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Motion Perception: Human Psychophysics

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Perceiving motion is a fundamental skill of any visual system: to analyze the form and velocity of moving objects; to avoid collision with moving masses; to navigate through our environment; to analyze the three-dimensional structure of the world we move through; and much more. Much progress has been made over the past few decades to learn how humans and other animals analyze visual signals of objects in motion. This chapter concentrates primarily on advances in human psychophysics. For an excellent review of imaging studies of human and nonhuman primates—and the homologies between them—the interested reader is referred to the excellent chapter (chapter 55) by Orban and Jastorff.

Over the last few decades many important conceptual and empirical advances have enormously expanded our understanding of the principles behind motion perception. Advances in the psychophysics of motion have been accompanied by important breakthroughs in physiology. This chapter concentrates on the main advances in motion psychophysics that have contributed to our understanding of human visual motion perception.

MOTION DETECTORS CONSIDERED AS SPATIOTEMPORAL FILTERS

One of the more important conceptual leaps for motion research was to apply the powerful technique of Fourier analysis to show how suitably tuned spatiotemporal filters can model motion perception (Adelson & Bergen, 1985; Burr, Ross, & Morrone, 1986; van Santen & Sperling, 1985; Watson & Ahumada, 1985). The details of the various models are probably less important than the general message they all convey: that many aspects of motion, thought to be mysterious, are well explained in the frequency domain.

Figure 54.1 illustrates the three stages of one representative model (Adelson & Bergen, 1985). It starts with spatiotemporal filters that integrate the motion input over space (A) and time (B). The outputs of these filters are combined by "quadrature pairing," a technique that produces direction selectivity (C). The outputs of the two classes of filters (sine and cosine) are then squared and summed together (C), to yield a smooth response, selective for direction and also weakly selective for speed. Figure 54.1D shows the resulting frequency response, clearly selective to a specific range of velocities.

This model describes perception of real motion and also accounts for many other phenomena, including *apparent* or *sampled* motion, previously thought to reflect separate processes (e.g., Kolers, 1972): The integration in space and in time causes the discrete motion sequence to become continuous. It also explains some motion illusions, including the "fluted square wave" illusion (Adelson & Bergen, 1985) and the reverse-phi illusion of Anstis (1970). In both cases the explanation of the illusions is that the stimuli contain motion energy in the direction in which they are perceived, even though this is not obvious without analyzing the spatiotemporal frequency spectrum. Interestingly, the reverse-phi illusion has recently been extended to demonstrate different transmission times of ON- and OFF-luminance channels (Del Viva, Gori, & Burr, 2006), again taking advantage of the fact that this illusion has spatiotemporal energy corresponding to the perceived direction of motion. Frequency-based models also provide the basis for explaining many illusions discovered more recently, such as Pinna and Brelstaff's (2000) powerful illusion.

Considering motion as spatiotemporal energy was an important conceptual breakthrough, but it is important to note that these more recent models build on the pioneering work of Werner Reichardt (1957, 1961), which compares the output from one part of space with the delayed output of another. Two such units operate together, mutually inhibiting each other to eliminate a response to flashes. The original Reichardt detector had no filters, just sampling two points of the retina and a simple delay line, although later adaptations included spatiotemporal filtering (Egelhaaf et al., 1988).

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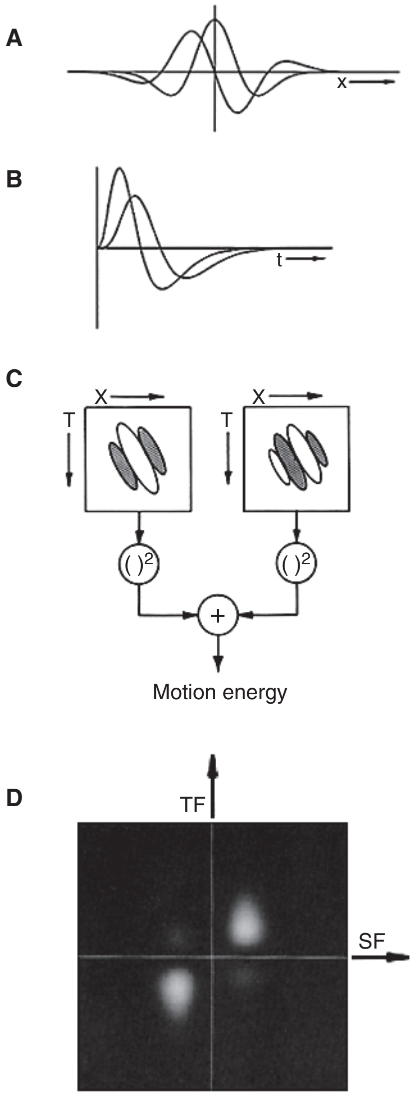

FIGURE 54.1 Constructing a spatiotemporally tuned motion detector. (A, B) The models of Adelson and Bergen (1985), Watson and Ahumada (1985), and van Santen and Sperling (1985) all start with separable operators (or impulse response functions) tuned in space (A) and in time (B), each both in sine and in cosine phase. Each spatial operator is multiplied with each temporal operator to yield four separate spatiotemporal impulse response functions of different phases. (C) Appropriate subtractive combination of these separable spatiotemporal impulse response functions yields two "quadrature pairs" of linear filters (Watson & Ahumada, 1985), oriented in space-time (hence selective to motion direction). In Adelson and Bergen's model these are combined after squaring to yield a phase-independent measure that is known as "motion energy." The full detector has another quadrature pair tuned to the opposite direction, which combines subtractively to enhance direction selectivity (and inhibition responsiveness to nondirected flashes). (D) The spatiotemporal energy spectrum of the motion detector in C. Responding only to one quadrant of spatiotemporal frequency gives the direction selectivity and broad selectivity to speed. (Reproduced with permission from Adelson & Bergen, 1985.)

