporal channels, can adequately explain human speed percepts (Jogan & Stocker, 2015). A notable exception to the rationale for the slow speed prior occurs in visual periphery, which tends to be exposed to faster speeds both when we are moving in the world (W. H. Warren, Kay, Zosh, Duchon, & Sahuc, 2001) and when tracking a moving object (Kowler, 2011). Moreover, because we mostly move forward, motion in peripheral vision is biased toward centrifugal motions. Thus, if priors are derived from experience (Sotiropoulos, Seitz, & Seriès, 2011), then our peripheral motion perception should have a centrifugal prior. Indeed, perception of high uncertainty peripheral motion is biased in the centrifugal direction (R. Zhang, Kwon, & Tadin, 2013).

However, there is also evidence that the Bayesian framework cannot fully explain human speed perception (Hammett, Champion, Thompson, & Morland, 2007; Hassan & Hammett, 2015). In particular, the existence of the slow speed prior in central vision is inconsistent with the finding that the Thompson effect is only observed at slower speeds. At higher speeds, the bias is attenuated or even reversed such that the apparent speed is increased even at low contrasts (P. G. Thompson, Brooks, & Hammett, 2006; P. G. Thompson, 1982; although see Hawken, Gegenfurtner, & Tang, 1994). To account for this result, a biologically plausible model has been proposed, known as the ratio model (Hammett, Champion, Morland, & Thompson, 2005). The ratio model assumes that the speed can be estimated from the ratio of the responses from two channels broadly tuned to temporal frequencies (i.e., low- and high-pass channels). Recent evidence

suggests that a model that combines the ratio model together with a Bayesian slow speed prior can provide an explanation for a wide range of speed phenomena (Sotiropoulos, Seitz, & Seriès, 2014), indicating that speed perception likely arises from both biological constraints in the visual system and Bayesian computational strategies.

Studies have revealed the visual area MT as the most likely place for encoding speed signals. MT neurons are speed-selective (Maunsell & Van Essen, 1983a) and neurons with similar speed tuning are spatially clustered together (J. Liu & Newsome, 2003). The area MT seems to be functionally related to perception of speed as well, as evidenced by trial-by-trial correlation between neuronal activity and speed percepts in monkeys (J. Liu & Newsome, 2005). Furthermore, consistent with the earlier-described Thompson effect, the speed tuning of MT neurons shifts to lower speeds at low contrasts (Krekelberg, van Wezel, & Albright, 2006; although see Pack, Hunter, & Born, 2005). Neuroimaging work in humans also supports a key role of hMT+ in speed perception (Lingnau, Ashida, Wall, & Smith, 2009). Disruption of hMT+ with TMS biases and impairs speed perception (McKeefry, Burton, Vakrou, Barrett, & Morland, 2008), and the activity in hMT+ is stronger when participants perform a speed discrimination task than when they perform a contrast discrimination task (Huk & Heeger, 2000). In addition to MT, neurons in macaque V3 (Felleman & Van Essen, 1987), and human V3A are also implicated in speed processing (McKeefry et al., 2008).

If MT truly represents object speed, then speed tuning of MT neurons should be invariant to variations in spatial frequency. Similar to motion direction, speed is a combined property of space and time; the speed of a visual stimulus (degree per second), by definition, can be characterized as its temporal frequency (cycles per second) divided by spatial frequency (cycles per degree). Therefore, a neuron's selectivity to how fast stimuli move for a given spatial frequency does not necessarily indicate that the neuron is tuned to speed. Stated differently, a true speed-selective neuron should respond to *speed* independently from spatial frequency. A temporal-frequency-tuned neuron, in contrast, would respond well to stimulus speed only if a certain spatial frequency is present in the stimulus, thus, being dependent on both the spatial structure of the stimulus and its speed—a behavior known to be observed in V1 neurons (Foster, Gaska, Nagler, & Pollen, 1985).

Perrone and Thiele (2001) showed that the speed-preference in MT neurons is independent of spatial frequency. They measured MT responses to moving sine-wave gratings defined by various spatial and temporal frequencies. This resulted in a 'spectral receptive field' of a neuron showing the neuron's sensitivity along a spatiotemporal frequency map (Figure 10.4). About 60% of the neurons in MT had peak sensitivity along an oriented line on the map, and the neurons preferred speed could be reliably predicted from this oriented spectral receptive field. This suggests that the neurons in MT are tuned to speed rather than to temporal frequency, invariant to spatial structure of the stimuli (for a related model see: Perrone & Thiele, 2002). Exactly how speed-selective MT is, however, is still under debate. Priebe, Cassanello, and Lisberger (2003) showed that only 25% of MT neurons are tuned to object speed (although, the neurons became less dependent on spatial frequency when more complex grating stimuli were used). Furthermore, Priebe, Lisberger, and Movshon (2006) found that some V1 complex cells had speed preference invariant to spatial frequency, suggesting that some of the speed-tuning in MT may be inherited from V1 inputs. Recent work shows that properties
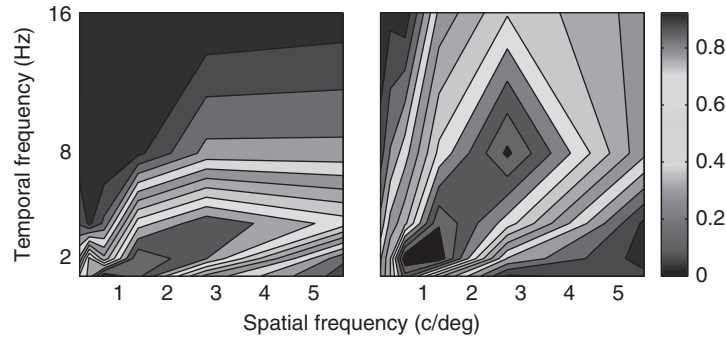
Figure 10.4   Example MT neurons with oriented spatiotemporal receptive fields (Perrone & Thiele, 2001). Shaded regions represent neurons' responses to a wide range of spatial and temporal frequency combinations. Orientedregions indicate that the optimal temporal frequency depends on stimulus spatial frequency. That is, these neurons are tuned to stimulus speed rather than to its temporal frequency. Color version of this figure is available at http://onlinelibrary.wiley.com/book/10.1002/9781119170174.
Source: Data courtesy of John A. Perrone.

of human speed perception, including spatially invariant speed tuning, may be optimal for encoding speed in natural image motions (Burge & Geisler, 2015). From this result, one can speculate that speed perception, and likely other aspects of motion processing, are constrained by strong evolutionary pressures to efficiently represent real world motion stimuli, eventually becoming optimal at extracting motion information from natural scenes.

GLOBAL MOTION ANALYSIS

Detection of local motion signals is a critical step in motion processing, yet it is grossly insufficient to account for our motion perception. As detailed in the next section, local motion signals can be very ambiguous and often differ from our perception. Nevertheless, we are able to accurately and effortlessly perceive a wide range of motion signals. Thus, a key question in motion research is elucidating how local motion signals are integrated into more global motion percepts that characterize our perceptual experience.

Ambiguity of Local Motion Signals: The Aperture Problem

A V1 neuron responds to stimuli over a small area of the visual field, known as the receptive field. That is, the receptive field of a V1 neuron works as an aperture through which the neuron monitors the world. In many cases, viewing motion through an aperture causes problems because the motion signal detected through this small aperture is ambiguous regarding both its direction and speed; numerous possible stimulus velocities can yield the same local stimulus within the receptive field. For example, imagine a vertically oriented bar moving rightward and viewed through an aperture that obscures its end points (Figure 10.5A). In this case, you correctly perceive the bar motion as rightward. However, the same perception can arise from a vertically oriented bar moving diagonally downward to the right (Figure 10.5B). In fact, if the diagonal motion is 1.41 times faster than the horizontal bar motion, the local motion information for the two situations in Figures 10.5A and B will be *identical*. The direction-selective cells in V1 encounter the same problem as they
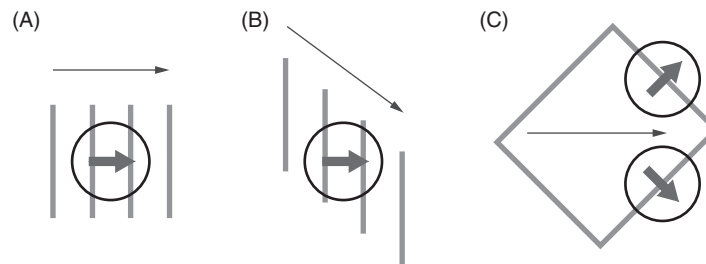
Figure 10.5   The aperture problem. In both (A) and (B), four vertical bars depict sequential positions of a single bar moving in directions given by thin arrows. When viewed through an aperture (circle), bar motions in (A) and (B) will be perceived as identical; moving horizontally to the right (thick arrow), despite large differences in their actual direction and speed (thin arrow). Similarly, global rectangle motion in (C; thin arrow) is not accurately represented when viewed through the two aperture locations. In fact, motion signals detected in the two apertures are different, despite arising from a coherently moving object. Apertures in these examples are equivalent to neurons' receptive fields, which, like these apertures, provide ambiguous information about the object's true motion. Color version of this figure is available at http://onlinelibrary.wiley.com/book/10.1002/9781119170174.

analyze local motion signals. This ambiguity about motion direction and speed is referred to as the aperture problem—it arises from V1 neurons viewing motion through an aperture smaller than the moving stimulus. The way our visual system solves this problem represents a long-standing question in motion research (Wallach, 1935) and remains an active area of investigation.
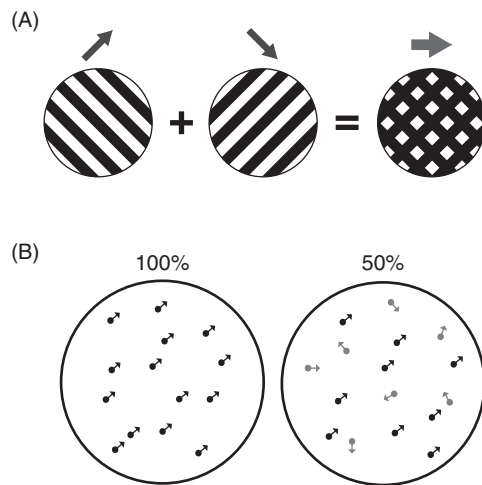
Motion Integration

The aperture problem illustrates the fact that small receptive fields of V1 neurons limit the ability of the visual system to accurately represent the velocity of large objects. For a rectangular object moving to the right (Figure 10.5C), two V1 neurons whose receptive fields are located at the edges will each encode the direction of the motion to be diagonally oriented toward the upper and lower right, respectively, incorrectly representing the global motion of the object. This is reminiscent of an old Hindu parable, where three blind men encounter an elephant in the forest. The first man touches the elephant's leg and concludes that it is a tree, phant's leg and concludes that it is a tree,

the second feels its ear and deduces it is a large leaf, while the third argues it is a snake after touching its tusk. Yet, if the men gather together and integrate their experiences, they can easily arrive to a correct decision. The same holds for ambiguous local motion signals—their ambiguity can be resolved by appropriate integration.

Indeed, perception of a moving object as a whole is often dissociated from the local motion signals within the object. This can be experienced in a class of stimuli known as plaids (Figure 10.6A; Adelson & Movshon, 1982); stimuli often used in studies investigating motion integration mechanisms. When two superimposed gratings are moving in different directions—say diagonally upwards and downwards to the right, the resulting global percept is a rightward moving plaid. This perceived pattern motion is not physically presented in the stimulus, but rather derived from the two individual component motions. Another type of a stimulus that shows such dissociation is the so-called random dot stimuli, in which a global motion percept arises from many, individually noisy, motion signals (Figure 10.6B). Imagine a

(A)

(B)

Figure 10.6   Examples of stimuli widely used to study motion integration. (A) A plaid stimulus is generated by superimposition of two moving gratings (diagonally upward and downward to the right). This arrangement results in a coherent rightward motion of the plaid stimulus. (B) Random dot stimuli consist of moving dots usually presented within an invisible circular aperture (shown here for illustration purposes only). Studies often manipulate motion coherence. A 100% coherent stimulus consists of only signal dots that all move in the same direction (left). At 50% coherence (right), half of the dots are coherent signal dots (black), while the other half are noise dots (gray) that move in random directions (dots are shown in different shades of gray for illustration purposes only).

school of fish or spots on a running leopard. Each of these stimuli can have a coherent global motion direction, even though directions of comprising components—individual fish and spots—may vary greatly from the global direction (for the leopard, local motion of individual spots will vary depending on their position on the leopard torso and limbs). Laboratory analogues of this situation are widely used motion coherence stimuli that are made up of individual signal dots that either move within a range of directions (Bisley, Zaksas, Droll, & Pasternak, 2004; Williams & Sekuler, 1984) or consist of

both coherently moving signal dots and randomly moving noise dots (Britten, Shadlen, Newsome, & Movshon, 1992).

Physiological studies have suggested that the middle temporal area (MT), which is known to be critical for motion perception (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Parker & Newsome, 1998; Salzman, Britten, & Newsome, 1990) is the neural locus of motion integration (Born & Bradley, 2005; Rust, Mante, Simoncelli, & Movshon, 2006; Simoncelli & Heeger, 1998; Stoner & Albright, 1992). MT neurons are broadly tuned to motion direction (Albright, 1984), inheriting responses from direction- (Movshon & Newsome, 1996) and speed-selective (Orban, Kennedy, & Bullier, 1986) neurons in V1. MT neurons have larger receptive fields than those in V1 (Dubner & Zeki, 1971; Maunsell & Van Essen, 1983b), making them suitable for integrating local signals across larger spatial extent. Indeed, neural responses in MT appear to be related to the perception of global motion. For instance, when presented with plaid stimuli, V1 neurons faithfully respond to component motion directions. However, a substantial portion of MT neurons responds to the pattern motion direction (Movshon, Adelson, Gizzi, & Newsome, 1985; Pack, Berezovskii, & Born, 2001; Rust et al., 2006). Similarly, representing global motion from random dots is too much of a challenge for V1 neurons, while the responses of MT neurons tend to match our corresponding perception of global motion (Britten et al., 1996; Parker & Newsome, 1998; Salzman et al., 1990). Using fMRI, such results have also been found in the human analogue of MT (hMT+) for plaids (Huk & Heeger, 2002; for a notable exception see Van Kemenade, Seymour, Christophel, Rothkirch, & Sterzer, 2014), as well as for random dots in which V1 responds better to incoherent motion while hMT+ responds better to coherent motion (Braddick et al., 2001).

To capture the transition from local motion detection in V1 to global motion detection in MT, Simoncelli and Heeger (1998) proposed a two-stage model of motion processing in which local motion is detected and integrated. The model starts with V1 simple cells, which detect local motion signals using linear spatiotemporal filters. Their responses are then rectified and normalized by the rectified responses of all cells to account for response nonlinearities, and pooled over local space to generate complex cell responses. In the next stage, responses of pattern-selective MT cells are modeled by linearly integrating responses of V1 complex cells, which gives rise to velocity preferences in MT. As in the first stage, MT responses are also rectified and normalized. This cascade of linear–nonlinear processes successfully explains responses of both V1 and MT neurons to component and pattern motion. Subsequent work elaborated on this model by, for example, incorporating surround suppression in V1 cells (Rust et al., 2006), and aiming to predict MT responses when viewing naturalistic movies (Nishimoto & Gallant, 2011). In particular, Rust et al. (2006) proposed a model where MT neurons linearly integrate responses of direction-selective V1 neurons that are affected by two kinds of divisive normalization, one deriving from a broad population of V1 neurons (untuned normalization) and the other deriving from each neuron's own responses (tuned normalization). A key strength of this model is that it can account for a wide range of pattern motion responses in MT by using a relatively simple and a biologically plausible architecture. For example, the tuned normalization component is consistent with surround suppression in V1 cells, which operates in a divisive manner and is selective for orientation and motion direction (J. R. Cavanaugh, Bair, & Movshon, 2002). In sum, this class of models strongly argues that nonlinear normalization mechanisms

likely play an important role in giving rise to complex motion sensitivity in MT.

