



Review

Motion psychophysics: 1985–2010

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ABSTRACT

This review traces progress made in the field of visual motion research from 1985 through to 2010. While it is certainly not exhaustive, it attempts to cover most of the major achievements during that period, and speculate on where the field is heading.

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1. Pre-history

This review of motion psychophysics picks up the story from where Ken Nakayama (1985) left off. Those with an interest in ancient history are recommended to go there for an excellent review of work in the 60s and 70s.

Our review starts at a fortunate time, when many seminal models of motion perception hit the scene, several in a single volume of the *Journal of the Optical Society*. These models changed the way people thought about motion perception, and set solid ground for the development of more complete models in the following years, as well as providing the impetus for further research.

The momentum for this new approach had been building for some time: our understanding of the underlying physiology of motion processing had been boosted by studies by Zeki (1980) and Albright (1984, 1984) who demonstrated the importance of area MT¹ and showed an elegant columnar organisation of directionally selective cells there. This work in the monkey was supported by the intriguing report by Zihl and colleagues (1983) of a 'motion blind' patient who, it was suggested, might have bilateral damage to the human analogues of MT.

If the early years of the 1980s were a golden age of motion processing then it was because of groundwork laid down in the years before. The 1960s and 70s were a time when our understanding of spatial vision leapt forward. Seminal papers by Robson (1966),

Campbell and Robson (1968), Blakemore and Campbell (1969), Graham and Nachmias (1971) and many others had established the sine-wave grating as the stimulus of choice for research in spatial vision. Tuned 'spatial frequency channels' seemed to be a reality (Braddick, Campbell, & Atkinson, 1978), established by a raft of psychophysical procedures and by single unit recording as well. The systems-theory approach had also been most successful in studies of the temporal sensitivity, primarily to flicker (DeLange, 1958; Robson, 1966; Roufs, 1972). Pioneering work by Tolhurst and others (Kulikowski & Tolhurst, 1973; Tolhurst, 1973, 1975) did much to promote the idea that perhaps human vision involved separate 'pattern' and 'motion' pathways, an idea that persists to this day, albeit under different guises, such as the parvocellular–magnocellular distinction, and dorsal and ventral streams. By the early 80s we had good psychophysical support for direction selective channels and even an idea of the temporal tuning of channels as well (Anderson & Burr, 1985; Thompson, 1983, 1984; Watson & Robson, 1981) though the speed tuning of these channels remained largely mysterious. David Marr, who had died tragically at the age of 35 in 1980 had left a rich legacy for our understanding of vision and for computational models of motion processing in his book *Vision*, published posthumously in 1982 (Marr, 1982) and in a wonderful paper with Shimon Ullman (Marr & Ullman, 1981).

Another force that drove the massive rise in research in motion perception was technology. Computers revolutionized the study of motion, allowing for dynamic and continual updating of frames, an enormous advance on pre-computer technology like the tachistoscope. In the early years, computer-generated motion stimuli were also somewhat limited, essentially one-dimensional patterns such as sine-wave gratings (generated by purpose-built machinery under computer control), or random-dot stimuli (usually only two-frame). Other possibilities did exist, using, for example, dynamic

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¹ Throughout this review we have used MT rather than V5. This is merely for convenience and in no way should be taken as an indication of the authors' loyalties on this matter.

frame-free point-plotting techniques (Ross & Hogben, 1974), but these did not prevail. Two-dimensional stimuli, even plaids, were beyond the scope of most labs. Purpose-built framestores, notably from Cambridge Research Systems, who have specialized in vision research equipment, made life much easier for all. In addition to advances in hardware, many software packages were developed by community-minded colleagues. An early one was Landy, Cohen and Sperling's (1984) comprehensive "HIPS" package under Unix. But for motion perception, Dennis Pelli's (1997) and David Brainard's (1997) *Psychtoolbox* package proved invaluable, both for the technically challenged and technically competent researchers, allowing them to create rapidly and at little expense interesting stimuli and run experiments on their Mac or PC. This package is continually being developed and improved, and is to this day one of the major tools for motion research.

So at the start of 1985 the big issues were: how is direction selectivity achieved in the visual system? What is the spatial tuning of direction selective channels? How do we encode speed? Where are these computations carried out in the visual system? Is second order motion really coded differently from first order motion? How are local-motion signals integrated into the coherent motion of objects (solving, amongst other things, the aperture problem)? How and why do we segregate different motion signals? How does motion interact with other attributes, such as perceived position and form?