Burr and colleagues (Burr & Ross, 1986; Burr, Ross, & Morrone, 1986) measured the characteristics of the spatiotemporal filters by the psychophysical technique of masking and used these results to account for how the form of moving objects is perceived. To make the results more intuitive they inverse-Fourier transformed the filter from frequency space to space-time, introducing the concept of the spatiotemporal receptive field, oriented in space-time (see figure 54.2). This representation makes obvious many of the phenomena that seemed mysterious, such as "motion smear" (Burr, 1980), "spatiotemporal interpolation" (Burr, 1979), and seemingly unrelated phenomena such as metacontrast (Burr, 1984). Interestingly, many similar issues have been reemerging recently (e.g., Boi et al., 2009), and it seems that these illusions too can be explained, both qualitatively and quantitatively, by receptive fields oriented in space-time (Pooresmaeili et al., 2012).

SECOND-ORDER, HIGHER-ORDER, AND FEATURE-TRACKING MOTION

"Second-order" motion was first demonstrated by David Badcock and colleagues (Badcock & Derrington, 1985; Derrington & Badcock, 1985; Derrington & Henning, 1987) with complex gratings comprising two drifting harmonics that caused "beats" as they came into and out of phase. The apparent direction of motion of these stimuli could vary, either in the physical direction of motion, as predicted by energy models, or in the direction of the beats (which contain no energy in Fourier space that would excite the energy models), and could not be explained by trivial nonlinearities such as distortion products (Badcock & Derrington, 1989). This class of motion stimulus, which contains no energy in the Fourier plane describing the direction of perceived motion, has variously been called "non-Fourier motion," "second-order motion" (a more correct term than had prevailed), higher-order motion, and sometimes "feature motion."

Zanker (1990, 1993) devised another motion stimulus, which he coined "theta motion," motion of motion-defined forms, for example, leftward drifting dots confined to a rectangular region that was itself drifting rightward. But second-order motion is most often associated with Chubb and Sperling (1988), who devised a clever series of "drift-balanced" stimuli that have no directed motion energy that energy detectors would pick up but are perceived clearly to move in one direction or another. They developed a simple model that will detect second-order motion, mainly because of a nonlinear rectifying stage after the linear filters, which renders the output visible to an energy-extraction stage.

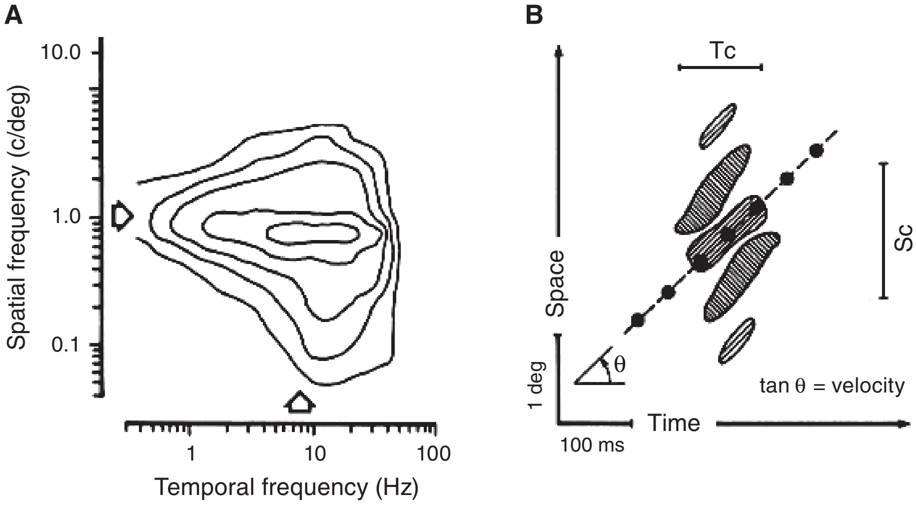

FIGURE 54.2 (A) Spatiotemporal tuning of a hypothetical unit of the human motion system measured by the technique of "masking" (Burr, Ross, & Morrone, 1986). The function is tuned to 1 cycle/deg, 8 Hz, and falls off steadily away from the peak (contour lines represent 0.5 log-unit attenuation). (B) Spatiotemporal receptive field derived from the filter (assuming linear phase). Forward cross-hatching represents excitatory regions; back cross-hatching represents inhibitory regions. The orientation in space-time means it has a preferred velocity, both direction and speed. Spatiotemporal operators of this sort (inferred from all the filter-based motion models of the mid-1980s) go a long way toward explaining many phenomena such as integrating the path of sampled motion (indicated by the series of dots) so it is perceived as smooth and "spatiotemporal interpolation" (see Burr & Ross, 1986). They also help to explain why we do not see the world to be as smeared as may be expected from a "camera" analogy. The field extends for over 100 ms in time (indicated by symbol T_C) and may be expected to smear targets by this amount. However, the analysis is not in this direction but orthogonal to the long axis of the receptive field, where the spread in space-time is considerably less.

