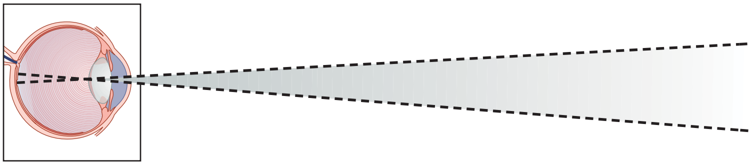

9

Motion Perception

Changes in the spatial distribution of light, over time, can lead to the perception of motion. Think of a person jogging across your field of vision. The spatial distribution of light that falls on your retina changes from moment to moment, causing the jogger to be perceived as moving.

Consider the jogger in more detail: The arms are swinging back and forth, moving in opposite directions. As one leg extends forward, the other leg moves relatively little. The torso is moving slower than the leg that is stepping forward. An analysis reveals that various components of the jogger's body are moving at different rates and in different directions, yet are perceived as a single, unified object moving forward.

A growing body of knowledge provides insight regarding the complex mechanisms underlying motion perception. It is becoming evident that motion is processed along a specialized visual pathway, the dorsal processing stream. This localization of function provides the basis for tests of motion perception that can be useful in the diagnoses of certain neurologic disorders. This chapter concentrates on psychophysical aspects of motion perception. Its physiological bases are discussed in Chapter 15.

STIMULI USED TO STUDY MOTION PERCEPTION

When we observe a jogger, we perceive real motion; the image slides across the retina. Much of the motion that we experience, however, can be classified as **apparent,** or **illusory, motion.** For instance, when spatially separated lights are sequentially flashed, with an appropriate interval between the flashes, a sense of motion is elicited (Fig. 9–1; Korte, 1915; Bartley, 1963). Referred to as **stroboscopic motion,** or the **phi phenomenon,** this effect is common in lighted signs that create the illusion of motion. A bowling alley sign, for example, might consist of a lighted

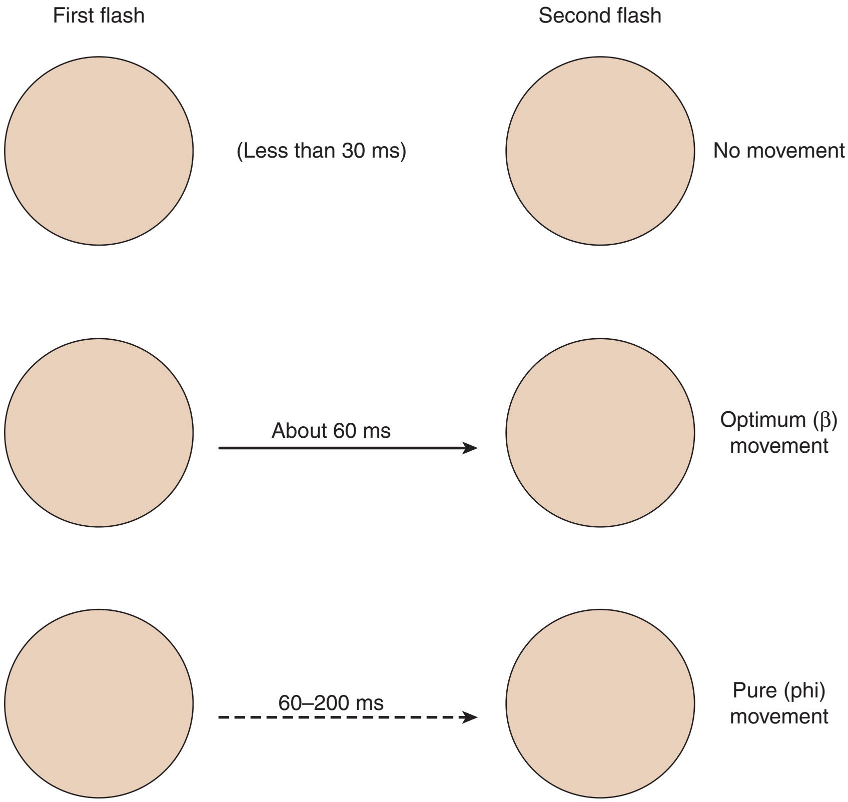

Figure 9–1. Stroboscopic movement. Various sensations of movement are produced by different intervals between the two flashes of light. An interval of 60 ms produces a realistic sensation of the spot moving from position A to position B **(optimum** or **beta movement).** An interval of less than 30 ms produces no sensation of movement, whereas durations of 60 to 200 ms produce a partial illusion of movement **(pure** or **phi movement).**

bowling ball that appears to move down an alley toward the awaiting pins. The sequential flashing, at the proper rate, of the various lights that constitute the sign elicits the illusion of movement.