In this review we shall trace the progress in our understanding of some of these key questions. There are thousands of papers that have made a contribution to progress (and a few that have made a contribution to our lack of progress) so this review will necessarily be very selective. There are some areas that, for space constraints, we have decided to omit completely, such as the perception of "biological motion", a fundamental motion task for social creatures: we refer the interested reader to an excellent recent review by Blake and Shiffrar (2007), and invite them to play with Nikolaus Troje's amusing demo. We note also the fundamental contributions of researchers such as Tony Movshon and Bill Newsome to understanding the physiological circuitry of motion pathways, but this was to be covered by separate review. And within the areas we have chosen to review, we will undoubtedly omit to mention some seminal papers and will mention others of only modest value (probably our own and those of close friends). We apologise for this, but this review would have fallen foul of just the same prejudices if you had written it, dear reader.

2. Motion detectors as spatio-temporal filters

1985 was a landmark year for research on motion perception. That year the *Journal of the Optical Society* published a special edition on motion perception, which included the influential contributions of Adelson and Bergen (1985), van Santen and Sperling (1985), Watson and Ahumada (1985) and others. These important papers (and another published in the Proceedings of the Royal Society: Burr, Ross, & Morrone, 1986), shared a common theme. Following the zeitgeist of the successful application of Fourier analysis to visual perception, they define motion in frequency space, and show how suitably tuned spatio-temporal filters can model well human motion perception (see Burr (1991, chap. 15), for a review of this approach). The details of the various models are probably less important than the general message: that many aspects of motion, thought to be mysterious, are well explained in the frequency domain.

The contributions are all subtly different, but perhaps Adelson and Bergen (1985) explain most clearly how motion can be represented as an orientation in x - y - t space, and readily extracted as spatio-temporal energy by suitable filters. Fig. 1 illustrates the

main aspects of this model. There are three important parts to their model: non-directionally tuned spatial and temporal filters (A and B), that smooth the motion input in space and in time; the "quadrature pairing" of the filters (complementary phase-tuning), that gives direction selectivity (C); and the squaring of the responses before summing (C), that smoothes out the ripples and gives a constant response to a drifting sinusoid. Perhaps the most important aspect is the quadrature phase arrangement of the filters, that gives the unit directional selectivity and, to a lesser extent (as we will discuss later) a certain degree of speed selectivity.

Adelson and Bergen show that their model is not only capable of analysing real motion but explains many other phenomena as well, including apparent, or sampled motion, previously thought to reflect separate processes (e.g. Kolers, 1972). They also explain some motion illusions that were popular at the time, including the "fluted square wave" illusion (Adelson, 1982), and the reverse-phi illusion of Stuart Anstis (1970). In both cases the explanation of the illusions is that the stimuli actually contain motion energy in the direction in which they are perceived, even though this is not obvious without analysing the spatio-temporal frequency spectrum. Interestingly, the reversed 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 spatio-temporal energy corresponding to the perceived direction of motion. These frequency-based models also provide the basis for the explanation of many illusions discovered more recently, such as Pinna and Brelstaff's (2000) powerful illusion, discussed in detail in a later section.

The other papers in the series attacked the problem from different viewpoints. Watson and Ahumada (1985) give an excellent summary of the known properties of motion perception, and rigorously develop their model of motion perception, constrained by this knowledge. The model differs subtly from Adelson and Bergen, in that their filters are assembled in series, and the output not squared, but the basic message is selectivity in space-time. van Santen and Sperling (1985) again come up with a very similar model, and analyse in detail the differences between the models. Importantly, they point out how all models build on the pioneering work of Reichardt (1957), Reichardt (1961), that compares the output from one part of space with the delayed output of another (see Fig. 2). 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 recognized the need from filtering: Egelhaaf, Hausen, Reichardt, & Wehrhahn, 1988). Van Santen and Sperling (1985) show the utility of spatial and temporal filters in producing the spatial and temporal offsets, and how this eliminates potential problems in point-sampling, like aliasing. They (and also Adelson & Bergen, 1985) show formally the mathematical similarities of the Reichardt models, and the new filter-based models. More recently, Morgan (1992b) varied the contrast in a two-frame motion sequence to demonstrate that the spatial filtering operation precedes the directional motion analysis.