There is still some debate on whether second-order motion requires a functionally distinct system for its analysis or whether both could be subserved by the same system. For example, Taub, Victor, and Conte (1997) claim that the most parsimonious explanation is that both types of motion are detected by a common mechanism, with a simple rectifying nonlinearity at the front end to convert the "non-Fourier" into "Fourier" motion energy (see also Cavanagh & Mather, 1989).

But evidence also exists for separate systems. Animation sequences that require integration of first-order and second-order frames do not give rise to unambiguous motion (Ledgeway & Smith, 1994; Mather & West, 1993). There are also qualitative differences between the two types of motion: Contrast thresholds for identifying motion direction are higher (relative to detection) for second-order than for first-order motion (Smith, Snowden, & Milne, 1994), as are temporal-frequency thresholds (Derrington, Badcock, & Henning, 1993; Smith & Ledgeway, 1998). Perhaps the strongest evidence is neuropsychological, as several patients have been described with selective impairment of either first- or second-order motion (Greenlee & Smith, 1997; Vaina & Cowey, 1996; Vaina & Soloviev, 2004).

In addition, another class of motion has been proposed, variously termed "third-order" (Lu & Sperling, 1995a, 1995b, 2001) or "attentional" motion (Cavanagh, 1992; Verstraten, Cavanagh, & Labianca, 2000). Third-order motion is thought to depend on psychological attributes of the stimuli, such as attention or "salience" (the probability that the image will be perceived as "figure" rather than "ground"; Lu & Sperling, 2001), so a perceptually salient figure is seen to move over a background. Examples can be constructed to which both the first- and second-order systems are blind, such as a moving stimulus that continually changes in orientation, contrast, or chromaticity. Interestingly, changing the salience of equiluminant drifting gratings causes activation of the inferior parietal lobule (IPL), implicating a different area in the analysis of third-order motion, one that is involved in attention (Claeys et al., 2003).

Attention has also been implicated in describing higher-order motion. Cavanagh introduced a new class of motion stimuli that he termed *attentional motion stimuli* (in many respects similar to Lu and Sperling's third-order motion stimuli). A typical example could be a luminance-modulated grating drifting in one direction with a superimposed chromatic-modulated grating

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drifting in the opposite direction: Attending to one or the other determines the direction of drift. Whether motion of this type is functionally distinct from third-order motion, or indeed whether either type really defines a unique class of motion, is, of course, subject to debate.

One question that many perplexed readers may wish to ask at this stage is, "What purpose does this second- and higher-order motion serve? When may we normally encounter a second-order motion stimulus modulated, say, in contrast but not luminance?" One approach has been to suggest that the higher-order motions represent a form of *feature tracking*, a system specialized to monitor the motion of salient features. This is reminiscent of Lu and Sperling's third-order motion but may in fact be a more general goal of motion mechanisms.

The early motion models of the Marr group were designed to track edges in two-dimensional motion (Hildreth, 1984; Marr & Ullman, 1981), and much experimental evidence is consistent with edge tracking or, more generally, feature tracking (Cavanagh & Mather, 1989; Derrington & Ukkonen, 1999; Morgan, 1992; Morgan & Mather, 1994; Seiffert & Cavanagh, 1998). Del Viva and Morrone (1998, 2006) developed a feature-tracking algorithm based on the "local energy" feature-detection algorithm (Morrone & Burr, 1988), which first detects salient features in scenes and then searches for peaks in space-time corresponding to the motion of these features. In some respects the model resembles Chubb and Sperling's (1988), in that the early nonlinearity converts the contrast features into energy detectable by basic Reichardt-type models. They show that their algorithm can predict qualitatively and quantitatively human perceptual performance on many interesting examples of motion stimuli that defy many other motion models. One key factor is "phase congruence" between harmonics of compound gratings in determining whether the harmonics will move as a block or be seen in transparency. Phase, also important for Fleet and Langley's (1994) model, has little effect on Fourier power but is fundamental in the formation of visually salient features.

SEGMENTATION AND INTEGRATION OF MOTION SIGNALS

A particularly challenging problem for motion perception is to understand when to integrate motion signals and when to segregate them (see Braddick, 1993, for an excellent discussion of this issue). Much evidence shows that motion mechanisms can integrate over a wide area. One clear example is what has been termed "motion capture" (Mackay, 1961; Ramachandran & Inada, 1984, 1985): A field of dynamic random dots moving in no clear direction can be "captured" by a moving frame or low-frequency grating or even a subjective contour to appear to move coherently. But motion mechanisms can also segregate, so that shapes defined solely by motion can stand out on stationary or reverse-moving backgrounds (Dick, Ullman, & Sagi, 1987; Julesz, 1971).