A number of theoretical accounts have been suggested as ways to solve the aperture problem. This includes the vector averaging (VA) hypothesis and the intersection of constraints (IOC) hypothesis. The VA hypothesis argues that the coherent plaid percept can be predicted by the simple average of the local motion vectors. On the other hand, the IOC hypothesis (Adelson & Movshon, 1982) builds on an observation that the possible true motion vectors that each component grating can yield lie on a constraint line (Figure 10.7A). For plaids, the point where the constraint lines derived from the two component gratings intersect determines the speed and the direction of the perceived pattern motion (Figure 10.7B). Both VA and IOC accounts are not perfect, that is, there are circumstances where they fail to predict the resulting percept. For instance, the IOC hypothesis is not able to predict the perception of type II plaids (i.e., when the perceived pattern motion falls outside of the component grating vectors), while the VA hypothesis largely fails to predict the speed of the pattern percept (for a review see Bradley & Goyal, 2008). Psychophysical evidence suggests that humans can adaptively switch between the two strategies (Amano, Edwards, Badcock, & Nishida, 2009), reflecting some flexibility in the use of integration mechanisms.

These notable failures of IOC and VA hypotheses suggest that the proposed strategies might not be the sole mechanisms that the visual system uses to integrate local motion signals. Other interesting possible mechanisms in solving the aperture problem were later introduced. Using a Bayesian framework (already described in the Local Motion Analysis section), Weiss and colleagues (2002) argue that many motion phenomena, including motion perception in plaids, can be explained under the assumption
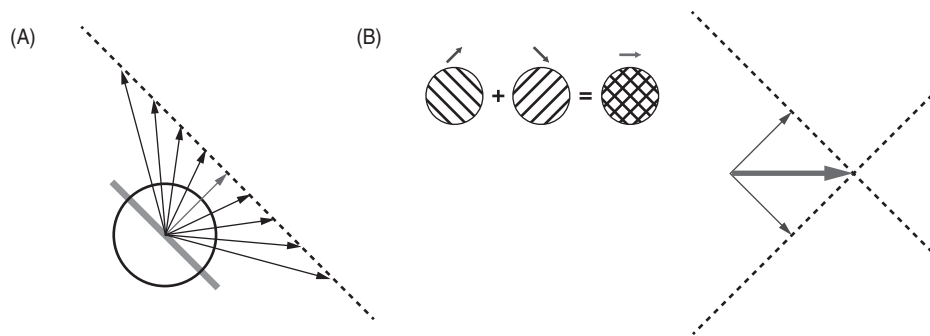
Figure 10.7   Intersection of constraints (IOC) hypothesis. (A) A range of possible motions (arrow angle and length represent direction and speed, respectively) of a moving bar that all result in the same perceived motion when viewed through an aperture (the arrow orthogonal to the dotted line). The dotted line, parallel to the orientation of the bar, represents the constraint on the possible velocities that are compatible with the motion of the bar. (B) The IOC hypothesis states that the perceived pattern motion (thick horizontal arrow) of a moving plaid is determined by the intersection of the constraints derived from its component gratings moving in orthogonal directions (oblique arrows). Color version of this figure is available at http://onlinelibrary.wiley.com/book/10.1002/9781119170174.

that our sensory measurements are noisy, and that the brain relies on a prior that slower motions are more likely to occur in the environment. The resulting Bayesian model effectively explains motion percepts under a wide range of uncertainty conditions. Another approach posits that the visual system makes use of *motion streaks* for estimating motion directions (Geisler, 1999). Motion streaks, analogous to speed lines used by artists to depict moving objects, are spatial orientation signals created by fast-moving objects that can be detected by motion-blind, orientation-sensitive mechanisms. The responses of these orientation-sensitive mechanisms could, in theory, provide additional information to canonical motion mechanisms. Recent evidence shows that spatial form information may indeed contribute to extracting pattern motion signals (Quaia, Optican, & Cumming, 2016).

Motion Segmentation

As outlined earlier, motion integration plays an important role in disambiguating local motion signals. However, such mechanisms

are only helpful if restricted to appropriate information. Integrating motion signals belonging to distinct objects or averaging motion from an object with that from background will degrade the effectiveness of motion perception. This raises an important question: How does the visual system determine which local motion signals should be integrated into a single coherent object or into the background? The answer involves finding a balance between two fundamental, but competing, processes: integration and segregation (Braddick, 1993). The goal of integration is to smooth variations in local motion signals and to connect them into a single surface, whereas segregation detects the changes in motion signals and parses the scene into different regions. Thus, effectiveness of motion processing strongly depends on the accomplishment of appropriate balance between the two conflicting demands of integration and segregation.

In contrast to motion integration, mechanisms of visual motion segregation are poorly understood. Previous studies have shown that there are various cues that we can rely on to

segment visual scenes. For example, visual form information can be used to determine whether or not local motion signals should be integrated (Lorenceau & Alais, 2001; Tadin, Lappin, Blake, & Grossman, 2002). However, even in the absence of other visual cues, segregation of objects using motion information can be remarkably effective (Nawrot, Shannon, & Rizzo, 1996). One way to achieve this is to take advantage of the spatial correlations. Because the neighboring regions of moving objects are likely to be correlated, the system can determine the extent to which a local signal should be assigned to an object by comparing it with nearby signals (Allman, Miezin, & McGuinness, 1985b; Rao & Ballard, 1999).

Such spatial (de)correlations of motion signals may be accomplished by ubiquitous center-surround mechanisms; responses of most visual neurons are affected not only by the stimulus falling on their classical receptive field centers, but also by the stimulus presented in the surrounding areas (Allman et al., 1985b). The effect can be both antagonistic and facilitatory. For example, in MT, the response is attenuated if the surround is filled with the neuron's preferred direction but facilitated when it is in the opposite direction (Allman, Miezin, & McGuinness, 1985a). Similar effects have been observed in a wide range of motion processing areas, indicating that center-surround mechanisms are general properties of visual motion processing (Tadin, 2015). Antagonistic center-surround mechanisms are particularly suitable for signaling object motion, since an object moving in the opposite direction from the background would reliably enhance neural responses (Nakayama & Loomis, 1974). Conversely, the motion of a large background, when presented alone, would result in a suppressed response. These hypotheses received some empirical support from an MT microstimulation

study (Born, Groh, Zhao, & Lukasewycz, 2000). Microstimulation applied to antagonistic center-surround neurons shifted the monkey's target pursuit eye movement towards the preferred direction of the neuron, while microstimulation of neurons without antagonistic surrounds shifted the pursuit towards the opposite direction. These results are consistent with coding of object motion by antagonistic center-surround neurons and coding of background motion by neurons preferring wide motion fields.

The existence of neural mechanisms that can subserve motion segregation, however, does not solve the issue of appropriately balancing conflicting demands of integration and segregation. In the absence of other explicit visual cues that can aid segregation (e.g., separation in depth, Nakayama, Shimojo, & Silverman, 1989), the visual system may rely on the quality of local motion signals to adaptively determine the appropriate extent of motion integration. If local signals are low in visibility or noisy, then aggressive integration may be necessary to average out noise. However, when local motion signals appear to be of high certainty, then there are clear advantages of employing earlier-described suppression mechanisms. Such adaptive balance between integration and suppression is evident in motion perception. At low contrast or high noise, increasing the size of a moving object results in improved motion perception. However, at high contrast, the observer's ability to discriminate motion direction of a high contrast grating becomes worse as the size of the stimulus increases (Tadin & Lappin, 2005; Tadin, Lappin, Gilroy, & Blake, 2003). This phenomenon, called spatial suppression, has been causally linked with hMT+ (Tadin, Silvanto, Pascual-Leone, & Battelli, 2011) and is consistent with contrast-dependent center-surround antagonism in area MT (L. D. Liu, Haefner, & Pack, 2016; Pack et al., 2005).

430   Motion Perception

Finally, we consider a special case of motion segregation that involves spatially overlapping stimuli. When two sheets of moving dots slide on top of each other in opposite directions, observers usually perceive two distinct moving stimuli—i.e., motion transparency is observed. This indicates that the visual system can correctly integrate and segment local motion signals even when presented in the same location. Spatial segregation seems to play a role in the perception of motion transparency, albeit on a much smaller spatial scale. If individual dots belonging to two normally transparent stimuli are paired such that pairs of oppositely moving dots occupy the same small region, the transparency percept changes into flicker (Qian, Andersen, & Adelson, 1994). In a companion article, Qian and Andersen (1994) found that MT responses were modulated in accord with perceptual changes in such stimuli, again supporting the role of MT in global motion analysis. However, there remain several challenges to be resolved to confirm the extent in which MT is involved in the perception of motion transparency. For instance, humans can perceive transparent motion from stimuli that are separated by smaller angular difference than the average tuning width of MT (Braddick, Wishart, & Curran, 2002). In addition, the speed selectivity (Masson, Mestre, & Stone, 1999) and the spatial scale (Mestre, Masson, & Stone, 2001) of motion segmentation in the perception of motion transparency match the receptive field characteristics of V1 neurons, indicating a possible role of V1. Recent evidence hints to a solution that selective pooling and nonlinear integration of MT neurons can explain the perception of transparency from stimuli consisting of smaller direction differences (J. Xiao & Huang, 2015).

HIGHER-ORDER MOTION

In addition to the distinction between local and global motion, there is another useful way to classify motion: first-order motion, second-order motion, and even higher-order processes that include third-order motion and feature tracking. In some cases, these distinctions are clearly defined and theoretically grounded, while in other cases, as detailed in the next section, they are still a subject of debate. This area of research peaked in 1990s, but the knowledge gained remains an important part of our understanding of motion perception.

Most of the studies described in this chapter involve first-order motion stimuli. Such stimuli involve movement of luminance-defined features (Figure 10.8a) that can be detected by a class of models described in the Local Motion Analysis section. While luminance-defined motion is arguably the most commonly occurring motion and certainly the most studied type of motion, we can perceive motion defined by modulations of other features, such as contrast and texture (Figure 10.8B; Badcock & Derrington, 1985, 1989; Cavanagh & Mather, 1989; Chubb & Sperling, 1988). In a typical contrast-defined motion stimulus (Figure 10.8B), the individual luminance-defined features (i.e., individual back and white checks) are randomly generated on each stimulus frame. Consequently, the stimulus contains no coherent first-order motion that can be detected by Fourier-based mechanisms. However, the spatial contrast envelope of luminance features is modulated such that contrast waves drift in one direction; leftward in this example.

Although there are some indications that first- and second-order motion could
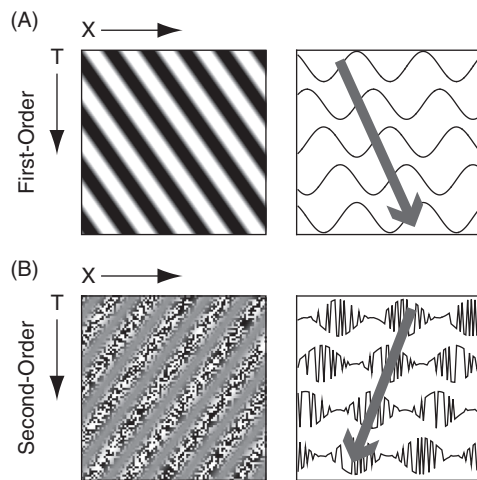
Figure 10.8 Schematic space-time illustrations of first- (A) and second- (B) order motion stimuli. (A) A luminance-modulated sinusoidal grating is shown as moving to the right. Its luminance envelope is depicted in the right panel. (B) A contrast-modulated dynamic random noise is shown as moving to the left. The spatial contrast envelope that modulates luminance features is depicted in the right panel. Thick arrows indicate the perceived motion direction. Color version of this figure is available at http://online library.wiley.com/book/10.1002/9781119170174. SOURCE: Figure courtesy of Davis Glasser.

be processed by largely overlapping neural mechanisms (Cavanagh & Mather, 1989; Hong, Tong, & Seiffert, 2012; Taub, Victor, & Conte, 1997), much of the evidence argues for at least a partial separation of first- and second-order motion processing. This includes psychophysical (Chubb & Sperling, 1989; Derrington & Badcock, 1985; Glasser & Tadin, 2011; Ledgeway & Smith, 1994; Nishida & Sato, 1995), neuroimaging (Ashida, Lingnau, Wall, & Smith, 2007), and neuropsychological studies. For example, Vania, Cowey and colleagues reported patients who had selective deficits in perceiving either first- or second-order motion (Vaina & Cowey, 1996; Vaina,

Soloviev, Bienfang, & Cowey, 2000). As detailed in the Motion Adaptation section later in this chapter, adaptation to first- and second-order motion results in different types of aftereffects. Basic properties of first- and second-order motion perception also differ. Our sensitivity to second-order motion is considerably weaker than our ability to perceive first-order motion (Ledgeway & Hess, 2002; Ledgeway & Hutchinson, 2005, 2008). These two types of motion perception also differ in their spatial and temporal properties. Perception of second-order motion is not only less efficient than our sensitivity to first-order modulations, but it is also more sluggish (Hutchinson & Ledgeway, 2006) and requires greater spatial integration (Glasser & Tadin, 2011).

Given the paucity of pure second-order motion stimuli outside of a handful of psychophysical laboratories and its earlier-described limitations, it is fair to question the functional role of dedicated second-order motion mechanisms. One argument is that, because of the high ecological importance of moving stimuli, it is advantageous to have mechanisms sensitive to even infrequent motion stimuli. For example, second-order motion perception dominates under conditions that suppress first-order mechanisms (Glasser & Tadin, 2011). Another argument is that second-order motion perception is related to a broader category that encompasses our ability to perceive motion based on attentional or feature tracking.

It is possible to design stimuli that have no unambiguous information available to the first- and second-order motion systems, but still yield a perception of motion. This includes motion percepts caused by changing the position of salient features and those caused by task instructions to track a cued feature. The former is commonly called

third-order motion (Lu & Sperling, 1995, 2001), while the latter is believed to reflect attentional feature tracking (Cavanagh, 1992; Verstraten, Cavanagh, & Labianca, 2000). Despite differences in how these two types of higher order motion are typically generated, they share a key defining characteristic in that both involve attention as a driving factor. These attentionally driven motion percepts share a number of properties with lower-order motion perception. Most notably, they yield a subjective impression of object motion. As such, attention-driven motion can, for example, induce different types of motion aftereffect (MAE; Culham, Verstraten, Ashida, & Cavanagh, 2000; Shim & Cavanagh, 2005). As both types of motion are driven by shifts in attention, they are considerably more sluggish than lower-order motion. However, they are differences in temporal dynamics. While third-order motion fails at frequencies higher than 3Hz (Lu & Sperling, 2001), subject-initiated feature tracking is even slower (Verstraten et al., 2000). More on links between attentional tracking and motion perception is in Motion Perception in the Context of Attention, Working Memory, Awareness, and Learning section.