Burr and colleagues (Burr, 1983; Burr & Ross, 1986; Burr et al., 1986) took a slightly different approach. They were less interested in developing a model of velocity perception as in explaining how the visual system manages to perceive veridically the form of objects in motion. Again their model was based on the spatio-temporal filter approach, but rather than assume the existence of separable filters, they measured them, using the psychophysical technique of masking. The resultant hypothetical spatio-temporal filter was not spatio-temporally separable, as others had assumed, but this probably made very little difference to the thrust of the idea. What was perhaps more useful was the transform of the filter

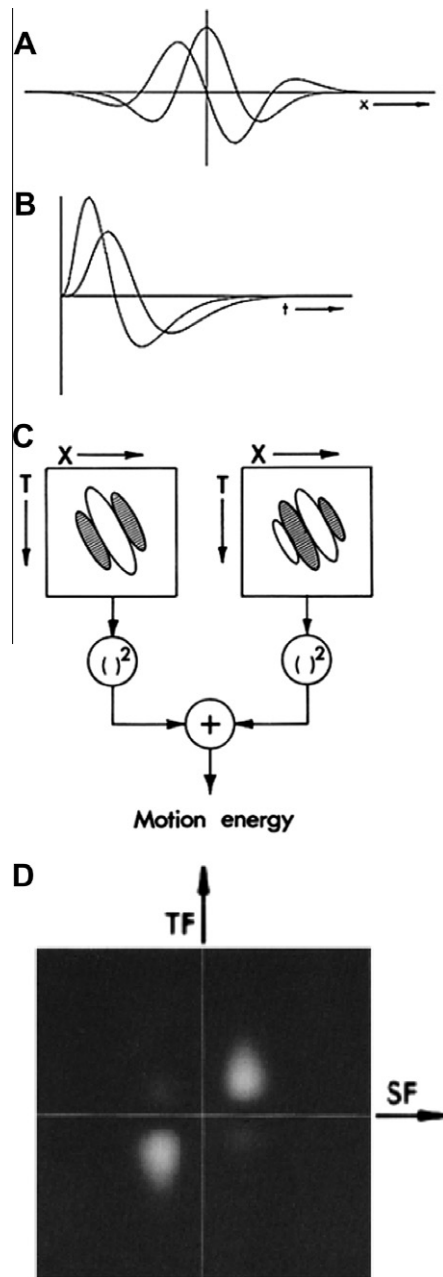


Fig. 1. Constructing a spatio-temporally tuned motion detector. (A and B) The models of Adelson and Bergen (1985), Watson and Ahumada (1985) and van Santen and Sperling (1985) all start with separable operators (or impulse response functions) tuned in space (A) and in time (B), each both in sine and in cosine phase. Each spatial operator is multiplied with each temporal operator to yield four separate spatio-temporal impulse response functions of different phases. (C) Appropriate subtractive combination of these separable spatio-temporal 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 what 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 non-directed flashes). (D) The spatio-temporal energy spectrum of the motion detector in C. Responding only to one quadrant of spatio-temporal frequency gives the direction selectivity, and a broad selectivity to speed. Reproduced with permission from Adelson and Bergen (1985).

from its representation in frequency space to the more intuitive representation in space–time: the spatio-temporal receptive field, oriented in space–time (see Fig. 3 and Burr & Ross, 1986). This rep-

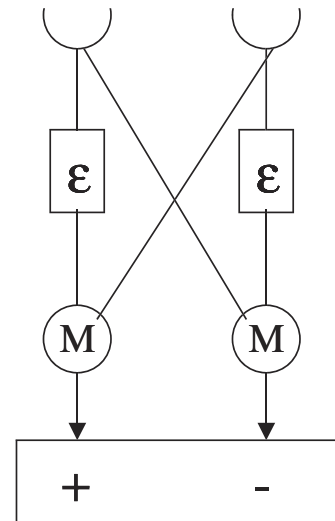


Fig. 2. The “Reichardt detector” in its simplest form. This schema effectively constitutes the backbone to any motion detector. The key is that it samples from two points in space connected by a delay line (indicated by ϵ). In this version, there are two opposed detectors that mutually inhibit each other, preventing a response to non-directed flashes. Adelson and Bergen (1985) demonstrate that this version of the Reichardt detector is formally equivalent to their model.