Nowhere is the conflicting requirement for segregation and integration more apparent than in the "aperture problem." Figure 54.3A illustrates the point. As a circle moves horizontally to the right, the local changes in the image can occur over a wide range of directions. Local measurements of motion (by neurons with small receptive fields) will all indicate motion perpendicular to the orientation of the edge passing through its field. To determine the true global motion of the object, local motions must be combined. The real problem here is for the system to know when to combine motions to yield a global percept of a moving object and when to segregate these motions to resolve a moving pattern from its background.

To tackle this problem Adelson and Movshon (1982) introduced the "plaid" stimulus—two sinusoidal gratings of different orientations moving, therefore, in different directions—and asked under what conditions the two gratings slide one over the other transparently, and when do they cohere into a single plaid pattern. They showed that, in vector space, the motion of each grating is consistent with a family of motions that lie along a line. Each motion has such a constraint line, and these two lines cross one another at "the intersection of constraints," which determines the single direction and speed of motion that can satisfy both components of the plaid (figure 54.3B). This notion predicted rather well the perceived direction of the plaids, even in the case where the intersection of constraints prediction is at odds with the vector sums of the components.

The intersection-of-constraints model has been questioned, with some evidence that the vector sum or vector average of the components gives a more accurate estimation of the direction of movement of the resulting plaid (Ferrera & Wilson, 1990; Wilson & Kim, 1994; Yo & Wilson, 1992). Other researchers have also suggested a role for local features such as blobs in the plaid patterns (e.g., Alais, Wenderoth, & Burke, 1994; Bowns & Alais, 2006). Although the details are still much under dispute, this research clearly exemplifies one of the real problems of motion perception: when to integrate components into a single motion and when to keep them segregated.