Movies, television, and computer monitors all create a sense of motion by the use of stroboscopic stimuli. Each frame in a movie, for instance, has a spatial configuration slightly different from that of the preceding frame. The frames are presented at a temporal rate that creates the illusion of smooth motion.

Motion pictures generally present 24 different images per second. Each image is displayed three consecutive times, for a total of 72 presentations per second (i.e., the shutter opens and closes 72 times per second). Why is it necessary to show each image three times? If there were only 24 presentations, the illusion of motion would be created, but the movie would flicker because the presentation rate is below the critical flicker fusion frequency (Chapter 8).

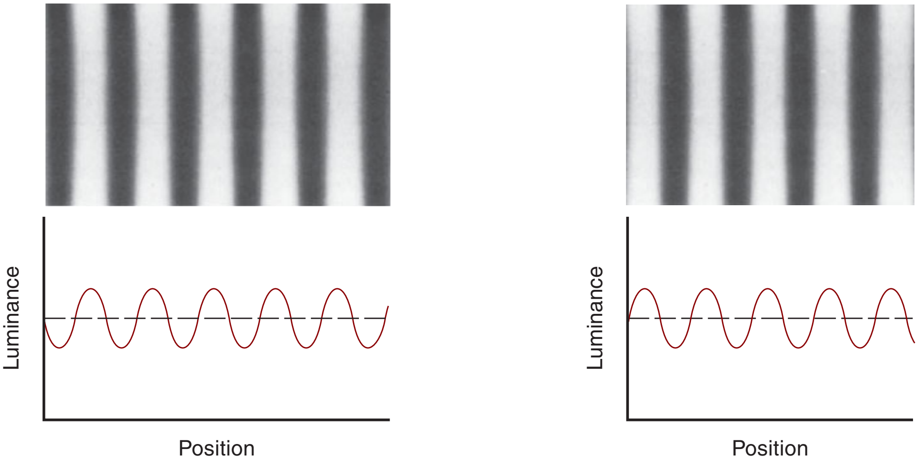

Figure 9–2. A sinusoidal grating is phase shifted (sinusoidally, over time) to produce a grating that appears to drift (move).

Although earlier studies of apparent motion used stroboscopic stimuli flashed in sequence, recent investigations frequently use sine wave gratings that undergo a phase shift (Fig. 9–2). The resulting sine wave grating may appear to drift in a given direction.

Since the stroboscopic and sine wave stimuli that we have discussed up to this point are comparatively simple, consisting of a linear exchange of light for dark (or vice versa), they are referred to as **first-order** stimuli for motion.

What are the physiological mechanisms underlying first-order motion perception? Consider a bright stimulus that is moving across the visual field, from left to right. As it moves, the stimulus sequentially activates the receptive fields of visual neurons in its path. Suppose that these neurons respond with different latencies such that those initially stimulated respond more slowly (i.e., have a longer latency) than those that are subsequently stimulated. When the stimulus is moving at the proper speed, the slower neurons, which are stimulated first, respond at the same point in time as the faster neurons, which are stimulated later. If these responses are added together, the resulting signal could encode stimulus speed and direction (Barlow and Levick, 1965; Wässle, 2001).

More complex stimuli that require the integration of motion cues across a wide expanse of visual space can be presented with **random dot kinematograms.** In panel A of Fig. 9–3, the dots are moving in random directions with respect to each other. By definition, the pattern shows no coherence. As we proceed from panel B to panel C, a higher percentage of the dots move in a common direction and the percent coherence increases from 50% to 100%. **Coherence threshold** is defined as the smallest percent coherence that results in the perception of motion in a defined direction (e.g., up, down, left, or right) (Newsome and Paré, 1988; Silverman et al., 1990). Humans do remarkably well on this task, manifesting coherence thresholds close to 1% (Burr and Santoro, 2001).