What is the functional significance of second- and higher-order motion systems? They are considerably slower, less efficient and more attentionally demanding than first-order motion. Unlike first-order motion, they are driven not by motion energy but by stimulus features, providing flexibility of utilizing features other than luminance to detect motion. This also links higher-order systems more directly to object motion. As such, they help accomplish an important goal of motion perception—tracking where relevant objects are in dynamic environments. Second- and higher-order motion systems can accomplish this ecologically important goal even in cases when first-order motion information is ambiguous, corrupted or simply not available. In this framework, second-order motion can be conceptualized as a transitional system that can still take advantage of some aspects of bottom-up motion processing. This makes second-order motion processing faster and less demanding for resources than attention-driven motion perception.

MOTION AND POSITION

When objects move in the world, motion generally cooccurs with changes in object position. Yet, motion and position perception are typically studied in isolation from each other. Research has largely focused on simple paradigms in which motion signals are fixed in space, as is the case with most studies cited in this review. Two most widely used motion stimuli—gratings and random dots—are, in nearly all cases, presented in fixed spatial envelopes. In biological motion research (reviewed later in the chapter), the most common stimulus has been the *treadmill walker*. There are several reasons for why this has been the case. In neurophysiology, spatially fixed receptive fields favor the use of spatially fixed motion stimuli. Analogous constraints are shared by many behavioral studies, where the aim often is to keep the stimulus location fixed (e.g., to study adaptation and to avoid complications deriving from variations in motion processing between fovea and different locations in visual periphery). Moreover, psychophysical studies historically aimed to isolate motion processing by minimizing contributions from changes in object position (psychophysicists are very good at isolating things). Consequently, despite inherent coupling of motion and position, current theoretical frameworks conceptualize motion processing as largely independent from position.

There are, however, numerous instances where motion and position interact (Whitney, 2002). As detailed later, motion signals can have substantial effects on perceived position of objects. These mislocalizations are not just laboratory curiosities, but also have real life consequences. For example, motion-induced mislocalization has been shown to affect judgments of professional tennis referees (Whitney, Wurnitsch, Hontiveros, & Louie, 2008). The relationship between motion and position is bidirectional; changes in object position can be sufficient to evoke visual sensation of motion, even in the absence of net local motion signals in the stimulus (attention-driven motion; Cavanagh, 1992; Lu & Sperling, 1995, 2001; Verstraten et al., 2000). Here, we largely focus on reviewing effects of motion on position, concluding with a model that proposes a unifying framework for understanding these two closely related aspects of our visual perception (Kwon et al., 2015). For more detail on attention-driven motion, see the Higher Order Motion section.

A moving grating viewed through a stationary Gaussian window (i.e., a drifting Gabor) is a common stimulus used to study motion perception. De Valois and De Valois (1991) showed that the perceived position of a drifting Gabor is not given by the location of its stationary window, but it is shifted in the direction of the grating motion (Figure 10.9). This phenomenon—called motion-induced position shift (MIPS)—has been extensively studied. It occurs for a wide range of motion stimuli, including random dots (Ramachandran & Anstis, 1990), second-order motion (Bressler & Whitney, 2006), radial motion (Whitaker, McGraw, & Pearson, 1999) and motion in depth (Edwards & Badcock, 2003). MIPS increases with stimulus speed and duration (Arnold, Thompson, & Johnston, 2007; but see Chung, Patel, Bedell, & Yilmaz, 2007 for a potentially interesting exception).
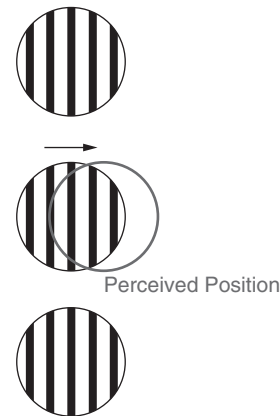
Figure 10.9 A schematic illustrating the motion-induced position shift described by De Valois and De Valois (1991). A rightward drifting stimulus presented in a stationary envelope is shown between two stimuli with no net motion. In this illusion, the perceived position of the center stimulus is shifted in the direction of its motion.

A seemingly related phenomenon occurs when a stationary target is flashed near a moving stimulus. Here, the target position shifts in the direction of the moving stimulus (Whitney & Cavanagh, 2000, 2002). This motion-induced mislocalization can occur even if the motion and the stationary flash are widely separated. Another phenomenon, called positional MAE, occurs when a stationary target is shown after motion adaptation (Nishida & Johnston, 1999; Snowden, 1998). Its position is shifted, but in the opposite direction from adapting motion (i.e., in the MAE direction). Notably, mechanisms underlying positional MAE are, at least in part, distinct those that account for traditional MAE (McKeefry, Laviers, & McGraw, 2006; Whitney & Cavanagh, 2003). Similar to motion-induced mislocalization, positional MAE is relatively resistant to spatial separation between the adapter and the test stimuli (McGraw & Roach, 2008; Whitney & Cavanagh, 2003). These findings indicate that motion can affect position coding over large spatial distances, both during

the stimulus motion and after it ends. Motion can also affect perceived object trajectory, as in the well-known curveball illusion (Shapiro, Lu, Huang, Knight, & Ennis, 2010; Tse & Hsieh, 2006). For example, a straight downward trajectory of a Gabor patch will be perceived as moving obliquely if (a) the Gabor patch contains horizontal pattern motion and (b) the stimulus is viewed in visual periphery. Interestingly, while the perceptual effect of the curveball illusion can be quite dramatic, resulting in trajectory deviations around 45 degrees, saccadic eye movements toward these moving objects are unaffected by the illusion (Lisi & Cavanagh, 2015). Thus, while motion affects perceived position of objects, these effects do not spill over to the action system.

Despite considerable research, mechanisms underlying motion-induced changes in position remain unclear. Arnold et al. (2007) found that apparent stimulus contrast is higher at the leading edge of a drifting Gabor and propose that this spatial modulation of stimulus contrast can account for MIPS. Although plausible, this account cannot fully capture MIPS phenomenology. For example, MIPS magnitude can be as big as the stimulus radius (Kwon et al., 2015), which can be hard to explain by modest shifts in the apparent stimulus contrast. Alternatively, MIPS could be explained by motion-induced shifts in visual receptive fields. Such receptive field shifts have been found in cat primary visual cortex, with properties broadly consistent with MIPS (Fu, Shen, Gao, & Dan, 2004). However, in human V1, positional BOLD signals evoked by Gabor drifting stimuli do not match perceived position shifts in MIPS (J. V. Liu, Ashida, Smith, & Wandell, 2006; Whitney et al., 2003). Studies have linked hMT+ with motion-induced changes in perceived position (Maus, Fischer, & Whitney, 2013; McGraw, Walsh, & Barrett, 2004)—findings consistent with our general

understanding of hMT+ as a key neural correlate of motion *perception* (as opposed to the physical motion stimulus). However, finding neural correlates of motion-induced changes in position only answers the "where" question, only providing hints about how to answer "how" and "why" questions.

A new framework for understanding MIPS and related phenomena re-conceptualizes the problem of motion and position coding as object tracking (Kwon et al., 2015). The assumption is that the brain exploits the intrinsic interdependency of motion and position, and integrates these signals into coupled perceptual estimates to adaptively track objects. Simply stated, the goal of the system is to estimate position of the object over time. This can be accomplished by considering both position signals and object motion. For example, rightward object motion is a good clue that the future object position will be in the rightward direction. When motion and position signals are in conflict (e.g., as in MIPS stimuli), the relative influence of each set of signals is determined by their reliability. This predicts larger influence of motion (i.e., larger MIPS) for blurred spatial envelopes and peripheral presentation—both being examples of degraded position signals. Computationally, this can be implemented as a Kalman filter (Kalman, 1960) that optimally weights sensory inputs based on their reliability. In fact, analogous computations are used for object tracking by the Global Positioning System (Challa, Morelande, Mušicki, & Evans, 2011). The resulting model (Kwon et al., 2015) accounts for MIPS over a range of stimulus conditions. Moreover, with no changes in model parameters, the same model can also account for perceptual speed biases (Stocker & Simoncelli, 2006), slowing of motions shown in visual periphery (Lichtenstein, 1963; Tynan & Sekuler, 1982) and the curveball illusion (Shapiro et al., 2010).

While these results still need to be replicated, Kwon et al. (2015) argue that we should be thinking about motion and position, not as two separate visual subdomains, but as two inherently related and inseparable stimulus properties (Burr & Thompson, 2011). Thus, rather than considering interactions between motion and position as surprising, we should be expecting those interactions to be ubiquitous.

We conclude with a consideration of the flash-lag effect—a phenomenon that is often discussed together with other motion-induced mislocalizations. When a static stimulus is flashed in spatial alignment with a moving object, the perceived position of the flash lags the perceived position of the moving object (Hazelhoff & Wiersma, 1924; Metzger, 1932). Since its modern rediscovery (Nijhawan, 1994), there has been a considerable amount of research on the flash-lag effect. Nijhawan's explanation centered around a fundamental constraint in neural processing. Given ubiquitous neural processing delays, sensory information is already ~100 ms old by the time it becomes perceptually available. This is particularly an issue for moving objects, which during those 100 ms, will move to different locations. To deal with this, the brain could simply extrapolate the position of moving objects, a solution that can account for the typical flash-lag effect (Nijhawan, 1994). However, we consider flash-lag separately from other motion-related mislocalizations because there is good evidence that the flash-lag effect is not best described as a motion phenomenon. It also occurs when the moving object is replaced with static changes in color or luminance (Sheth, Nijhawan, & Shimojo, 2000). Moreover, analogous effects occur for auditory and cross-modal stimuli (Alais & Burr, 2003; Arrighi, Alais, & Burr, 2005). Subsequent research has suggested explanations that are based on differential

latencies for flashed and moving stimuli (e.g., Whitney & Murakami, 1998), "postdictive" averaging of position (Eagleman & Sejnowski, 2000), as well as a range of other explanations. For in-depth reviews on this topic, see Hubbard, (2014), Shimojo (2014), Eagleman and Sejnowski (2007), Krekelberg and Lappe (2001), Nijhawan (2002), and Whitney (2002).

MOTION ADAPTATION

Our perception of the world depends not only on the current sensory input, but also on past stimulus history. For example, following a prolonged exposure to a moving stimulus, a stationary object will appear to be moving in the opposite direction from the previously viewed motion. This phenomenon, first documented by Aristotle, is known as the motion aftereffect (MAE; Anstis, Verstraten, & Mather, 1998) and it is a prototypical example for demonstrating consequences of visual motion adaptation. A famous real world example of MAE is the waterfall illusion (Addams, 1834). Prolonged viewing of a waterfall (i.e., downward motion) will result in the perception of illusory upward motion when one shifts his or her gaze to nearby stationary rocks. In the laboratory, the stimulus that induces adaptation (e.g., waterfall) is called the adapting stimulus, or the adapter. The subsequently presented stimulus for testing adaptation-induced changes in perception (e.g., stationary rocks) is called the test stimulus.

Adaptation to moving stimuli can actually lead to several different perceptual consequences. First, as in the waterfall illusion, it alters the perception of static or motion-balanced stimuli to be moving in the opposite direction from the adapting stimuli. Second, motion adaptation decreases visual sensitivity to the stimuli that share the same

visual properties as the adapting stimuli. For instance, detection of a low-contrast moving grating becomes more difficult after adapting to a high-contrast stimulus that moved in the same direction and had the same spatial frequency (Tolhurst, 1973). Third, motion adaptation can shift the perceived direction of a test stimulus either toward (attraction) or away from (repulsion) the adapting direction, depending on the angular difference between adapting and test directions (e.g., Levinson & Sekuler, 1976). This phenomenon, often called the direction aftereffect, is similar to the tilt-aftereffect in the orientation domain (Clifford, 2002).

Several factors can influence motion adaption and its effects. Like other types of visual adaptation, motion adaptation is selective. For instance, the strength of adaptation is the greatest when the adapting and test gratings have the same spatial frequency (Bex, Verstraten, & Mareschal, 1996). It also varies with stimulus properties. Peak adaptation effects, for example, have been found for stimuli with a temporal frequency of 5 Hz (Pantle, 1974) and stronger MAEs are perceived for complex (e.g., rotation and radiation) stimuli than translational motion (Bex, Metha, & Makous, 1999). Stimulus context also plays an important role (Day & Strelow, 1971; Murakami & Shimojo, 1995; Sachtler & Zaidi, 1993). Surround motion in the opposite direction from the adapter enhances adaptation strength, while high contrast surround moving in the same direction weakens it—a pattern of results consistent with center-surround suppression in the motion system (Murakami & Shimojo, 1995; Tadin, Paffen, Blake, & Lappin, 2008).

Motion adaptation is also influenced by other visual mechanisms such as attention and awareness. Given the known effects of attention on enhancing neural responses (e.g., Connor, Preddie, Gallant, & Van Essen, 1997), it can be hypothesized that attending to adapting motion direction should increase MAE strength (although see Morgan, 2012)—a hypothesis supported by Alais and Blake (1999). Using bivectorial stimuli, in which two sets of dots moved in different directions, the researchers showed that the perceived MAE direction can be modulated by selectively attending to one of the two sets of dots. Similar results are found for awareness. Reversing early findings that showed no effects of awareness on motion adaptation (Lehmkuhle & Fox, 1975), Blake and colleagues found that adapting to a motion stimulus that is suppressed from visual awareness results in attenuated MAE (Blake, Tadin, Sobel, Raissian, & Chong, 2006), revealing that MAE strength is modulated by perceptual awareness.

Adaptation has been widely used as the "psychophysicist's microelectrode" (Frisby, 1979)—a unique tool to investigate visual motion processing. Depending on types of stimuli and measurements used, psychophysical studies can tap into different levels of processing in the motion hierarchy. For example, Nishida and Sato (1995) showed that the use of different adaptation test stimuli—static vs. dynamic (e.g., flickering)—can reveal properties of low- and high-level motion mechanisms, respectively. Adaptation to second-order motion induced strong MAEs only for flickering test stimuli, while adapting to first-order motion induced MAE regardless of the test stimulus. Remarkably, when the authors used a compound adapting stimulus that contained first-order motion energy in one direction and a second-order motion signal in the opposite direction, the direction of the resulting MAE depended on the test stimulus. A static test appeared to move in the direction opposite to first-order adapting motion, while a dynamic test appeared to move in the opposite to the second-order motion signal. These results indicate that static and dynamic MAEs reflect

distinct motion processing mechanisms in the visual system, with dynamic MAEs tapping into higher levels of motion processing (Maruya, Watanabe, & Watanabe, 2008).

To further infer processing stages involved in motion adaptation, researchers utilized monocular adaptation paradigms and examined eye specificity of various MAEs. If the effect of adaptation transfers to the non-adapted eye, this indicates that the adaptation takes place at a relatively late stage in the motion processing hierarchy where the inputs from the two eyes are combined (Wade, Swanston, & de Weert, 1993). Supporting Nishida and Sato's (1995) conclusions, MAEs measured with a flickering test show a strong transfer between the eyes, while a static MAE exhibits a significant amount of eye specificity (Nishida & Ashida, 2000; Nishida, Ashida, & Sato, 1994). Generally, more complex motion stimuli result in greater interocular transfer (Steiner, Blake, & Rose, 1994). The interocular transfer of dynamic MAE, however, is abolished when the adapting stimulus is suppressed from awareness—further supporting the high-level nature of dynamic MAE (Maruya et al., 2008).