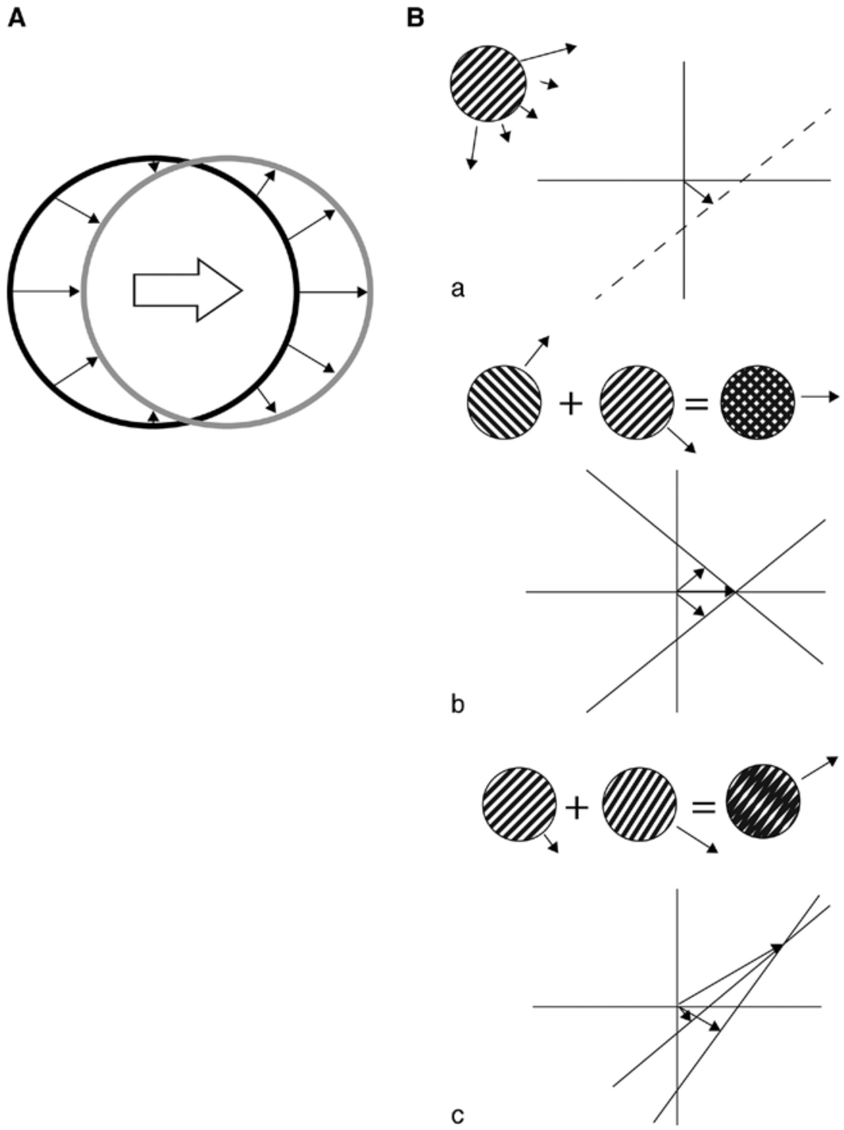

FIGURE 54.3 (A) Illustration of the aperture problem. When a circle moves horizontally, the local movement of the contours may be in a wide range of directions. If only the vector of motion perpendicular to the local edge orientation is seen, the range of motions of the circle will extend from vertically downward through rightward movement to vertically upward. This gamut of motion directions must be integrated to give the global movement. (B) The intersection of constraints model of plaid motion (from Adelson & Movshon, 1982). (a) A 45° grating with a motion vector perpendicular to its orientation is ambiguous in that the size of the vector of motion parallel to its orientation is not knowable. The dotted constraint line provides the locus of all the motion vectors. (b) When added to a second grating orthogonal to the first and moving upward to the right, a single point marks the intersection of the two constraint lines, which predicts correctly the perceived horizontal movement of the plaid. (c) A so-called type 2 plaid in which the intersection of constraints prediction of motion lies outside the component vectors. This prediction is, therefore, very different from a vector sum or vector average model of plaid motion.

The simplest mechanism for integration is the simple linear filtering incorporated into most modern models of motion energy detection, which blur together all signals falling within their receptive fields (figures 54.1 and 54.2). Psychophysical studies suggest that the size of the receptive fields of motion detectors increases with velocity and spatial frequency preference, can be quite large, up to 8° for low-frequency, fast-moving gratings (Anderson & Burr, 1987, 1991), and can extend over around 100 ms in time (Burr, 1981). But the situation is more complex than predicted by the spatial and temporal extent of the front-end filters. Motion signals from these front-end Reichardt-like detectors are combined at a later, intermediate stage of motion

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processing to mediate global perception of coherent motion of random-dot and other complex patterns (Bex & Dakin, 2002; Yang & Blake, 1994).

Coherence thresholds for random-dot patterns seem to tap into a higher level of processing. For example, detection thresholds for discriminating motion coherence improve with exposure duration up to 3 s, compared with 100–300 ms for contrast detection thresholds. The 100–300 ms agrees well with the temporal properties of neurons in primary visual cortex (Duysons et al., 1985; Tolhurst & Movshon, 1975), whereas integration times beyond 1 s are quite beyond what would be expected in primary cortex, implying the action of higher mechanisms such as prefrontal cortex and the functional link with area MT (Zaksas & Pasternak, 2006). Random-dot patterns also reveal spatial summation fields much larger than that revealed by contrast sensitivity measurements, up to 70° (Burr, Morrone, & Vaina, 1998), particularly for flow motion.

It is important to note that although the motion systems can summate over large regions, up to 70° for complex optic-flow motion (Burr, Morrone, & Vaina, 1998), the summation is not obligatory but under clear attentional control (Burr et al., 2009). When regions of moving stimuli are cued, the noncued regions can be ignored, even when the cued regions are not contiguous in space. This shows that the summation does not reflect a large, hard-wired receptive field of a high-level mechanism but flexible summation under attentional control. Indeed, there is evidence that summation between patches of motion stimuli is more effective than within a single contiguous patch of comparable area (Verghese & Stone, 1995, 1996).

Motion is a powerful cue for scene segregation: A field of dots moving coherently stands out clearly from a background comprised of stationary dots, forming a clear shape defined by motion information alone (Julesz, 1971). The resolution of motion as a cue to segregation is less than that of luminance but is nevertheless quite fine, in the order of 2' arc (Loomis & Nakayama, 1973; Nakayama et al., 1985; Regan & Hong, 1990). Motion-defined resolution varies with both filter frequency and image speed, with performance for unfiltered patterns moving at 1–4°/s yielding a stripe resolution of about 3' (Burr, McKee, & Morrone, 2006), similar to the smallest receptive size of motion units. However, "vernier acuity" under similar conditions was about 2' arc, only slightly better than grating acuity (whereas standard luminance-based vernier acuity is typically 3–10 times better than resolution). Imaging studies show that many areas, including motion areas V3a and V5, as well as V4, show shape selectivity for motion-defined contours (Braddick et al., 2000; Mysore et al., 2008).

Not only is motion integration under voluntary control, but it is strongly subject to contextual influences. Lorenceau and Alais (2001) devised a stimulus from a diamond figure orbiting behind an occluding surface. The local signals within the separate apertures have completely ambiguous direction, but the global impression is of an orbiting diamond outline. However, when the stimuli within the local windows are swapped (leaving the local stimulation patterns unaltered), the pattern is perceived as a sliding motion rather than as a rotating diamond. This demonstration provides a clear example of the resourcefulness of the system in integrating motion signals appropriately and also demonstrates the tight links between form and motion perception (often considered to be independent "modules"), where form provides a clear veto for motion integration in the absence of closure.

Tadin and colleagues (2003) have described a clever technique for investigating the neural mechanisms underlying the segregation of motion signals. They use a variant of the summation technique, varying the size of visual stimuli and measuring direction discrimination thresholds (by varying exposure duration). Their counterintuitive result is that, for high-contrast stimuli, increasing the size of the stimulus (over about 3°) decreases sensitivity for direction discrimination. Large stimuli are also less effective for inducing the motion-after effect. They suggest that these results reflect the action of center–surround neural mechanisms like those that have been described for area MT (Born et al., 2000; Born & Tootell, 1992; Raiguel et al., 1995) and MSTl (Eifuku & Wurtz, 1998): Large stimuli activate the inhibitory surround, weakening the response of these units.