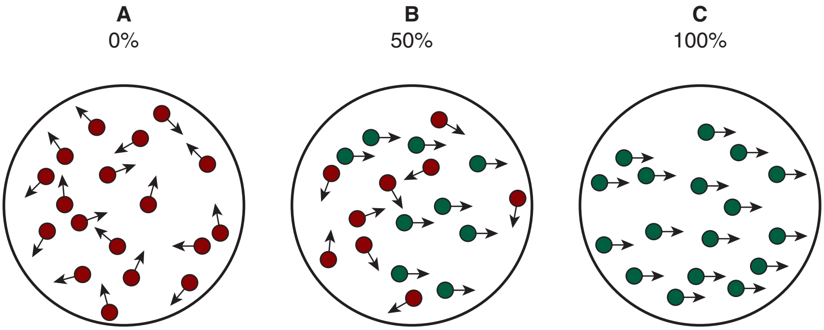

Figure 9–3. Random dot kinematograms used to study motion perception. **A.** When the dots are moving in random directions, there is no coherence. **B.** At 50% coherence, the direction of movement of 50% of the dots is correlated. **C.** All the dots are moving in the same direction when the coherence is 100%. Human subjects show coherence motion thresholds as low as 1% (Burr and Santoro, 2001).

Similar stimuli can be used to study other aspects of motion perception (Fig. 9–4; Nakayama, 1985). The minimum distance that the dots must move in a given direction to elicit the perception of motion is referred to as the **minimum displacement threshold (D_{min}).** Likewise, the maximum distance the dots can move and still elicit motion perception is called the **maximum displacement threshold (D_{max}).**

Compared to stroboscopic stimuli, the processing required for random dot kinematograms to produce a motion signal is more complex because the visual system must integrate information from many dots over a broad expanse of the retina. (Nakayama and Tyler, 1981). This so-called **global motion** perception may involve higher-level cortical motion centers (Newsome and Paré, 1988; Logothetis, 1994).

Whereas first-order motion perception is elicited by local luminance changes on the retina, motion perception can also occur for more complex stimuli, such as

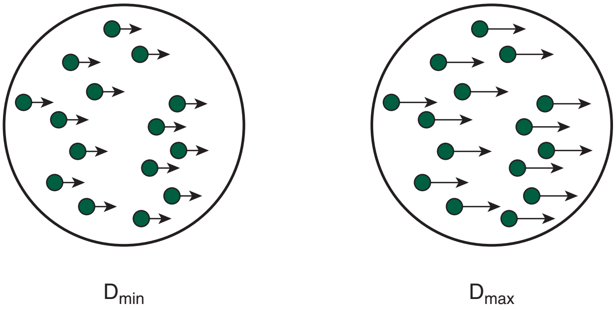

Figure 9–4. The minimum movement that elicits the perception of motion is referred to as the minimum displacement threshold (D_{min}), and the maximum movement that elicits the perception of movement is the maximum displacement threshold (D_{max}) (Bullimore et al., 1993).

texture-defined contours. These second-order motion stimuli may be processed by different pathways than first-order stimuli (Nishida et al., 1997).

DORSAL PROCESSING STREAM

From the retina to striate cortex, motion information—particularly high-velocity motion—is processed primarily along the magno pathway (see Chapter 15). Although the parvo pathway is not blind to motion cues, it apparently plays less of a role and may be involved in processing low-velocity stimuli (Newsome and Wurtz, 1988; Maunsell et al., 1990). Interestingly, amblyopes (see Chapter 17) show reduced sensitivity to low velocities, apparently because of an impairment of the parvo pathway (Steinman et al., 1988).

Motion information is disseminated from striate cortex to neighboring cortical areas, with a convergence of motion information seemingly occurring in **visual area 5,** which is also known as the **middle temporal area, MT, V5, or MT/V5** (see Figs. 14–2 and 15–1). The cortical pathway that originates at striate cortex and continues through visual area 5 to prefrontal cortex is variously referred to as the **parietal** pathway, the **dorsal** processing stream, or the **where** system (Mishkin et al., 1983).

Cells in MT/V5 have features that make them well suited to play a major role in motion perception (Maunsell and Van Essen, 1983). They respond to global stimuli, including random dot kinematograms. Electrical stimulation of cells in MT/V5 of a monkey alters the animal's motion perception (Salzman and Newsome, 1994). Underscoring the centrality of this area to motion perception, damage to MT/V5 can impair the perception of motion (akinetopsia) (Zihl et al., 1983; Barton et al., 1996). The functional physiology of MT/V5 is discussed in more detail in Chapter 15.

We began this chapter with a discussion of the motion perceived when viewing a jogger. This represents a special case of motion perception—**biological motion** perception. There is evidence that the natural movements of humans and other animals may be processed differently than other forms of motion. Functional magnetic resonance imaging (fRMI)[1] reveals that an area of the human cortex, the **posterior superior temporal sulcus (STC),** is activated when viewing biological motion, but not artificial motion (Grossman and Blake, 2001).