What neural mechanisms give rise to MAE and other effects of motion adaption? Early theories viewed MAE as a consequence of selective reductions in neural responses in motion processing areas in the brain—so-called the neural fatigue hypothesis. Sutherland (1961) proposed that perception of illusory motion following adaptation is driven by the ratio of responses among the direction-selective cells with opposite direction preferences. The idea is that neural responses of cells tuned to the adapting direction will be attenuated after adaptation, shifting the population response to a subsequently presented static stimulus in the opposite direction. Indeed, postadaptation response reductions that

are specific to the adapting direction have been observed both for single neurons in macaque area MT (Kohn & Movshon, 2003, 2004; Perge, Borghuis, Bours, Lankheet, & van Wezel, 2005; van Wezel & Britten, 2002) and in hMT+, as measured by fMRI (Huk, Ress, & Heeger, 2001; Krekelberg, Vatakis, & Kourtzi, 2005; H. A. Lee & Lee, 2012; Nishida, Sasaki, Murakami, Watanabe, & Tootell, 2003). Earlier studies of MAE using fMRI reported the neural response in hMT+ increases in response to a stationary stimulus after motion adaptation, which has been taken as evidence for the neural correlate of illusory motion perception in MAE (He, Cohen, & Hu, 1998; Tootell et al., 1995). However, it has been later shown that such increase in hMT+ response were confounded by attention (i.e., attention is required to perceive illusory motion from stationary stimuli), and that adaptation rather causes direction-selective reduction in neural response (Huk et al., 2001). Together, these results are consistent with perceptual desensitization that is observed following adaptation and suggest that cortical area MT may be a neural correlate of MAE.

However, more detailed investigations of adaptation-induced changes in neural responses paint a more complex and, arguably, interesting picture (for detailed reviews: Kohn, 2007; Krekelberg, Boynton, & van Wezel, 2006; Solomon & Kohn, 2014). Kohn and Movshon (2004) showed the reduction in responsiveness of MT neurons depends on the relationship between each neuron's preferred motion direction and adapting motion direction. Specifically, a neuron's post-adaptation response is most attenuated for motion directions that are near, but not identical to the adapting stimulus direction. Consequently, this results in narrowing of tuning width when the adapting motion is in neurons' preferred direction. On the other hand, when adapting direction is on

a flank of a neuron's turning curve (which, for any supra-threshold motion, would be most neurons responding to the adapter), the result is shifting the neuron's overall tuning *toward* the adapted motion direction. Notably, a simple population-coding model shows that such shifts in tuning curves can account for repulsive direction aftereffects observed in perception. Although Kohn and Movshon's (2004) findings are in contrast with earlier literature on how V1 neurons' tuning shift away from adapted orientation following adaptation (Dragoi, Sharma, & Sur, 2000; Felsen et al., 2002), a more recent work suggests that this discrepancy likely arises from different stimulus parameters used across studies. Using identical set of stimulus ensembles for both V1 and MT neurons, Patterson, Duijnhouwer, Wissig, Krekelberg, and Kohn (2014) revealed similar effects of adaptation in the two areas. In particular, adaptation in both V1 and MT resulted in either attractive or repulsive shifts, depending on stimulus size and adapting duration. In a separate project, Kohn and Movshon (2003) examined the contrast tuning of motion adaptation and found that the adaptation-induced reduction in the responsiveness of MT neurons was primarily due to changes in contrast gain. That is, adaptation to high-contrast gratings moving in the preferred direction of tested neurons had little effect on the maximum post-adaptation response, but rather it shifted the semisaturation point of the contrast response function to higher contrasts. This change in contrast gain following adaptation speaks against a simple account that adaptation merely reduces the overall neural response due to fatigue. Instead, it suggests an important functional role. Namely, by shifting the contrast response function, motion adaptation may allow a neuron to more efficiently encode a wider range of stimulus strengths in a manner similar to well-known light adaptation in retina (Shapley & Enroth-Cugell, 1984).

A strong argument against the conventional view of adaptation as related to neural fatigue is evidence for rapid motion adaptation. Traditionally, motion adaptation has been studied using prolonged periods of adaptation, ranging from several seconds to minutes. This is in contrast with natural viewing of motion, where, with a notable exception of smooth pursuit eye movements, neurons, and their receptive fields are typically exposed to moving stimuli for only a fraction of a second. However, even brief exposure to motion is sufficient to cause adaptation effects. Adapting to a moving grating for only a few tens of milliseconds can reliably produce MAEs in human observers (Glasser, Tsui, Pack, & Tadin, 2011). This perceptual observation is consistent with rapid adaptation observed in MT neurons (Glasser et al., 2011; Priebe, Churchland, & Lisberger, 2002; Priebe & Lisberger, 2002) and likely reflects adaptation at relatively early visual processing stages (Glasser et al., 2011). Given the dynamic nature of moving stimuli in the natural environment, this form of rapid adaptation may be particularly important in everyday visual motion perception. Namely, it indicates that motion adaptation occurs essentially every time we see motion. Whether motion adaptation effects observed at different timescales rely on distinct or same mechanisms remains largely unknown.

The functional role of motion adaptation, both rapid and prolonged, is an open research question. Similar to other visual adaptation mechanisms, motion adaptation may have both neural and perceptual functional significance (Clifford et al., 2007; Solomon & Kohn, 2014; Webster, 2011). Theories broadly suggest that adaptation can normalize stimulus-response relationships, adjusting the dynamic range of neural responses to the prevailing stimulus strength in the environment (Kohn & Movshon, 2003;

Ohzawa, Sclar, & Freeman, 1985), reduce redundancy in sensory responses (Wainwright, 1999) and increase saliency to novel stimuli (Gepshtein, Lesmes, & Albright, 2013; Solomon & Kohn, 2014; Webster, 2011). A long-standing hypothesis postulates that visual adaptation should increase discriminability around the adapting stimulus features (e.g., Clifford, 2002). However, in contrast with other visual domains such as orientation (Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001; Wissig, Patterson, & Kohn, 2013), perceptual benefits from motion adaptation have been difficult to find. Some studies report slight increases in sensitivity to speed (Clifford & Wenderoth, 1999; Kristjánsson, 2001) and either impaired or enhanced direction discriminability after an exposure to different stimulus distributions (Price & Prescott, 2012) but the results are not conclusive. More work is needed to better elucidate functional roles of motion adaptation, over both longer and shorter timescales.

MOTION IN THREE DIMENSIONS

The world we live in is three-dimensional (3D). Visual objects and scenes are structured in depth, and most of us are able to effortlessly perceive the rich three-dimensionality of our environment. The same is true for motion in the world. So far, we have discussed motion in two dimensions, largely focusing on translational motion in the frontoparallel plane. This represents a bulk of motion perception research. Yet, most moving stimuli arise from motion in depth (e.g., objects moving toward or away from the observer). Moreover, motion cues contribute significantly to our depth perception. This section focuses on two important aspects of motion perception: mechanisms that subserve our ability to perceive 3D motions and those that aid our ability to see 3D structures in the environment based on motion.

Structure From Motion

If we think about the computations necessary to perceive the world in three dimensions, it is quite remarkable how readily the visual system accomplishes this complex task. The sensory inputs for vision—the retinal images—are two-dimensional (2D). As discussed in Chapter 9 of this volume, the visual system uses a range of strategies to recover the 3D structure that gives rise to these flat retinal images. Among these strategies, motion can be particularly effective. An easy way to visualize this is to use shadows. Imagine a shadow of a bent paper clip projected on a wall by a single light source. The 3D structure of the paper clip is difficult to discern from the flat shadow, but it becomes instantly apparent if we start rotating the paper clip (in fact, motion is the only cue that allows you to infer the 3D structure in this case). This effect is known as *structure-from-motion* (or the kinetic depth effect; Wallach & O'Connell, 1953) and demonstrates that motion is a powerful cue for seeing 3D structure of objects.

To study the mechanisms of structure-from-motion, researchers mostly rely on random dot displays similar to the one depicted in Figure 10.10. It is a 2D projection of a transparent rotating cylinder whose curved surface is covered with opaque random dots. Similar to the paper clip shadow example above, observers are able to readily perceive a 3D cylindrical structure solely from the motion of such stimuli (R. A. Andersen & Bradley, 1998). However, because there are no other depth cues, the direction of the cylinder rotation is ambiguous; the depth ordering of the cylinder surfaces (i.e., which surface is in the front) cannot be specified by 2D motion of dots. Thus, as in other cases
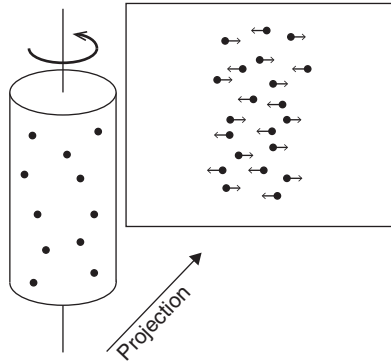
Figure 10.10   2D projection of dots placed on the surface of a transparent 3D rotating cylinder. The resulting 2D stimulus consists of dots moving to either to the left or right.

of visual ambiguity (Leopold & Logothetis, 1999), the visual system selects one of the two competing interpretations at a time, with the resulting percept of rotation direction switching every few seconds.

Other primates, such as rhesus monkeys, can also detect structure from motion in a similar manner to humans (Siegel & Andersen, 1988). Neurophysiological studies in monkeys point to MT as a neural locus for perceiving structure-from-motion. Responses of the MT neurons correlate with monkeys' perceptual report of the rotation direction of the ambiguous rotating cylinders (Bradley, Chang, & Andersen, 1998; Dodd, Krug, Cumming, & Parker, 2001). Furthermore, microstimulation of disparity-selective cells in MT (i.e., cells sensitive to stereo depth) can bias monkeys' depth perception toward the preferred disparity of stimulated neurons, indicating a role of MT in discerning depth in structure-from-motion stimuli. Similarly, activity in hMT+ is stronger when humans view motion stimuli that imply 3D structure than when the stimulus is 2D motion (Orban, Sunaert, Todd, Van Hecke, & Marchal, 1999). Such increased activity seems to reflect the role of hMT+ in disambiguating motion surfaces, rather than processing the 3D form

per se. To distinguish between the two, E. Freeman, Sterzer, and Driver (2012) used two types of motion stimuli—cylindrical and flat—where both contained two different motion surfaces, but only the cylindrical stimulus implied a coherent 3D form. They found that the lateral occipital cortex (LOC), as measured by fMRI, distinguished between the two types of stimuli, whereas hMT+ did not. The result is consistent with the well-established role of LOC in processing 3D form (Grill-Spector, Kourtzi, & Kanwisher, 2001), and suggests that MT may be more important for segmenting spatially overlapping motion surfaces.
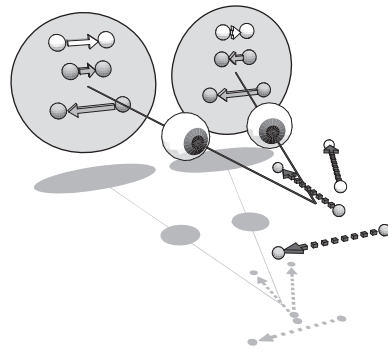
Motion in Depth

Motions of moving objects in the world rarely move along a single, frontoparallel 2D depth plane. That is, most object motion also occurs with changes in depth (i.e., moving toward or away from the observer). This type of motion is commonly called motion in depth, or 3D motion. To perceive motion in depth, the visual system can rely on both monocular and binocular cues (Brenner, van den Berg, & van Damme, 1996; Regan & Beverley, 1979), with each being informative under different conditions (Gray & Regan, 1998). A well-known monocular cue is "looming" (Beverley & Regan, 1983). As an object approaches the observer, the size of its retinal image increases rapidly. The rate of this retinal expansion gives the observer information about time-to-collision—the time when the looming object will hit the observer (D. N. Lee, 1976). Geometric rules governing looming are similar to those underlying optic flow patterns that result from self-motion (discussed later in this section). Looming, however, is distinct from optic flow. Human observers are sensitive to looming-like changes in stimulus size, which can be used to estimate the rate of expansion independently from the optic flow

cues (Schrater, Knill, & Simoncelli, 2001). Processing of looming is automatic and precise. Looming stimuli that are on a collision path with an observer capture attention, while those that would result in a close miss do not. Notably, this occurs even when the stimuli are suppressed from perceptual awareness (Lin, Murray, & Boynton, 2009).

Binocular cues can also provide reliable information for perceiving motion in depth (for a review see Harris, Nefs, & Grafton, 2008). Here, the visual system takes advantage of the fact that motion in depth creates different motion signals in each eye. For example, the retinal motion in each eye will be in opposite directions when an object moves directly towards an observer (Figure 10.11). On the other hand,

◐ 3D (direct)   ● Frontoparallel   ○ 3D (oblique)

Figure 10.11   Illustration of various 3D motion trajectories and corresponding retinal motions in each eye. An object moving directly towards the observer produces opposite retinal motion (the middle set of arrows within large gray circles), while a three-dimensional oblique motion causes signals in same direction, but at different speeds in the two eyes (white arrows and circles). Frontoparallel motion creates similar retinal motion in each eye (the bottom pair of arrows). Color version of this figure is available at http://onlinelibrary.wiley.com/book/10.1002/9781119170174.
SOURCE: From Czuba, Huk, Cormack, and Kohn (2014). Reproduced with permission of The Society for Neuroscience.

if the object moves obliquely to the left of the observer, the retinal motion in the two eyes will have an identical direction but different speeds (Figure 10.11, white arrows and circles). This cue is called the interocular velocity difference (IOVD). Differences in motion signals in each eye invariably create another binocular motion cue that is coupled with IOVD—changes in binocular disparity (CD). An object moving in depth causes changes in its relative retinal location between the two eyes—a binocular cue that contains information about its 3D motion. Studies have shown that motion in depth based on these two types of binocular cues may be processed by mechanisms that are distinct from those involved in processing 2D motion. Czuba, Rokers, Guillet, Huk, and Cormack (2011) found that human observers adapt to motion in depth, which, notably, could not be explained by separate adaptation to 2D motion in each eye. This finding indicates the existence of specialized motion in depth mechanisms that integrate motion inputs from the two eyes. Perception of motion in depth also has distinct temporal integration profiles (Katz, Hennig, Cormack, & Huk, 2015), showing less temporal integration than 2D frontoparallel motion.

To elucidate contributions of IOVD and CD cues to perception of motion in depth, researchers commonly use random dot displays where each cue can be experimentally isolated. CD cues can be isolated by randomly repositioning dots in each frame while smoothly changing disparity over time. This effectively removes coherent monocular motions and thus eliminates IOVD cues. On the other hand, IOVD cues can be isolated by anticorrelating the dots between the two eyes, which substantially reduces CD cues without affecting IOVD. Using this strategy, studies have found that human observers can rely on both types of cues for perceiving motion in depth (Cumming & Parker, 1994;

Fernandez & Farell, 2005; Shioiri, Kakehi, Tashiro, & Yaguchi, 2009), but with different sensitivity profiles that depend on speed and eccentricity (Czuba, Rokers, Huk, & Cormack, 2010); sensitivity to CD cues is best near the fovea and for slower speeds, while IOVD cues become more important with increasing with eccentricity and speed. Overall, however, empirical evidence indicates that IOVD cues are a better source of information for discriminating motion in depth (Czuba et al., 2010). A recent fMRI study revealed that hMT+ may play a key role in representing motion in depth based on both CD and IOVD (Rokers, Cormack, & Huk, 2009). However, work in both awake and anesthetized monkeys showed that the contribution of IOVD cues to MT responses seems to be greater than that of CD cues (Czuba, Huk, Cormack, & Kohn, 2014; Sanada & DeAngelis, 2014). In humans, an area anterior to hMT+ selectively responds to CD cues (Likova & Tyler, 2007), suggesting an involvement of multiple brain areas in perceiving motion in depth.