MOTION TRANSPARENCY

An important practical example of selective segregation and integration is *motion transparency*, where a foreground field slides over a stationary or differently moving background. Here the visual system has to represent multiple motions in the same part of the visual field. However, not all stimuli with opposing local-motion signals are seen as transparent. Qian, Andersen, and Adelson (1994) devised a stimulus with two patterns of pseudorandomly positioned dots moving in opposite directions over the same region. When the patterns were constrained so the opposing motion signals were *locally* coincident (paired), there was no perceptual impression of transparency. To produce transparency the displays have to have locally unbalanced motion signals with some microregions containing motion in one direction, others in the other direction. Provided there are some regions with net motion in a given direction, the system can segregate these from those moving in the other direction and then integrate these disparate regions to yield one or more coherent surfaces moving in particular directions.

In a companion paper Qian and Andersen (1994) show how cells in V1 and MT respond to these patterns. In general, V1 cells do not distinguish between the stimulus conditions in which the dots of opposite motion direction were constrained to fall within a local region (paired) and those in which the patterns contained locally unbalanced signals (unpaired). MT cells, on the other hand, reliably distinguished between the two conditions, responding well only to the nonpaired stimuli. They suggest that this is consistent with a two-stage model. The first stage, like a simple Reichardt detector responding only to motion energy, corresponds well to the behavior of V1 cells. The second stage introduces local inhibition between opposing directions of motion within a local region, presumably for noise suppression and preventing flicker producing a sense of motion. fMRI studies reveal similar differences in humans: V1 responds more strongly to counterphase flicker (the sum of two opposed drifting gratings) than to a single drifting grating, but for MT the reverse is true (Heeger et al., 1999).

What remains to be explained, of course, is how the signals of directed motion—some leftward, others rightward—combine appropriately with each other to yield the impression of a surface in motion. This clearly recalls the idea of "common fate" of Wertheimer (1912). What it points to, however, is a very clear example of how the visual system needs to segregate stimuli on the basis of their direction of motion and then to integrate these same signals. No linear system can achieve both at the same time. Some intermediate nonlinearity—which we can describe as a *feature extraction*—is necessary.

There is also evidence (Del Viva & Morrone, 2006; Meso & Zanker, 2009) that transparency is determined by *phase congruency*, which to a large extent governs visually salient features (Morrone & Burr, 1988). When two extended patterns with clear features drift in opposite directions (for example, two square waves), those Fourier components in the composite, bidirectional stimulus that are not coherent in phase are seen to drift in transparency. To model the effect it is necessary to introduce an oriented spatiotemporal filter that operates after feature extraction (discussed above) and is selective to phase congruency. With this scheme, pooling of motion signals occurs between components that produce features and segregation of the different transparent surfaces by analyzing along fixed directions the trajectories of the features.

APPEARANCE OF OBJECTS IN MOTION: MOTION BLUR AND SPEEDLINES

Many of the *modular* models of vision assume that form and motion are processed separately by different brain areas (e.g., Marr, 1982; Mishkin, Ungerleider, & Macko, 1983; Zeki, 1993). Although this may or may not be to some extent true (see, for example, Burr, 1999; Lennie, 1998), motion and form are clearly interconnected. The most obvious example is "biological motion" (see Blake & Shiffrar, 2007), where it is the motion itself that defines the form. But even for simple objects in motion, the mechanisms that analyze their form must be capable of taking the motion into account.

One very basic aspect of form analysis of moving objects is that they do not seem to be as smeared as would be expected on a simple "camera analogy" (Burr, 1980). Early visual mechanisms integrate information for around 100 ms, whether stationary (Barlow, 1958) or in motion (Burr, 1981). This integration may be expected to smear the images over time, like opening the shutter of a camera for this period. However, as mentioned earlier, motion mechanisms are tuned to the motion and hence are oriented in space-time (figure 54.2). This means that they do not simply integrate over time, but they integrate in the direction of the receptive field in space-time. The spatial structure of the image in motion is analyzed not normal to the space axis (as static objects would be) but normal to the axis of slant of the spatiotemporal receptive field (see also Burr & Ross, 1986, and figure 54.3). That is, they rotate space-time, effectively annulling the smearing effects of the motion. The relevant smear is not given by the duration over which these detectors spread but by the width normal to their axis. Detectors not tuned to the motion cannot do this and will cause smear much the same as a still camera will. Since these initial experiments a great deal of work has been done on motion smear, largely by Beddel and his group, showing that many factors contribute to smear, such as the presence of multiple rather than single targets (Chen, Bedell, & Ogmen, 1995) and pursuit eye movements (Bedell, Chung, & Patel, 2004; Tong, Stevenson, & Bedell, 2008).