ROLES OF LUMINANCE AND COLOR

As previously highlighted, ample evidence suggests that the magno pathway plays an important role in the perception of motion, particularly rapid motion. Can motion perception be elicited by stimuli defined solely by color, such as isoluminant gratings, that are thought to be poor stimuli for the magno pathway (Livingstone and Hubel, 1987, 1988)? These gratings consist of bars of various hues, with each

---

[1] Functional magnetic resonance imaging is discussed in more detail in Chapter 15.

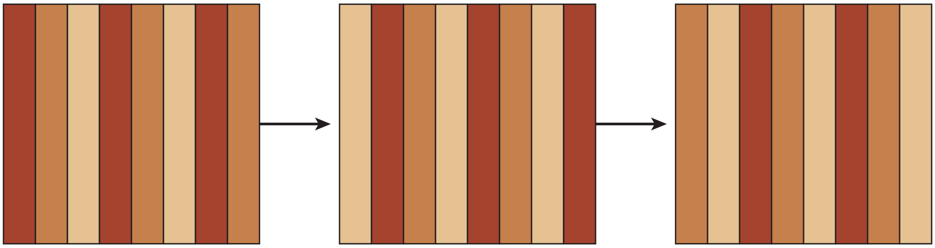

Figure 9–5. The bars that constitute an isoluminant grating all have the same luminance. The perception of movement as the bars drift to the right is impaired by the absence of luminance contrast.

bar having the same luminance (see Chapters 5 and 13). The grating is visible only because the bars that constitute it have different hues, creating chromatic contrast.

Consider the isoluminant grating that is schematically represented in Fig. 9–5. If the bars were drifting to the right, would they be seen as moving? The answer is complicated (Cavanagh, 1996). Under certain isoluminant conditions, the perception of motion is impaired—it may be weak or slower than the actual movement of the bars. Adding luminance contrast (i.e., changing the stimulus so that the red, orange, and yellow bars have different luminances) improves the perception of motion. This psychophysical finding is consistent with a predominant role for the magno pathway in processing motion information. Under certain other isoluminant conditions, however, the perception of motion is robust, pointing to a role for the parvo pathway in coding motion (Cropper and Derrington, 1996).

What do we know about motion perception under scotopic conditions?[2] Psychophysical studies show that objects appear to move slower (approximately 25% slower) under rod-mediated vision than under cone-mediated vision (Gegenfurtner et al., 1999). This raises the possibility that for certain conditions—such as driving at night—objects that are illuminated by the vehicle's headlights and viewed with cone-mediated vision may be perceived as moving faster than objects that are not illuminated by the headlights (i.e., objects falling on the peripheral retina). Such a circumstance could be confusing to a driver, creating the potential for an accident.

DYNAMIC VISUAL ACUITY

Many of the visual stimuli that humans encounter are not stable, but are moving. What effect does the velocity of a moving stimulus have on visual acuity? As stimulus velocity increases, resolution acuity remains relatively constant until the stimulus

---

[2] Under scotopic conditions, rods feed primarily into the magno pathway (Lee et al., 1997).

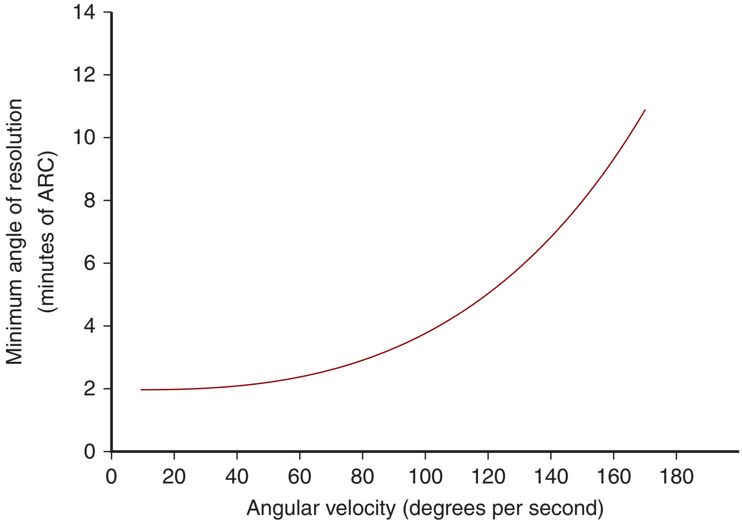

Figure 9–6. The minimum angle of resolution remains relatively constant as the velocity of an acuity target increases up to about 60 to 80 degrees/second. Beyond this velocity, there is a degradation in resolution acuity (Miller and Ludvigh, 1962).

velocity reaches approximately 60 to 80 degrees/second (Miller and Ludvigh, 1962). Beyond this velocity, the ability to resolve a moving stimulus, commonly referred to as **dynamic visual acuity,** deteriorates (Fig. 9–6). The reduction in dynamic visual acuity at increasing target velocities is apparently because of the inability to accurately follow the stimulus with tracking (or following) eye movements, referred to as **smooth pursuit eye movements** (Barmack, 1970).