Motion Parallax

When we make head-movements, compensatory eye rotations allow us to keep our eyes fixated on an object. Such self-movements create very informative changes in retinal image patterns. For instance, if you move your head side-to-side while trying to fixate on an object in a cluttered visual scene, the retinal motion of objects in the scene will depend on their depth relative to the object you are fixating. The objects that are near will create retinal motion in the opposite direction from your head movement, while the retinal image of far objects will move in the same direction. In addition, the speed of the retinal motion will be inversely related to the distance of the objects from the fixation point; retinal motion of objects that

are near the fixation object will be slower than the motion of objects that are more distant. Clearly, the retinal motion pattern in this situation—commonly called motion parallax—contains a wealth of information about the 3D structure of the world. An analogous situation occurs when an observer is translated though the environment—for example, when fixating on a landscape feature while riding a train.

Researchers have found that motion parallax can provide a remarkably strong depth cue, allowing similar levels of perceptual sensitivity to depth from binocular cues (B. Rogers & Graham, 1979, 1982; but see (Bradshaw, Hibbard, Parton, Rose, & Langley, 2006) within only about 30 ms (Nawrot & Stroyan, 2012). The activity of MT neurons have been linked to perceptual sensitivity in discriminating depth based on motion parallax (H. R. Kim, Angelaki, & DeAngelis, 2015); the most sensitive neurons in MT showed a level of sensitivity close to that of behavior. Furthermore, responses of MT neurons predicted trial-by-trial variability in the animal's perceptual decisions.

While motion parallax can provide sufficient information for depth perception, it has been suggested that the visual cues alone may not be enough to disambiguate depth from motion parallax (Ono & Steinbach, 1990; S. Rogers & Rogers, 1992). Specifically, in the absence of pictorial depth cues (e.g., size or occlusion), objects that are located near or far from the fixation plane can create identical retinal motions for opposite directions of observer motion; a near-object will create rightward retinal motion as the observer translates to the left, and the same retinal motion will be produced for a far-object as the observer translates to the right. In such cases, the visual system needs to rely on extra-retinal information, critically, the efference copy of eye-movement signals (Aytekin & Rucci, 2012;

Nadler, Nawrot, Angelaki, & DeAngelis, 2009; Nawrot, 2003a, 2003b). Resolution of this ambiguity appears to take place in the cortical area MT, which has been shown to integrate extra-retinal eye-movement signals with retinal image motion to represent depth from motion parallax (Nadler, Angelaki, & DeAngelis, 2008; Nadler et al., 2009). Using a virtual-reality platform that translates monkeys in space, Nadler et al. (2008) recorded MT responses to a visual stimulus during simulated or physical translation (i.e., extra-retinal signals available). The visual stimulus was made ambiguous to depth signs (i.e., near or far relative to fixation) and identical across movement conditions, such that any differences in MT responses could only be accounted by the presence of extra-retinal signals. Their results showed that the responses of many MT neurons were stronger for their preferred depth sign when the motion parallax was caused by physical translation than when motion parallax was simulated, providing the evidence that MT neurons integrate extra-retinal signals to represent depth. Inversely, a more recent work shows that retinal image motion, namely dynamic perspective cues, can be used to infer the eye-rotation and disambiguate depth sign in MT (H. R. Kim, Angelaki, & DeAngelis, 2014).

Optic Flow

When we move through a stationary environment, a large pattern of motion is produced on the retina, which depends on both our own movement and the structure of the environment. This global pattern of retinal motion is known as the optic flow (Koenderink, 1986). A prototypical example can be found during driving. When you are driving a car, stationary objects in the visual scene create a flow of expanding retinal motion. As you have probably experienced from a 3D movie, optic flow can often give you a strong illusory sense of self-motion.

Neurophysiological studies have linked many different higher-level visual areas with optic flow processing, including the areas MST (medial superior temporal; Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Tanaka, Fukada, & Saito, 1989), VIP (ventral intraparietal; Bremmer, Duhamel, Ben Hamed, & Graf, 2002; T. Zhang, Heuer, & Britten, 2004), 7a (Siegel & Read, 1997), STP (superior temporal polysensory; Anderson & Siegel, 1999), and V6 (Fan, Liu, DeAngelis, & Angelaki, 2015). Among these areas, MST (specifically, the dorsal section; MSTd) has been the core of numerous investigations. The neurons in MST have large receptive fields, which can extend up to $100°$ in diameter (Duffy & Wurtz, 1991), making it suitable for spatially integrating motion signals over large areas. Mathematically, optic flow can be broken up into translation, expansion (or contraction), rotation, and shear (Koenderink, 1986) Notably, MST contains neurons that have receptive fields sensitive to these optic flow components (Duffy & Wurtz, 1991; Saito et al., 1986), with many of them showing comparable or better neuronal sensitivity than the animal's perceptual thresholds in optic flow discrimination (Heuer & Britten, 2004). These further suggest a key role of MST in optic flow processing. Human homologues of MST have been identified as subsections within hMT+ that respond to the optic flow components (Morrone et al., 2000) and have large receptive fields that include both ipsilateral and contralateral regions (Huk, Dougherty, & Heeger, 2002).

One of the most important functions of optic flow is to help us estimate the current direction of our self-motion—also known as our heading. Assuming no additional eye and head movements, the focus of expansion in the optic flow signals heading. Human

observers are remarkably accurate at perceiving heading from optic flow, with thresholds ranging between just 1–2 degrees (W. H. Warren & Hannon, 1988). MST seems to be closely related to the perception of heading from optic flow. Microstimulation of MST neurons biases monkeys' heading judgments (Britten & van Wezel, 1998), showing causal involvement of MST in heading perception. During natural behavior, optic flow stimuli are typically paired with matching vestibular signals. MST neurons also show responses selective to the translation of the body even in the absence of visual inputs (Duffy, 1998; Gu, Watkins, Angelaki, & DeAngelis, 2006), which reflect the presence of vestibular signals in the area. Together with the visual information, these vestibular signals contribute to the perception of heading (Dokka, DeAngelis, & Angelaki, 2015; Gu, Angelaki, & DeAngelis, 2008; Gu, DeAngelis, & Angelaki, 2007; see the Multisensory Motion Perception section for more details).

Heading estimation from optic flow becomes complicated when we make head- or eye movements. For instance, in the driving example above, if you make an eye movement while driving, translational retinal motion from the eye rotation will be added to expanding optic flow. The visual system needs to disambiguate the two sources of retinal motion in order to correctly perceive the heading direction (aka the rotation problem; Britten, 2008; Lappe, Bremmer, & van den Berg, 1999; W. H. Warren, 2008). Both visual and nonvisual accounts have been proposed in solving the rotation problem. The visual account suggests that the visual signals alone can provide sufficient information for the perception of self-motion. A support for this can be found in studies where researchers exploited optic flow that simulated eye rotations (i.e., without the extraretinal signals available) and found unimpaired performance in heading perception (Stone &

Perrone, 1997; van den Berg, 1992; W. H. Warren & Hannon, 1988). However, other studies have shown that nonvisual, extraretinal signals are needed to compensate for eye rotation for accurate heading perception (Banks, Ehrlich, Backus, & Crowell, 1996; Royden, Crowell, & Banks, 1994). Neurophysiological studies suggest that neurons in MST partially compensate for eye rotations during self-motion (Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Shenoy, Bradley, & Andersen, 1999), with the degree of compensation increasing with pursuit speed (Shenoy, Crowell, & Andersen, 2002).

While global, wide-field mechanisms are well suited for representing optic flow and inferring heading, the visual system must solve another computational problem, namely, detecting moving objects during self-motion. Here, the visual system must determine which local motion vectors in the optic flow field are caused by the observer's movement through a stationary environment and/or by a moving object (Rushton & Warren, 2005; P. A. Warren & Rushton, 2009). This is an ecologically important problem—correct perception of other moving objects is arguably even more crucial during self-motion in order to avoid obstacles and interact with other objects. To separate object motion from optic flow, observers can globally subtract out the optic flow motion pattern, which is likely caused by self-motion (P. A. Warren & Rushton, 2009; Figure 10.12). This global flow parsing process, if successfully accomplished, effectively isolates external object motion signals, and thereby facilitates their detection. Layton and Fajen (2016) recently showed that a simple model that implements feedback connections from MST to MT and disinhibition of opponent signals in MT can explain the perceived object motion in the presence of optic flow, providing insights into possible neural mechanisms of flow parsing. In addition, object motion
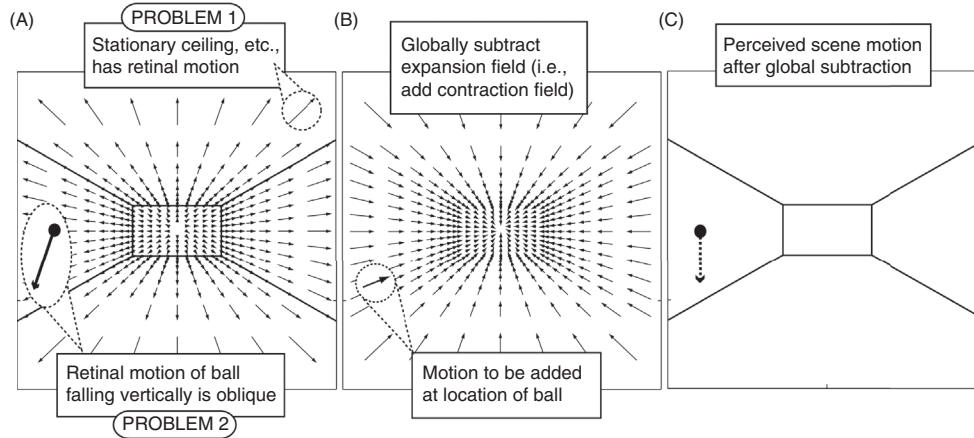
Figure 10.12 Flow parsing hypothesis. (A) Forward self-motion down a hallway creates a pattern of optic flow derived from the structure of the hallway (thin arrows). A vertically falling object creates an oblique retinal motion (thick arrow) due to the addition of local optic flow signals. (B) To correctly perceive the object motion, the visual system can subtract the global flow pattern. This is equivalent to the addition of a contraction field that is opposite to the induced optic flow. (C) This global subtraction results in a correct perceived vertical motion of the object.
SOURCE: From P. A. Warren and Rushton (2009). Reproduced with permission of Elsevier.

discrimination during self-motion can also be improved when vestibular self-motion signals accompany optic flow (MacNeilage, Zhang, DeAngelis, & Angelaki, 2012). Current psychophysical evidence suggests that flow parsing and heading perception may rely on similar neural computations (Foulkes, Rushton, & Warren, 2013), however, more studies are necessary to reveal the similarities, differences, and interactions between the two.
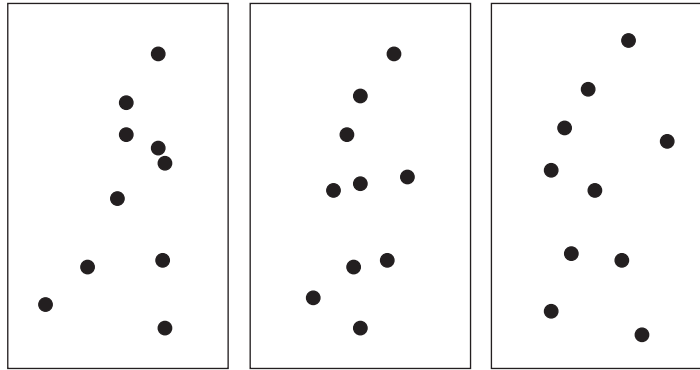
BIOLOGICAL MOTION

Perceiving the actions and intentions of other biological creatures is a fundamental neural function, especially for social animals. This ability allows us, for example, to distinguish between friendly and threatening situations and deduce emotional states of conspecifics. These inferences, which can be quite complex, are based on a wide range of visual and other sensory cues. Among them, visual motion plays a critical role. In fact, we are so sensitive to certain types of biological movement that the mechanisms behind this exceptional sensitivity have been dubbed *life detectors* (Troje & Westhoff, 2006).

Empirical study of biological motion has relied heavily on point-light (PL) animations (Figure 10.13). Popularized by Johansson (1973), these animations are composed of a small number of dot markers usually placed on the head and major joints of the body. When presented as static single frames, observers typically report perceiving meaningless groups of dots, but when presented in succession, dot motions create a vivid global percept of an animal in action. Here, we cover the major themes relevant to visual motion processing in biological motion perception. More details can be found in Chapter 11, this volume, and in reviews by Blake and Shiffrar (2007), Troje (2008), and Yovel and O'Toole (2016).

PL animations can convey much more than simply the presence of a biological creature.

Figure 10.13   A typical stimulus used to study biological motion. Each rectangle represents a frame of an animation. Dot markers in each frame may seem random, but a coherent form (a treadmill walker) is perceived when the frames are shown in succession. These stimuli are called point-light animations because the same effect is seen when viewing an actor moving in a dark room with small lights attached to various points on her or his body.

Within a brief period of time, we can extract detailed information about the actor from PL animations (Johansson, 1973). Human observers can recognize identity (Cutting & Kozlowski, 1977), gender (Hill & Johnston, 2001; Mather & Murdoch, 1994), type of activity (Dittrich, 1993) and emotional states of a PL person (Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Pollick, Paterson, Bruderlin, & Sanford, 2001). Even facial expressions can be easily discerned from corresponding PL animations (Bassili, 1978; Pollick, Hill, Calder, & Paterson, 2003). In fact, perceiving facial movements can help with speech perception: viewing PL faces facilitates speech understanding when there is uncertainty in auditory signals (Rosenblum, Johnson, & Saldaña, 1996). This ability to perceive living creatures from biological motion appears to be shared among different animal species and is present over nearly the entire human lifespan. Infants as young as 3 months are sensitive to biological motion (Fox & McDaniel, 1982), and this ability remains preserved in senescence (Norman, Payton, Long, & Hawkes, 2004). Other animals, including cats (Blake, 1993) and newly hatched chicks (Regolin, Tommasi, & Vallortigara, 2000), also perceive biological motion from PL displays. Biological motion, even when depicted with just a handful of dots, is rich in stimulus information (J. M. Gold, Tadin, Cook, & Blake, 2008), which, as detailed earlier, can be used for a remarkably wide range of visual functions.

Visual information in PL animations largely consists of local motion signals derived from individual dot motions, as well as dynamic global cues arising from relative motion of the same dots (J. Kim, Jung, Lee, & Blake, 2015). Therefore, by design, visual form perceived in these displays derives almost exclusively from motion cues (see below for a notable exception; Beintema & Lappe, 2002). Given the significant separation of form and motion processing in the brain (Mishkin, Ungerleider, & Macko, 1983), this makes studying PL displays particularly interesting as they offer a prominent example demonstrating extensive interactions between form and motion (Kourtzi, Krekelberg, & van Wezel, 2008). However,

this also makes it harder to pinpoint mechanisms underlying biological motion, with research revealing influences of both low- and high-level motion mechanisms, as well as interactions with visual form cues.

A role of low-level motion mechanisms is indicated by the observation that the perception of biological motion is degraded when low-level motion processes operating over short timescales are disrupted (Mather, Radford, & West, 1992). Subsequent work, however, has shown that biological motion perception is possible even with deteriorated low-level motion cues, although such stimuli require focused visual attention (Thornton, Rensink, & Shiffrar, 2002). Biological motion processing also requires considerably longer integration times than simple translational motions (Neri, Morrone, & Burr, 1998), again suggesting involvement of higher-level mechanisms. It is worth noting that most biological motion studies rely on stimuli that do not involve global changes in the position of the body (e.g., a commonly used treadmill walker; Figure 10.13). This helps isolate motion information from individual body parts, and, notably, the relative limb movements. However, this also ignores potentially important information contained in the global body motion (Thurman & Lu, 2016)—locomotion usually results in global changes of an animal's position.