There is another side to the motion-smear coin, one that has come to be known as *motion streaks* or *speedlines*. Geisler (1999) pointed out that the motion streaks left behind by moving stimuli provide potentially important information about the direction of motion, particularly in conditions where direction is made ambiguous by

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the aperture problem. Moving objects of finite size will stimulate two classes of cell: those tuned to the direction of motion and also cells without motion tuning, oriented orthogonally (in space-space) to the direction of motion. Wilson proposed a simple model in which the broad direction tuning of motion units could combine with the fine orientation tuning of other units to enhance direction selectivity.

Ross, Badcock, and Hayes (2000) reported a motion illusion in which random sequences of Glass patterns (pairs of dots all aligned in a coherent fashion) appear to move in coherent directions following the direction of the dot pairs. There is no actual motion energy in this direction, and it is easy to show that the motion energy is completely random. A likely explanation for this illusion is that it results from the dot pairs stimulating the hypothetical motion-streak or speed-line mechanisms. The randomly positioned dot pairs should generate a strong but noncoherent sense of motion, equally strong in all directions, exciting many broadly tuned motion detectors. However, only very limited classes of static, orientation-selective neurons will be stimulated, those parallel to the dot-pair alignment. This mechanism will signal local motion parallel to the direction of dot alignment (in both directions), which will lead to global coherent motion that follows the coherent Glass pattern. Interestingly, the apparent direction of motion of these Glass patterns is not fixed but alternates, as would be expected by the random changes in average motion energy.

Much evidence, both psychophysical and neurophysiological, has accumulated in favor of motion streaks. Noise or Glass patterns oriented near the direction of motion strongly degrade motion discrimination thresholds (Burr & Ross, 2002). Furthermore, motion induced by Glass patterns adds vectorially with real motion, suggesting that common mechanisms are being stimulated (Krekelberg et al., 2003). The streaks left by fast motion interact with stationary oriented patterns in interesting ways, causing motion aftereffects and tilt illusions (Apthorp & Alais, 2009), raising contrast thresholds in an orientation-specific manner (Apthorp, Cass, & Alais, 2010) and even causing orientation-selective suppression in rivalry (Apthorp, Wenderoth, & Alais, 2009).

There is also good electrophysiological evidence that motion streaks activate neurons in early visual cortex. Geisler and colleagues (2001) reported that cells in V1 of cat and monkey respond to dot motion orthogonal to their preferred direction (producing motion streaks parallel to their preferred orientation) and that the relative strength of the response to this direction increases with stimulus speed. Just as dynamic Glass patterns (that contain no coherent motion energy) are seen by humans to move coherently (Ross, Badcock, & Hayes, 2000), they also stimulate cells in MT and MST of monkey (Krekelberg et al., 2003). The direction preference of these STS cells was tuned for both real and “implied” motion and to combinations of them, suggesting that these cells did not distinguish between them. Taken together these results suggest that the implied motion streaks of dynamic Glass patterns generate motion signals in early visual cortex, to which the cells in STS respond, in the same way that they do to real motion signals.

The studies on motion streaks have clearly illustrated the *resourcefulness* of the visual motion system and its capacity to use all available information—even a cue that might normally be thought of as a hindrance to motion rather than a feature—to help it uncover the direction of moving objects and solve the aperture problem.

INFLUENCE OF MOTION ON POSITION AND SPACE

The previous section described interactions between motion and form processing in human vision. This section explores how motion also has a profound influence on perceived position of objects.

Perhaps the clearest and best-known example of motion influencing the perceived position of a target is the *flash-lag illusion*: a stimulus moving continuously seems to lead a briefly flashed light. It is one of the more robust visual illusions, easily demonstrated in the classroom by mounting a translucent card in front of a photographic flash and moving it around in normal lighting, periodically setting off the flash: the flash lags behind the moving card.

The illusion dates back at least to the 1930s, when Metzger (1931) reported that rotating stimuli seemed to move ahead of brief flashes of the stimulus moving behind adjacent slits. Donald Mackay rediscovered the effect by observing that, under strobe lighting, the glowing head of a moving cigarette moved ahead of the base (Mackay, 1958). But Nijhawan’s (1994) recent rediscovery and new interpretation of the illusion has spurred a surge of interest. Nijhawan’s original explanation was that the illusion compensated for the various delays in processing visual stimuli by extrapolating the motion trajectory forward in time, so a moving target seems to lead a stationary target. Certainly an interesting idea, but it has not stood up to rigorous testing. For example, if a moving stimulus is abruptly stopped or reversed, the extrapolated trajectory should go beyond the reversal point, but this was not observed experimentally (Brenner & Smeets, 2000; Whitney, Cavanagh, &

Murakami, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000).