SACCADIC SUPPRESSION

Place your two index fingers at arms length, separated by approximately 1 foot. Now, look back and forth between them. This ballistic eye movement between two fixation points is referred to as a **saccadic eye movement.** Note that as you move your eyes from finger to finger, or from any one object to another object, the visual world remains still and clear. This is in spite of the movement of images across your retina as you move your eyes.

Vision is suppressed shortly before, during, and shortly after saccadic eye movements. These phenomena, variously referred to as **saccadic suppression** and **saccadic omission,** enable us to look from one object to another without a smearing of our vision that would otherwise be caused by the rapid movement of images across the retina (Matin, 1974; Ciuffreda and Tannen, 1995).

Saccadic suppression is apparently caused by selective inhibition of the magno pathway. This makes sense when you consider that image movement across the retina during saccades is very fast, consisting of high temporal frequencies. Because the magno pathway is very sensitive to these frequencies, it is presumably suppressed to avoid a smearing of vision (see Chapter 13).

What are the mechanisms underlying saccadic suppression? Neural activity (in cortical motion areas) that would otherwise occur during a saccadic eye movement must somehow be suppressed. Where does the neural signal that is responsible for this suppression originate? Some investigators suggest that image movement across the retina acts as a mask. In this view, the signal for saccadic suppression originates within the retina. Other researchers believe that brain areas associated with the genesis of saccadic eye movements also send signals to cortical areas involved with motion perception. In this latter view, an extraretinal signal (i.e., the signal does not originate in the retina) leads to the suppression of motion perception (Matin et al., 1972; Burr et al., 1994; Schwartz and Godwin, 1996).

To address this interesting question, Thiele et al. (2002) recorded the activity of isolated neurons in the monkey cortical area MT/V5 and the nearby middle superior temporal area (MST) under two conditions. Under condition one, the monkey viewed a scene on which there were two spots and made a saccadic eye movement from one of these spots to the other. In condition two, the monkey did not move her eyes, but the scene was shifted so that it moved across the retina as it did during condition one. In both cases, the scene moved across the retina: In condition one, the movement was caused by a voluntary saccade and in condition two, it was because of movement of the scene. If saccadic suppression is caused by an extraretinal signal, one would expect to find neurons in the cortical motion areas (MT/V5 and MST) that are activated when the scene moves, but suppressed during saccades. Theile et al. (2002) found such neurons, providing strong evidence that a primary contributor to saccadic suppression is an extraretinal signal.

ADDITIONAL CLINICAL CONSIDERATIONS

As previously discussed, there is evidence that the neural damage in glaucoma may be selective for the magno pathway. Given the data in support of a critical role for this pathway in motion perception, it should not be surprising that tests of motion perception have been evaluated to determine if they are useful for the early diagnosis of glaucoma (Trick et al., 1995).

Clinical Highlight

Studies using random dot kinematograms have found that minimum displacement thresholds are elevated in patients with suspected glaucoma (Bullimore et al., 1993). In patients with glaucomatous field defects, motion coherence thresholds are higher in those regions of the visual field showing glaucomatous damage than in comparatively unaffected regions (Bosworth et al., 1997). These results suggest that motion deficits may occur relatively early in the disease process and that measures of motion perception might prove to be valuable for early diagnosis.

SUMMARY

First-order motion stimuli are characterized by changes in luminance over time. Such stimuli include flashing lights, drifting gratings, and random dot kinematograms. While the motion perception elicited by such stimuli can be modeled by relatively simple neural circuits, the processing of second-order stimuli is more complicated and may occur along a separate pathway.

Area MT/V5, part of the dorsal cortical processing stream, is thought to play a central role in processing motion information. (Additional evidence in support of this view is discussed in Chapter 15.) The dorsal stream originates in striate cortex, passes through MT/V5, and continues on to prefrontal cortex. Its major precortical input is the magno pathway.

It has been proposed that disease processes resulting in selective damage to the magno pathway may lead to deficits in motion perception. This hypothesis has led to studies that demonstrate impaired motion perception in the early stages of glaucoma. The practicality of tests of motion perception for routine clinical practice awaits further study.

Self-Assessment Question

1. Describe an experiment that would allow you to locate the areas of the human cortex that are most responsible for analyzing motion information. (Hint: See Chapter 1.)