Global form information, although only implicit in typical PL animations, also plays a key role. Form cues present in PL animations can provide an efficient reference frame for encoding other visual stimuli (Tadin et al., 2002). Observers can perceive biological motion even in modified PL displays devoid of coherent local motion information (Beintema & Lappe, 2002). In these displays, dots defining a PL walker could appear anywhere on the walker's limbs, and, critically, would randomly change positions each animation frame—eliminating coherent local motion cues, but preserving dynamic form information. The role of global form cues in biological motion perception is further supported by the inversion effect (Dittrich, 1993; Reed, Stone, Bozova, & Tanaka, 2003). Similar to face processing, action perception from PL animations deteriorates when the stimulus is flipped upside down (Pavlova & Sokolov, 2000; Sumi, 1984). However, even this inversion effect can be explained, at least in part, by low-level motion processing (Troje & Westhoff, 2006). It appears clear that both local and global mechanisms contribute to biological motion perception (Boxtel & Lu, 2015), and it is likely that their relative contributions may depend on the nature of the task (Chang & Troje, 2009). Such complexity in biological motion perception makes it necessary to investigate the phenomenon at different levels of processing (Troje, 2008), broadly encompassing lower-level visual mechanisms as well as top-down contributions, such as attention (Cavanagh, Labianca, & Thornton, 2001; Tyler & Grossman, 2011) and learning (Grossman, Blake, & Kim, 2004).

Mirroring behavioral findings reviewed in the previous paragraph, neural mechanisms of biological motion perception also indicate the involvement of multiple levels of processing. Evidence from patients with posterior brain lesions shows double dissociations between performance on simple motion coherence tasks and biological motion perception—clearly indicating that the mechanisms underlying biological motion perception are distinct from canonical motion processing discussed elsewhere in this chapter (Battelli, Cavanagh, & Thornton, 2003; Cowey & Vaina, 2000; Schenk & Zihl, 1997; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990). In fact, biological motion processing has been linked with a network

of brain areas (Grosbras, Beaton, & Eickhoff, 2012), with a critical role of posterior superior temporal sulcus (pSTS). The involvement of pSTS in biological motion perception is supported by neuroimaging (Bonda, Pestrides, Ostry, & Evans, 1996; Grossman et al., 2000, 2004), neurophysiology (Oram & Perrett, 1994) and brain stimulation studies (Grossman, Battelli, & Pascual-Leone, 2005; Vangeneugden, Peelen, Tadin, & Battelli, 2014). Other studies have observed activations in ventral areas, including fusiform and occipital face areas (Grossman & Blake, 2002) and the extrastriate body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001). These results are consistent with a role of form processing outlined in above described behavioral studies, although it is unclear to what extent ventral areas are critical for biological motion perception (Gilaie-Dotan, Saygin, Lorenzi, Rees, & Behrmann, 2015). Aiming to dissociate neural correlates of form and motion processing in PL animations, Vangeneugden et al. (2014) used TMS and multivoxel fMRI to investigate roles of pSTS and EBA in biological motion perception. Both TMS and fMRI revealed a double dissociation between pSTS and EBA. Namely, pSTS was critical for processing body motion but not body form information, while the opposite pattern of results was observed for EBA.

In sum, research on biological motion perception reveals a system that is remarkably effective at detecting a wide range of information, ranging from a basic task of spotting other living creatures to complex tasks such as discerning one's emotional state. This is accomplished, with some notable exceptions, by taking into account both motion cues and form cues. More broadly, biological motion processing can be conceptualized as a component of real-life person recognition, an inherently multimodal process that also relies on cues from body, face and voice perception (Yovel & O'Toole, 2016).

MOTION PERCEPTION IN THE CONTEXT OF ATTENTION, WORKING MEMORY, AWARENESS, AND LEARNING

Motion perception is determined not only by bottom-up sensory processing, but also by other factors such as attention and learning. For example, you might have experienced that focused attention can make slight movements appear more conspicuous. Guided by our ample experience with social situations, we tend to attribute elaborate social meanings to movements of simple shapes (Gao, McCarthy, & Scholl, 2010; Heider & Simmel, 1944). These examples illustrate that perception of motion, similar to other sensory modalities, is an active process that integrates bottom-up sensory information with top-down modulations driven by higher-level visual and cognitive mechanisms. Work on elucidating these interactions has been a major area of motion perception research in the last two decades. Here, we review key findings from this broad and growing line of research.

Attention

The brain can accurately represent only a small portion of the vast amount of incoming sensory input (Cowan, 2001; Luck & Vogel, 1997; Pashler, 1988; Rensink, 2002). As discussed in Chapter 6 in this volume, to deal with this inescapable constraint, the brain relies on attention as a key mechanism to select behaviorally relevant information (Kastner & Ungerleider, 2000). By employing visual attention, we can selectively focus on specific locations, features, and/or objects
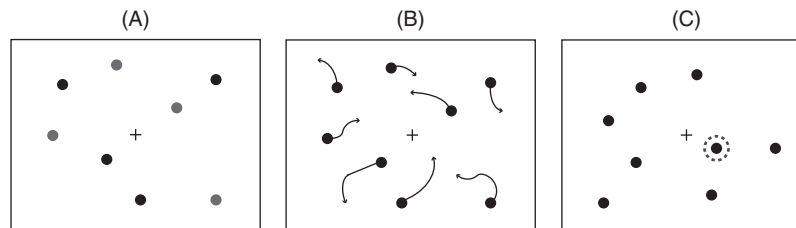
Figure 10.14   A typical multiple object tracking task. (A) Target objects (gray) are highlighted at the beginning of each trial. (B) As the trial starts, objects (now all with identical appearance) start moving in random trajectories. Participants are asked to track the target objects. (C) At the end of the trial, participants report whether a selected object (marked with adotted circle) was a target. In other versions of this task, participants are asked to click on what they believe are the target objects. Color version of this figure is available at http://onlinelibrary.wiley.com/book/10.1002/9781119170174.

in the visual field (usually called spatial, feature-based, and object-based attention, respectively), and, consequently, prioritize their visual processing (Carrasco, 2011). This also applies to motion perception (for a review of relevant older work see Raymond, 2000). In displays with many moving objects, we can use attention to simultaneously track up to four to five objects—a well-studied paradigm called multiple object tracking (Figure 10.14; Pylyshyn & Storm, 1988; for reviews see Cavanagh & Alvarez, 2005; Scholl, 2009). Tracking of multiple dynamic objects is critical for many visual activities that involve motion (e.g., tracking other players in a soccer match). In fact, multiple object tracking is a key component of several training interventions that aim to improve both vision and attention (Nyquist, Lappin, Zhang, & Tadin, 2016; Parsons et al., 2014). The ability to attentively track multiple objects greatly varies across individuals (Oksama & Hyönä, 2004), with individuals who play action video games being particularly good at this task (Green & Bavelier, 2003). More information about links between attentional tracking and motion perception is in the Higher-Order Motion section.

In addition to facilitating processing of attended moving objects, visual attention can also substantially alter their perception. For example, in bistable apparent motion stimuli, attention can alter (Kohler, Haddad, Singer, & Muckli, 2008) and significantly delay (Verstraten & Ashida, 2005) reversals in perceived motion direction. Motion repulsion—a phenomenon where directions of overlapping motion surfaces are perceived to be repulsed away from each other—can also be modulated by attention (Yuzhi Chen, Meng, Matthews, & Qian, 2005; Tzvetanov, Womelsdorf, Niebergall, & Treue, 2006). Furthermore, attention has strong effects on motion adaptation. It affects the duration (Chaudhuri, 1990), strength (Lankheet & Verstraten, 1995), and perceived direction (Alais & Blake, 1999) of MAE (but see Morgan, 2012). MAE is affected even when attention is allocated to a task-relevant motion direction shown at a location distant from the adapting stimulus (Arman, Ciaramitaro, & Boynton, 2006; Zirnsak & Hamker, 2010)—results that demonstrate the spatial reach of feature-based attention.

Behavioral effects of attention on motion perception are paralleled by attentional modulations of neural responses to moving stimuli. Attended motion directions can be decoded from fMRI signals in several visual areas, including both V1 and

hMT+ (Kamitani & Tong, 2006). Consistent with earlier-described behavioral effects of feature-based attention, attention to a motion direction modulates hMT+ responses across the visual field, including retinotopic regions with no bottom-up visual stimulation (Serences & Boynton, 2007). Attentional effects can even spread across visual features. For example, attending to a color in one visual hemifield can modulate the hMT+ responses to a task-irrelevant moving stimulus in the other hemifield if it is shown in the attended color (Sohn, Chong, Papathomas, & Vidnyánszky, 2005). This fMRI effect was also accompanied by an increase in MAE duration for the motion stimulus (Sohn et al., 2005), revealing a correspondence between perceptual and neural effects of attention.

A number of mechanisms have been proposed to explain the influence of attention on neural responses. Notably, the nature of the observed effects depends on the type of attention deployed. For instance, spatial attention increases MT responses to the attended motion directions (Treue & Maunsell, 1996)—a modulation that appears as a change in multiplicative gain (Cook & Maunsell, 2004; Seidemann & Newsome, 1999). Behavioral results in human subjects also indicate that spatial attention mostly operates via gain changes (Ling, Liu, & Carrasco, 2009). In addition, spatial attention shifts receptive fields toward the attended location (Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006) and changes the center-surround structure of receptive fields (Anton-Erxleben, Stephan, & Treue, 2009). Feature-based attention similarly modulates MT response via multiplicative gain, whose magnitude is determined by the similarity between attended and preferred motion directions (aka feature-similarity gain model; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996). The consequence of such modulations is an improvement of population

selectivity around the attended direction (Martinez-Trujillo & Treue, 2004). This link between feature attention and sharper tuning is corroborated by behavioral results in human subjects (Ling et al., 2009). In addition, different types of attentional modulation vary in their temporal dynamics. Relative to the endogenous (i.e., top-down) attention, exogenous (i.e., stimulus-driven) attention exerts much faster effects on neural responses in MT (Busse, Katzner, & Treue, 2008). Recent evidence shows that attention may also aid global motion perception by facilitating interhemispheric integration (Akin et al., 2014) and by mediating the transfer of motion information between V1 and MT (Saproo & Serences, 2014).

In sum, it is clear that attention plays a critical role in visual processing of motion. This relationship, however, is bidirectional. As mentioned in the introduction to this chapter, motion is remarkably effective at exogenously capturing attention. We wave our arms when wanting to be seen and remain motionless when attempting to go unnoticed. A single moving object quickly stands out from a background of stationary objects (Dick, Ullman, & Sagi, 1987). It is easy to argue why this is advantageous. If one needs to act in response to a moving object, often that action needs to be fast or, for example, a potential prey will escape. Given this ecological constraint, motion perception can especially benefit from rapid recruitment of processing enhancements associated with attention.

Working Memory

Everyday visual functions often require us to briefly remember motion of an object. For example, after checking your blind spot while driving, it is helpful to remember directions and speeds of any vehicles in your blind spot. Accomplishing this task requires integration

of motion processing and working memory. In the laboratory, this is commonly studied by employing delayed discrimination tasks where a temporal delay (typically lasting 1–3 seconds) is inserted between the presentations of two stimuli. Thus, observers must encode and maintain the first stimulus in working memory in order to successfully compare it with the second stimulus.

While, in principle, working memory tasks could be accomplished independently from sensory processing (i.e., by storing remembered information outside of sensory areas), there is growing evidence that sensory mechanisms are recruited during working memory tasks (Harrison & Tong, 2009). This also seems to be the case in working memory for motion. The nature of stored working memory is stimulus specific. For example, storage for visual motion is specific to stimulus locations (Zaksas, Bisley, & Pasternak, 2001), and to speed and direction (Pasternak & Zaksas, 2003). These findings are consistent with the idea that sensory mechanisms that encode visual motion may be involved in working memory for motion (Pasternak & Greenlee, 2005). Indeed, studies have observed transient responses during the working memory delay period in area MT (Bisley et al., 2004; Zaksas & Pasternak, 2006; although see Mendoza-Halliday, Torres, & Martinez-Trujillo, 2014). This is consistent with fMRI studies that show successful decoding of working memory contents from the delay period signals both in early visual areas (Harrison & Tong, 2009; Sneve, Alnæs, Endestad, Greenlee, & Magnussen, 2012) and in hMT+ (Riggall & Postle, 2012). A recent study showed that applying TMS over hMT+ during the delay period alters working memory for motion (Zokaei, Manohar, Husain, & Feredoes, 2014), suggesting a causal role of MT in these tasks. Moreover, MT responses to the second stimulus in the delayed motion

discrimination task are influenced by the direction of the first stimulus, indicating a possible role of MT in signaling similarities/differences between motion stimuli in working memory (Lui & Pasternak, 2011). Additionally, motion information stored in working memory can influence perception of subsequently presented stimuli, creating illusions such as motion repulsion (Kang, Hong, Blake, & Woodman, 2011) and biasing the perceived direction in ambiguous structure-from-motion stimuli (Scocchia, Valsecchi, Gegenfurtner, & Triesch, 2013). This again implies that motion-processing mechanisms are recruited for storing motion in working memory.

If low-level sensory areas are critically involved in working memory, then they should interact with key working memory areas, such as lateral prefrontal cortex (LFPC). Indeed, during delayed motion discrimination tasks, neurons in LPFC show direction- and speed-selective responses that are similar to those typically observed in MT (Hussar & Pasternak, 2009, 2013; Zaksas & Pasternak, 2006). The stimulus selectivity in LPFC, however, can adaptively and flexibly change depending on behavioral context (Hussar & Pasternak, 2009), which is consistent with the established role of LFPC in executive functions (Tanji & Hoshi, 2008). Recent evidence shows that, during working memory for motion, activity in LPFC is coherent in phase with the local field potential oscillations in MT (Mendoza-Halliday et al., 2014). This further supports the idea that LPFC exerts top-down modulations on MT. The specific role of LPFC in working memory—whether it is actually used for storage or for attentional allocation—is still in debate (e.g., Lebedev, Messinger, Kralik, & Wise, 2004). Regardless, this area seems to be critically involved in the maintenance of remembered stimuli, as evidenced by impaired working memory performance after

unilateral lesion in LPFC (Pasternak, Lui, & Spinelli, 2015). It is worth noting that the observed impairment is specific to the hemifield contralateral to the lesion (Pasternak et al., 2015), which may be indicative of the importance of the interaction between LPFC and the retinotopic area MT. That is, it is likely that the two areas function together to underlie working memory for motion.

Awareness

Understanding the mechanisms that subserve visual awareness of motion is an important, but challenging task in vision science. Neurophysiological studies in macaque area MT have consistently linked MT responses to motion perception (Britten et al., 1996; Parker & Newsome, 1998; Salzman et al., 1990). Brain stimulation techniques, such as TMS, allowed us to understand a possible role of feedback projection from MT to V1 in the subjective awareness of motion (Pascual-Leone & Walsh, 2001; Silvanto, Cowey, Lavie, & Walsh, 2005). However, the mechanisms underlying conscious experience of motion are not yet well understood.