Whitney and co-workers put forward a simpler explanation for the flash-lag effect, the "differential latency hypothesis," suggesting that the visual system responds with shorter latency to moving than to flashed stimuli. Although this explanation has the appeal of simplicity, it again fails to account for many of the complexities of the flash-lag phenomenology. For example, increasing the number of flashes (in a repetitive sequence) or the duration of the flash leads to a reduction in the magnitude of flash lag (difficult to reconcile with a simple latency). Furthermore, the flash-lag effect is far more general than was originally thought. Indeed, it does not require that objects actually move in space but can change in other dimensions, such as color or luminance (Sheth, Nijhawan, & Shimojo, 2000) and even works for streams of changing letters (Bachmann & Poder, 2001). Indeed, it is not even restricted to vision. Analogous phenomena of even greater magnitude occur in audition, both for moving sound sources and "chirps," sounds that increase or decrease in pitch over time (Alais & Burr, 2003), with leads of up to 200 ms (compared with the far more modest 20 ms in vision). Flash-lag phenomena also occur cross-modally, probing auditory motion with a visual flash and vice versa. For these effects differential latencies seem particularly implausible. Indeed Arrighi, Alais, and Burr (2005) tested the latency hypothesis directly and showed not only that the latencies are insufficient to explain the measured flash-lag results but actually go in the wrong direction.

Murakami (2001) devised a particularly clever adaptation of the flash-lag effect. Rather than using continuous motion, he presented bars in random positions over time, and subjects judged whether they appeared to the left or right of a marker; again, this produced a robust flash-lag effect, with the additional advantage of being an objective technique, not possible to predict by cognitive reasoning. The results with this were difficult to reconcile with interpolation or spatial averaging but did seem reasonably consistent with differential latencies.

Despite the enormous research effort expended on the flash-lag effect, no single clear explanation has emerged. In the end the flash-lag effect has probably opened more problems than it has solved, in particular the general question of how time and temporal order are encoded in the brain. This has proven to be a profitable line of research, outside of the scope of this chapter, but discussed in chapter 53 by Johnston. And whatever the explanation of the flash-lag effect may be, it appears to have one crucial consequence in everyday life: Baldo, Ranvaud, and Morya (2002) provided convincing evidence that soccer assistant referees' errors in flagging offsides are consistent with the flash-lag effect influencing their decisions.

When a grating drifts behind a stationary window, the window appears to be displaced in the direction of the motion. The effect, described by De Valois and De Valois (1991), is extremely compelling, with shifts up to 15 min for low-frequency gratings drifting at 4–8 Hz. Ramachandran and Anstis (1990) also reported that random dots moving within a stationary window displace the position of the window and that the effect is strongest when the patterns are equiluminant. These demonstrations go to show that motion affects space perception: position and motion are not completely independent for the brain. It is still not exactly clear how this occurs, but presumably it is related to the signal that spatiotemporal receptive fields give about the location in space of objects stimulating them.

Snowden (1998) and Nishida and Johnston (1999) have shown independently that motion can distort position indirectly, via the motion aftereffect. After viewing a drifting grating (or rotating windmill) for some seconds, a grating patch displayed to the adapted region seems to be displaced in the direction of the motion aftereffect. Interestingly, the spatial distortions caused by motion extend beyond the range of the moving stimulus. Whitney and Cavanagh (2000, 2002) showed that moving stimuli affect the perceived position of stimuli briefly flashed to positions quite remote from the motion; they also influence fast-reaching movements (Whitney, 2002; Whitney, Westwood, & Goodale, 2003; Yamagishi, Anderson, & Ashida, 2001) and saccades (Zimmermann, Morrone, & Burr, 2012). Very brief motion displays are sufficient to create large spatial distortions, maximum at motion onset, suggesting very rapidly adapting mechanisms (Roach & McGraw, 2009). Interestingly, the spatial distortions produced by motion and by adapting to motion are clearly distinguishable from the classical motion aftereffects. Whitney and Cavanagh (2003) have demonstrated clear shifts in spatial position, with no corresponding aftereffect. McKeefry, Laviers, and McGraw (2006) have more convincing evidence: Although the motion aftereffect is chromatically selective, motion-induced spatial distortions were completely insensitive to chromatic composition. The dissociation between chromatic selectivity of aftereffects suggested that chromatic inputs are segregated during initial analysis but are later integrated, before the site where motion affects spatial position. Along these lines, Turi and Burr (2012) have shown that whereas the motion aftereffect is *retinotopic* (moving with the eyes), the positional motion

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aftereffect is *spatiotopic*, specific to position in external space, not to the retinal region stimulated.

The studies reviewed in this section show that form, motion, and position cannot be thought of in isolation. Form can influence motion—most clearly shown in the motion-streak studies—and motion can influence form, in reducing blur in moving objects and in strongly affecting the perceived position of objects in motion and objects flashed near moving stimuli.

CONCLUDING REMARKS

One clear conclusion to emerge from the wealth of studies is that the visual motion system is extremely resourceful in the face of very challenging problems. Another is that motion and position and form interact strongly with each other and are difficult to study in isolation. We need to segregate moving objects from their background, but this segregation involves the integration of local movement signals, many of which have, seemingly, little in common; sometimes we need to keep these local signals separate so that we can distinguish separate objects, as, for example, in transparency. It seems certain that our motion system uses any and all the information it can to make the best bet of what is out there in the real world. For example, the "speed lines" familiar from comics and cartoons can be used to disambiguate and refine our estimation of motion direction. That such a novel mechanism of motion perception can be discovered so recently, after it seemed that much of what could be learned of motion perception had already been learned, suggests that there may well be many other surprises around the corner.

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