One approach to addressing this long-standing question is to investigate how conscious and/or unconscious visual processing influences motion perception. Various psychophysical paradigms allow us to achieve this by making visual stimuli disappear from awareness (C. Y. Kim & Blake, 2005). For instance, binocular rivalry (i.e., presenting two stimuli separately in each eye results in a temporary perceptual suppression of one of them) and visual crowding (i.e., presentations of nearby distractors prevents conscious awareness of a stimulus in visual periphery) are effective ways to render stimuli invisible over relatively sustained periods of time, while keeping low-level stimulus characteristics constant. Using these techniques, we can investigate whether perceptually suppressed motion can still have an effect on motion processing mechanisms. For example, motion-induced position shift can occur even without conscious perception of stimulus motion (Whitney, 2005; but see K. Watanabe, 2005). In contrast, MAE strength is modulated by awareness of the adapting motion (Blake et al., 2006; see Motion Adaptation section for detailed discussions on this topic).

The oculomotor system is a good example of a neural system that has access to perceptually inaccessible motion information. For example, ocular following responses (OFR; small, but rapid eye movements that are caused by motion onset) follow low-level motion signals even if those signals differ from perceived motion (Masson, Yang, & Miles, 2002; Sheliga, Chen, FitzGibbon, & Miles, 2005, 2006). Reflexive eye movements can be evoked by motion directions that are not consciously perceived (Spering, Pomplun, & Carrasco, 2011). In fact, stimulus motion direction can be decoded from OFRs even when observers' perceptual discriminations are at chance (Glasser & Tadin, 2014). These results are not limited to reflexive eye movements. Velocity changes can be tracked by smooth pursuit eye movements more accurately than predicted by the perceptual sensitivity to the same velocity changes (Tavassoli & Ringach, 2010). Taken together, these results reveal that the oculomotor system has access to motion information that is, at least in part, distinct from information used to support conscious motion perception. This indicates a certain degree of modularity within motion processing (Glasser & Tadin, 2014), and likely reflects distinct computational goals of perceptual and motor processing of motion.

The perception of motion is not only influenced by visual awareness, but motion can also make other stimuli invisible. Motion-induced blindness (MIB) is a phenomenon

where salient small objects in the foreground become perceptually suppressed in the presence of a continuously moving background (Bonneh, Cooperman, & Sagi, 2001). The mechanisms that give rise to MIB are not yet clear, with studies arguing for involvement of adaptation (Gorea & Caetta, 2009), perceptual filling-in (Hsu, Yeh, & Kramer, 2004, 2006), motion streak suppression (Wallis & Arnold, 2009), and effects of sensory and decision-related factors (Caetta, Gorea, & Bonneh, 2007). Regardless of its underlying mechanisms, MIB provides us with a new tool to investigate neural correlates of visual awareness by causing the changes in conscious states over constant sensory input (Hsieh & Tse, 2009; Mitroff & Scholl, 2004; Montaser-Kouhsari, Moradi, Zandvakili, & Esteky, 2004). Recent evidence shows that MIB fluctuations continue even when MIB stimuli are suppressed from awareness using continuous flash suppression (Dieter, Tadin, & Pearson, 2015). This indicates that MIB fluctuations are better understood as fluctuations in stimulus strength. Under typical viewing conditions, these fluctuations result in visibility fluctuations, but are not exclusively linked with visual awareness. Similar results were recently reported for a related phenomenon of binocular rivalry (Zou, He, & Zhang, 2016).

Together, studies covered in this subsection provide new clues about an important question of elucidating the relationship between motion processing and conscious perception of motion as well as cases when motion directly affects visual awareness of other stimuli.

Learning

Similar to the effects of perceptual learning on other visual features (T. Watanabe & Sasaki, 2015), our ability to perceive motion improves with training (Ball & Sekuler,

1982, 1987). In fact, human observers become more sensitive to motion stimuli even when motion is not task relevant (T. Watanabe et al., 2002; T. Watanabe, Náñez, & Sasaki, 2001; for limitations see Huang, Lu, Tjan, Zhou, & Liu, 2007; Tsushima, Seitz, & Watanabe, 2008) and when simply visualizing motion through mental imagery (Tartaglia, Bamert, Herzog, & Mast, 2012). Effects of perceptual learning on motion discrimination have been traditionally considered to be specific to trained location and direction—with only partial or no transfer to untrained stimulus features (Ball & Sekuler, 1987). However, recent work shows that, under certain conditions, perceptual learning of motion can in fact transfer to untrained features. For instance, transfer to untrained motion directions is observed when training with an easy task (e.g., motion discriminations with relatively larger direction differences; Z. Liu, 1999; Wang, Zhou, & Liu, 2013; although see Jeter, Dosher, Petrov, & Lu, 2009). Training methods have been developed to facilitate learning transfer across retinal locations (L. Q. Xiao et al., 2008), however, to what extent these methods work for training of motion direction is still debated (J. Liang, Zhou, Fahle, & Liu, 2015).

A key question in perceptual learning research involves elucidating neural changes that underlie observed perceptual improvements. Two main accounts have been proposed, and both have been investigated in the context of motion perception. One account argues that perceptual learning causes changes in sensory areas. Supporting evidence has been found in MT, where direction selectivity of neurons increases as the behavioral performance improves (Zohary, Celebrini, Britten, & Newsome, 1994). In humans, perceptual learning can lead to sharpening of direction tuning in V3A as well as connectivity between V3A and the intraparietal sulcus (N. Chen et al.,

2015). These results are consistent with analogous results for perceptual learning of visual orientation, which has been linked with changes in neuronal selectivity in monkey V4 (T. Yang & Maunsell, 2004) and in V1–V4 in humans (Jehee, Ling, Swisher, Bergen, & Tong, 2012). In contrast, the other account argues that perceptual learning changes how neurons in decision-related areas read out information from sensory areas such as MT (Law & Gold, 2008, 2009). These studies observed training-related changes in neural responses in the lateral intraparietal area, a region known for formation of perceptual decisions (J. I. Gold & Shadlen, 2007). Furthermore, Gu et al. (2011) found that, although interneural correlations in MSTd are reduced after monkeys trained on a heading discrimination task, the observed reduction was not sufficient to increase the efficiency of population coding. The conclusion is that changes in sensory areas (e.g., MT and MSTd) following perceptual learning may not fully account for improved motion sensitivity. In sum, mechanisms of perceptual learning for motion, as well as the factors that determine its specificity and generalizability remain active areas of research.

In conclusion, motion perception is influenced by and interacts with a wide range of critical brain functions. One can speculate that this is, at least in part, due to the ubiquity of motion in the environment and its high relevance to our behavior. Links covered in this section only cover major research themes. Motion, for example, is an important component of research in decision making (J. I. Gold & Shadlen, 2007), statistical representation (Watamaniuk & Duchon, 1992), visual imagery (Winawer, Huk, & Boroditsky, 2010), intelligence (Melnick, Harrison, Park, Bennetto, & Tadin, 2013), and even attractiveness (Winkielman, Halberstadt, Fazendeiro, & Catty, 2006). As we advance

our knowledge of bottom-up motion processing, characterizing relationships between motion perception and these higher-level factors will be essential for a comprehensive understanding of motion perception in the context of natural behavior.

MULTISENSORY MOTION PERCEPTION

Movement in the world often yields physical signals that can be detected by multiple sensory modalities. For example, a visual image of a moving car is usually paired with a moving sound and, if the car is sufficiently close and/or large, with vibrations. Optic flow generally cooccurs with corresponding vestibular sensations. Speech sounds are typically paired with the visual motion of the lips. These multisensory pairings generally provide redundant sensory information—information that can be exploited by neural mechanisms tuned to more than one sensory modality. Indeed, our perception of congruent multisensory events is more accurate than our sensitivity to unisensory cues. These multisensory enhancements can often go above and beyond those predicted by statistical probability summation, indicating genuine sensory summation (Alais, Newell, & Mamassian, 2010; Murray & Wallace, 2011). Despite the established benefits of multisensory processing, until recently, motion researchers have largely ignored this topic. For example, the motion perception chapter in the previous edition of this handbook devotes just one sentence to this topic (Sekuler et al., 2002). Here, we highlight recent developments in this growing area of research. For more comprehensive coverage, see Soto-Faraco and Väljamäe (2011) and Chapter 14 in this volume.

Among all sensory modalities, motion has the closest relationship with sound (Alais et al., 2010). If you try to sneak up on a wild animal, it is easy to realize that object movement is often accompanied with sounds. On an even more basic level, all sounds are caused by movement, albeit too small to be seen in most cases. There are, indeed, many examples of interactions between motion and sound. Arguably, one of the most important multisensory pairings of motion and sound occurs during speech. Speech comprehension significantly improves when the observer also views corresponding lip motions, especially under conditions when sound quality is poor (Sumby & Pollack, 1954). In fact, seeing lip motion that is mouthing a phoneme different from the simultaneously presented auditory phoneme can dramatically change the perceived sound—the well-known McGurk effect (McGurk & MacDonald, 1976). The opposite effect is also observed; sound can affect motion perception. Sekuler, Sekuler, and Lau (1997) conducted a clever experiment with two balls that start in two of the top corners of a rectangle and move along the two diagonals. This is usually perceived as two balls passing over each other in the middle of the rectangle. However, if a click sound is played as the balls pass over each other, most observers perceive the balls as bouncing off of each other. This also occurs even if sounds are subliminal (Dufour, Touzalin, Moessinger, Brochard, & Després, 2008), ruling-out conscious inference and arguing for a basic cross-modal interaction between sounds and motion. Even sound pitch can modulate motion perception. Motion direction of a counterphasing grating is normally ambiguous. However, when paired with ascending pitch it is generally perceived to move upward, while descending pitch biases perceived motion in the downward direction (Maeda, Kanai, &

Shimojo, 2004). This is likely because of our tendency to associate falling objects with descending and upward moving objects with ascending pitch.

As in the aforementioned Maeda et al. (2004) study, effects of other senses on motion are most readily demonstrated for ambiguous motion stimuli (e.g., E. Freeman & Driver, 2008). For instance, a bistable rotating globe can be strongly biased in the direction that is consistent with the physical rotation of a tactile globe (Blake, Sobel, & James, 2004). This study also showed that somatosensory sensations from touching a rotating globe are sufficient to activate hMT+, a finding that implicates hMT+ in the observed interaction between touch and motion. More recent work shows that, in hMT+, tactile motion is encoded in a direction-specific way (Van Kemenade, Seymour, Wacker, et al., 2014). Using multivariate pattern analysis, the authors are able to decode motion direction for both tactile and visual stimuli. This result, along with other related evidence (Poirier et al., 2005; Wolbers, Zahorik, & Giudice, 2011), indicates an important role of hMT+ in multisensory motion processing. However, it appears that, at least for somatosensory motion, it is not MT but rather the putative human MST region of hMT+ that responds to tactile motion (Beauchamp, Yasar, Kishan, & Ro, 2007). This is consistent with strong neurophysiological evidence for multisensory coding in MST; namely, a critical role of MST in processing visual and vestibular information during movement (Fetsch, DeAngelis, & Angelaki, 2013; Gu et al., 2007). Noncanonical motion areas are also involved in multisensory motion perception. For example, the superior temporal gyrus activates more strongly to audiovisual motion than either visual or auditory motion alone (Baumann & Greenlee, 2007).

Self-generated actions also affect motion perception. Treadmill walking biases a counterphasing grating (shown in front of the observer's feet) in the downward direction—that is, consistent with optic flow normally experienced during walking (Yabe & Taga, 2008). If two dynamic stimuli are presented one to each eye, the perceptual awareness will alternate between the two stimuli—a phenomenon known as binocular rivalry. However, if motion of one of the stimuli is controlled by self-generated actions (e.g., by moving a computer mouse), then its dominance periods will be prolonged and, remarkably, its suppression periods will be shortened (Maruya, Yang, & Blake, 2007). The effects of action on motion, however, are not restricted to bistable stimuli. As mentioned earlier in this chapter, grating motion viewed through a circular aperture will appear to move in the direction perpendicular to the orientation of the grating, regardless of the actual grating motion. However, if an observer actively moves the grating, perceived motion follows the hand motion (Hu & Knill, 2010). Our actions can, in fact, be solely sufficient to generate normally concomitant motion perceptions. When making hand movements in total darkness, most observers report *seeing* their own hand motion (Dieter, Hu, Knill, Blake, & Tadin, 2014). Notably, only those observers who reported seeing their own hand while blindfolded were also able to execute smooth pursuit eye movements while tracking their own hand motion in total darkness—providing an objective confirmation that motion was indeed experienced.

An important question in multisensory research is whether the observed interactions indicate decision level processes that, for signals near the detection threshold, are best explained by probabilistic summation or indicate more basic sensory integration (Alais et al., 2010). The evidence with respect to multisensory motion processing is mixed, with evidence for both sensory and decision level interactions (Alais & Burr, 2004; Gori, Mazzilli, Sandini, & Burr, 2011; Meyer, Wuerger, Röhrbein, & Zetzsche, 2005; Soto-Faraco, Spence, & Kingstone, 2005), where the outcome likely varies with stimulus conditions (Sanabria, Spence, & Soto-Faraco, 2007). Further evidence for strong multisensory processing of world motions comes from studies showing cross-modal transfer of motion adaptation. Adapting to motion in depth causes a subsequently perceived steady sound to modulate in loudness (Kitagawa & Ichihara, 2002). Adaptation to visual motion results in a tactile motion aftereffect, and vice versa (Konkle, Wang, Hayward, & Moore, 2009). While these adaptation studies cannot directly distinguish whether the associated cross-modal processing occurs at sensory- or decision-level stages, the results certainly indicate that motion information from different modalities is likely represented via shared or overlapping neural mechanisms.

MOTION PERCEPTION IN SPECIAL POPULATIONS

There is a substantial and growing literature focused on elucidating motion perception differences in special populations. This work has twofold benefits. It helps reveal atypical motion processes, providing new clues into underlying deficits in studied populations. At the same time, it often provides unique insights into basic mechanisms of motion perception. Here, we consider major foci of this broad and growing line of research.

Akinetopsia

Akinetopsia, also known as motion blindness, is a neurological condition where a patient is unable to perceive motion. One of

the earliest and most extensive reports of akinetopsia was on LM, a female patient who had bilateral damages in the brain affecting the hMT+ complex (Zeki, 1991; Zihl, von Cramon, & Mai, 1983). LM had spared primary visual cortex and no visual field deficits. Yet, she showed selective impairments in visual tasks that involved motion stimuli, including direction discriminations of suprathreshold moving gratings (Hess, Baker, & Zihl, 1989) and visually guided finger and eye movements (Zihl et al., 1983). Notably, she was able to perceive the direction of coherently moving random dots, albeit for a limited velocity range (Hess et al., 1989). However, her performance severely worsened even when a slight amount of noise dots was added to the stimulus (Baker, Hess, & Zihl, 1991). Similarly, the presence of noise dots was also shown to deteriorate LM's perception of structure from motion (Rizzo, Nawrot, & Zihl, 1995). This pattern of perceptual impairments is similar to that reported in monkeys with MT lesions (Aaen-Stockdale & Thompson, 2012; Baker et al., 1991). Shortly following MT lesions, monkeys showed pronounced deficits in motion perception, but over time, their direction discrimination performance improved except in the presence of noise (Rudolph & Pasternak, 1999). Together, these findings argue for the importance of MT in perception of motion, and in particular, the segregation of signal and noise in motion stimuli.

Cortical Blindness

Patients with cortical blindness typically exhibit a pattern of visual abnormalities that can be seen as approximately opposite to deficits associated with akinetopsia. Such individuals have damage in the primary visual cortex (or its afferents), which leads to profound losses of visual fields and perceptual abilities. Despite this, several studies report that there are residual visual abilities in the blind fields of the patients, a phenomenon termed *blindsight* (Cowey, 2010; Weiskrantz, Warrington, Sanders, & Marshall, 1974). These spared visual abilities in cortically blind patients are usually restricted to a very limited spatiotemporal range that includes low spatial frequencies below 4 cycles/deg (Sahraie et al., 2003), and at high temporal frequencies with a peak around 10 cycles/second (Barbur, Harlow, & Weiskrantz, 1994). Consequently, these patients are impaired in the perception of static, fine-grained stimuli, but have relatively spared ability to detect transient and moving stimuli—ability that is often unconscious, showing up only under forced choice paradigms (Morland et al., 1999; Weiskrantz, Harlow, & Barbur, 1991). This residual ability to process motion stimuli appears to be based on the first-order motion detection system, and not a mere detection of sequential changes in position (Azzopardi & Hock, 2011). This suggests that, with appropriate training, a complete recovery of motion processing may be feasible. Indeed, recent efforts in recovering the visual function in cortically blind fields have shown positive results (for a review see Melnick, Tadin, & Huxlin, 2016): With extensive behavioral training, patients with cortical blindness are able to relearn coarse motion direction discrimination to levels indistinguishable from performance in their intact visual fields. However, residual motion processing deficits remain (M. R. Cavanaugh et al., 2015; Das, Tadin, & Huxlin, 2014). Thus, further studies should investigate the mechanisms underlying observed vision recovery and the factors that limit and facilitate the effects of training.

Amblyopia

Amblyopia is a neurological disorder that is characterized by reduced visual acuity in one

(or both) eye(s) due to various factors such as misalignment in the eyes, chronic blur in one eye, or form deprivation. This condition results from abnormal visual experience in early development, which can lead to persistent impairments in cortical processing (Barrett, Bradley, & McGraw, 2004; Birch, 2013). Although amblyopia is generally studied as a disorder of spatial vision (Levi, 2013), growing experimental evidence has revealed notable deficits in motion perception (Hamm, Black, Dai, & Thompson, 2014; although see B. Thompson, Aaen-Stockdale, Mansouri, & Hess, 2008). Increased motion coherence thresholds have been reported in amblyopic adults (Constantinescu, Schmidt, Watson, & Hess, 2005; Simmers, Ledgeway, Hess, & McGraw, 2003), and children (Ho et al., 2005). This abnormality appears to be spatial-scale invariant (Aaen-Stockdale & Hess, 2008), to be present for both first- and second-order stimuli (Aaen-Stockdale, Ledgeway, & Hess, 2007), and to involve a specific deficit in segregation of signal from noise (Mansouri & Hess, 2006). These perceptual characteristics of motion deficits in amblyopia suggest the area MT as a possible neural locus of observed impairments. Indeed, fMRI studies have shown decreased hMT+ activity in response to motion stimuli in the amblyopic eyes, as compared to the fellow eye (Bonhomme et al., 2006; B. Thompson, Villeneuve, Casanova, & Hess, 2012). Consistent results have been observed in experimentally induced amblyopic monkeys, whose MT neurons exhibit reduced sensitivity to coherent motion (El-Shamayleh, Kiorpes, Kohn, & Movshon, 2010). In these amblyopic monkeys, MT neurons also showed a tendency to prefer slower speeds, similar to observed changes in perceptual sensitivity in the same amblyopic monkeys (Kiorpes, Tang, & Movshon, 2006). Together, these findings suggest that neural underpinnings of amblyopia extend beyond early visual areas and include other visual functions, such as global motion perception.

Autism Spectrum Disorder

Growing numbers of studies report atypical motion abilities in individuals with autism spectrum disorder (ASD; Simmons et al., 2009). Earlier studies investigated the ability to perceive global motion from random dots and generally showed impaired sensitivity to motion in ASD (Milne et al., 2006; Spencer et al., 2000). These observations led to a theory arguing for a broad impairment in dorsal visual processing function in ASD (Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005; Spencer et al., 2000). However, more recent evidence paints a more complex picture (Koldewyn, Whitney, & Rivera, 2010; Spencer & O'Brien, 2006). Some researchers argue that the impairment only occurs with complex visual stimuli (Bertone, Mottron, Jelenic, & Faubert, 2003), such as second-order motion (Bertone et al., 2003) and biological motion (Blake, Turner, Smoski, Pozdol, & Stone, 2003). Moreover, a recent study suggests that the ability to integrate local motion signals in random dot stimuli is actually enhanced in ASD (Manning, Tibber, Charman, Dakin, & Pellicano, 2015), providing a contrary view to the existing literature. Manning et al. (2015) argue that the ability to integrate local motion signals should be considered separately from research questions about segregation of signal and noise, which provides a possible explanation for elevated motion coherence thresholds measured in earlier studies (e.g., Spencer et al., 2000). Enhanced motion perception in ASD has also been found with moving gratings (Foss-Feig, Tadin, Schauder, & Cascio, 2013). This enhancement was limited to high contrast stimuli, suggesting an impairment in gain control mechanisms that normally saturate neural

and behavioral responses at high contrast stimuli (Foss-Feig et al., 2013; Rosenberg, Patterson, & Angelaki, 2015). The proposed gain control abnormality in ASD is consistent with a prominent hypothesis that postulates a broad impairment in the balance between neural excitation and inhibition in ASD (Rubenstein & Merzenich, 2003).

Schizophrenia

Impaired motion perception in schizophrenia has been widely observed across a variety of tasks (Butler, Silverstein, & Dakin, 2008), including motion detection (Yue Chen, Nakayama, Levy, Matthysse, & Holzman, 2003; Li, 2002), speed discrimination (Yue Chen, Levy, Sheremata, & Holzman, 2004; Yue Chen, Norton, & McBain, 2014; D. Kim, Wylie, Pasternak, Butler, & Javitt, 2006), and perception of biological motion (J. Kim, Norton, McBain, Öngür, & Chen, 2013; J. Kim, Park, & Blake, 2011). Such a broad impairment in motion perception will necessarily affect other brain functions that rely on motion processing. For example, impairments in motion processing may explain the well-established deficit in smooth pursuit eye movements present in the majority of patients with schizophrenia (Yue Chen, 2011; Holzman, Proctor, & Hughes, 1973). Patients with schizophrenia are impaired at predicting motion trajectories, and do not benefit from pursuit eye signals when performing such tasks (Spering, Dias, Sanchez, Schütz, & Javitt, 2013), suggesting a possible interplay between the two mechanisms.

Impaired integration and segregation of local motion signals appear to play a key role in motion perception abnormalities in schizophrenia. For example, there is evidence for increased motion coherence thresholds (Li, 2002) and impaired ability to extract average speed from a set of moving dots (Yue Chen et al., 2014; but see Tibber et al.,

2015). Tadin et al. (2006) found that spatial suppression, a mechanism linked with adaptive spatial integration and segregation of motion signals (Tadin, 2015), may be abnormal in schizophrenia. Such a finding is also consistent with evidence that patients with schizophrenia have trouble segmenting moving forms from the background (Schwartz, Maron, Evans, & Winstead, 1999). More recent evidence argues that the impairments in the integration of local visual information in schizophrenia might be more selective, not generalizing across visual domains (Tibber et al., 2015).

Aging

Aging is associated with deteriorating performance in a large number of visual tasks (G. J. Andersen, 2012; Owsley, 2011), including those associated with visual motion processing. Studies have shown aging-related impairments in motion detection and discrimination (Bennett, Sekuler, & Sekuler, 2007) and in perceiving biological motion (Pilz, Bennett, & Sekuler, 2010). Notably, these impairments in visual sensitivity do not appear to be caused by general decline in the optics of the eyes (Weale, 1961), but rather reflect abnormal motion mechanisms in the brain (Betts, Sekuler, & Bennett, 2009, 2012). For instance, spatial suppression of motion signals is considerably weakened in older adults, resulting in a counterintuitive perceptual improvement in seeing motion direction of large, high-contrast stimuli (Betts et al., 2012; Betts, Taylor, Sekuler, & Bennett, 2005)—moving stimuli that young adults typically have trouble perceiving (Tadin et al., 2003). This atypical enhancement for perceiving large, moving stimuli might have a substantial influence on everyday visual tasks like driving, where insensitivity to background motion might be an important mechanism for segmenting moving objects

(Tadin, 2015). Indeed, older adults exhibit difficulty perceiving motion-defined objects (Wist, Schrauf, & Ehrenstein, 2000). More recent efforts in studying the effects of aging on motion perception have focused not only on further characterization of deficits, but also on a possible recovery of motion sensitivity through perceptual training (Bower, Watanabe, & Andersen, 2013). Complementing human work, neurophysiological research in aging monkeys has focused on identifying aging-related changes in area MT, reporting abnormalities in direction selectivity (Z. Liang et al., 2010), speed-tuning (Y. Yang, Zhang, et al., 2009), contrast response functions and adaptation (Y. Yang et al., 2008), and neural response variability (Y. Yang, Liang, Li, Wang, & Zhou, 2009). Evidently, aging has widespread effects on a wide range of motion mechanisms.

Other Populations

For brevity, here we focused on only a few, notable areas of special population research in motion perception. Motion processing abnormalities, however, have been found in a wide range of populations and special groups. For example, patients with a history of depression exhibit abnormally weakened spatial suppression similar to the results observed in older adults (Golomb et al., 2009). Various motion perception abilities also have different developmental trajectories, as evident by a range of motion perception deficits in young children (for a review see Braddick, Atkinson, & Wattam-Bell, 2003). Furthermore, abnormalities in visual motion processing are frequently reported in patients with dyslexia (Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Demb, Boynton, Best, & Heeger, 1998; Eden et al., 1996; although see Goswami, 2015; Sperling, Lu, Manis, & Seidenberg, 2006). These abnormalities may derive from close links between

motion perception and eye movements, and a key role of the latter in reading (Stein, 2014). In addition, abnormal global motion perception is often found in individuals with migraine (McKendrick, Badcock, & Gurgone, 2006; Tibber, Kelly, Jansari, Dakin, & Shepherd, 2014).

Studies on atypical motion perception abilities in special populations are beginning to uncover the characteristics that are distinguishable across populations as well as those that are shared. As mentioned in the beginning of this section, this can help us both with increasing our understanding of studied conditions and with getting new insights into mechanisms of motion perception. Observations of motion perception abnormalities in a wide range of populations is consistent with a view that the human motion system is readily affected by conditions that broadly affect brain function, especially during development (Braddick et al., 2003; Grinter, Maybery, & Badcock, 2010). If true, this makes motion perception an important topic of study for a wide range of special populations research.

CONCLUSION

Since the most recent edition of the Steven's handbook, in 2002, there has been a considerable increase in motion research, now numbering roughly 1,000 papers a year that include both "motion" and "perception" in their titles or abstracts. This work can be largely split into two broad areas. The first is a continuation of a long-standing research focus on bottom-up motion mechanisms. Galvanized by theoretical foundations laid out in the 1980s, this line of mostly psychophysical, neurophysiological, and computational research has been very successful at explaining how different types of motion stimuli are processed by the visual

system. The other broad area of research has involved elucidating the numerous interactions between motion processing and other sensory and cognitive processes. This work has grown in parallel with our increasing understanding of, for example, multisensory processing, attention, decision processes, learning, memory, and various special populations. Here, motion research has both provided empirical paradigms for the study of other brain processes (e.g., an important role of motion coherence stimuli in decision research; J. I. Gold & Shadlen, 2007) and also been a model system for getting key insights into other fundamental brain functions (e.g., see Motion Perception in the Context of Attention, Working Memory, Awareness, and Learning section). In addition to their significant contributions to basic science, these advances have practical implications. For example, the effects of motion on perceived position should be considered in the judgments of sports referees (Whitney et al., 2008), while the effects of motion speed on perceived intent have clear implications when deciding culpability based on video evidence (Burns, Caruso, & Converse, 2016).

Moving forward, we expect that future research directions will continue in the same two broad areas: motion perception per se and interactions between motion perception and other brain functions. Despite significant theoretical and empirical progress, there are still key unanswered questions with regard to motion mechanisms:

- Although we have a reasonably solid understanding of how local motion signals are detected, we know considerably less about how motion perception operates in real world environments where motion signals can arise from a wide range of sources. To what extent findings obtained with, for example, moving dots presented on featureless backgrounds generalize to real world motion perception is a largely unexplored question. Recent results, however, are encouraging; properties of human speed estimates from natural image movies predict speed perception with sinewave gratings (Burge & Geisler, 2015).

- Expanding on the previous argument, real world motion signals include both motions in the world and those caused by our own eye and body motions. Any comprehensive model of motion perception must be able to factor out retinal motions caused by our own movements. This problem has been studied in the context of smooth pursuit eye movements and, more recently, detection of object motion in optic flow. However, an analogous problem occurs for a stationary observer that is fixating on a small target. In this case, retinal image motion is caused by fixational eye movements. Recent work shows that these small but ubiquitous eye movements may play a role in our ability to resolve fine spatial detail (Rucci & Poletti, 2015). However, little is known about their effects on motion perception.

- What are the functional roles, if any, of motion adaptation? In contrast to considerable research on characterizing motion adaptation and associated aftereffects, very little is known about its functional role. One possibility is that motion adaptation, unlike, for example, light adaptation in the retina, is better construed as a side effect of motion processing with no clear functional role. It should be noted that, likely, critical experiments have yet to be performed on this topic. Most motion adaptation studies use long stimulus presentations—durations much longer than ecologically valid brief time scales at which key aspects of motion processing occur.

- Most real world motions are in three dimensions, yet we are only beginning to understand the computational and neural mechanisms that underlie the combination of motion signals from two eyes. This is of importance not only for elucidating 3D motion perception, but for also understanding how motion perception is linked with our actions. For example, catching a baseball requires the close coordination of one's actions with his or her ability to perceive motion in depth.

Although there is important progress to be made in the study of motion perception per se, we suspect that a broader set of novel findings and new directions will emerge as we continue to consider how motion perception interacts with other brain functions. Here are some underexplored research topics:

- We are only beginning to appreciate large individual differences in motion perception. This individual variation can be exploited to reveal links between motion perception and other brain functions. Examples include using individual differences in speed perception to make inferences about mechanisms of smooth pursuit eye movements (Wilmer & Nakayama, 2007) and a finding that performance on a simple motion perception task can be a strong predictor of IQ scores (Melnick et al., 2013). We speculate that there is much more to be learned from applying the individual differences approach to motion perception.

- Much of basic motion research, including most of our own work, is based on moving stimuli that do not undergo global changes in position. This is in contrast with real world object motion, which is almost always paired with changes in position. Recent empirical and theoretical work argues that we should conceptualize motion and position as two inherently related and inseparable stimulus properties (Kwon et al., 2015; details in the Motion and Position section). Future work should further explore this new theoretical framework and determine to what extent our current understanding of motion has been limited by a dominant preference in our area of research to study motion while minimizing position cues.

- Significant motion perception deficits occur in a wide range of special populations. This appears to be consistent with a hypothesis that human motion processing is particularly fragile, especially during development (Braddick et al., 2003; Grinter et al., 2010). This is potentially a very important hypothesis, which, if confirmed, would argue for a central role of motion perception in the study, diagnosis, and assessment of a number of conditions. Future work in special populations should better address the extent to which the observed atypicalities can be accounted for by specific impairments in motion processing, as opposed to reflecting general changes in neural processing.

Here, we have highlighted some of the key areas where we believe future work will bring important advances in motion perception research. We realize that future motion perception reviews will surely include discoveries that were not anticipated by us or by our colleagues. Some of those discoveries might force reinterpretation of the studies and conclusions included in this review. What is easy to predict is that our understanding of motion perception and its links with other neural processes will continue to advance.

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