resentation makes immediately obvious many of the phenomena that seemed mysterious, such as motion smear (Burr, 1980, see also Section 6.1), “spatio-temporal interpolation” (URL: see movie 1) (Burr, 1979) and even point to explanations of seemingly unrelated phenomena, like metacontrast (Burr, 1984). Interestingly, many similar issues are re-emerging as “problems” in recent times (e.g. Boi, Ogmen, Krummenacher, Otto, & Herzog, 2009). Preliminary work has suggested that these illusions can be explained, both qualitatively and quantitatively, by spatio-temporal filters oriented in space–time (Pooresmaeili, Cicchini, Morrone, & Burr, 2010).

Perception of sampled motion as continuous can be envisaged as an integration within homogenous regions of the receptive field. This was not the first time that sampled motion had been explained in terms of the frequencies generated by sampling, but it is possibly more intuitive to some than the more rigorous and quantitative explanations in frequency space (Burr, Morrone, & Ross, 1985; Watson, Ahumada, & Farrell, 1983).

3. Second-order, higher-order and feature-tracking motion

Since the beginning of the formal study of motion perception, researchers have classified motion into a variety of types. The Gestaltists (e.g. Wertheimer, 1912) used letters of the alphabet to define the various motion phenomena they devised. In more recent times, it has long been thought that “apparent” motion was distinct from “real” motion (e.g. Kolers, 1972). And in a very influential paper, Oliver Braddick (1980) introduced the distinction between what he termed “short range” and “long range” motion.

We now know that many motion phenomena, from simple motion of real objects through to apparent motion and a range of classical illusions are readily explicable in terms of the motion energy in the stimulus, rendering many of the classical distinctions of the Gestaltists less useful. However, some phenomena are clearly not immediately accountable for by the energy of the stimulus. These include bi-stable motion displays like the Ternus Effect (Pantle & Picciano, 1976; Ternus, 1950), and also the “short range” and “long-range” division of Braddick (1980). But more challenging were the effects that came to be called *second-order motion*, followed by *third-order* and many other more subtle types of motion.

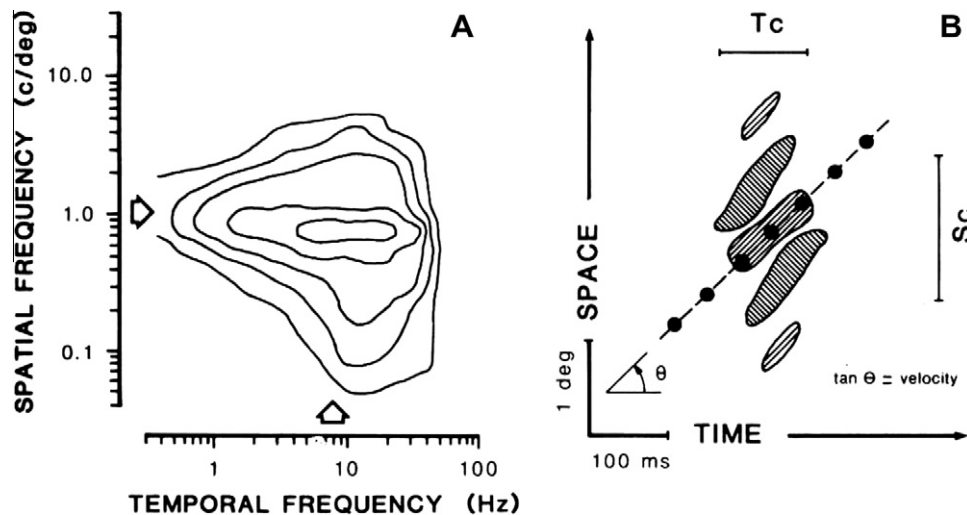


Fig. 3. (A) Spatio-temporal tuning of a hypothetical unit of the human motion system, measured by the technique of “masking” (Burr et al., 1986). The function is tuned to 1 c/deg, 8 Hz, and falls off steadily away from the peak (contour lines represent 0.5 log-unit attentions). (B) Spatio-temporal receptive field derived from the filter (assuming, somewhat unrealistically, linear phase). Forward cross-hatching represents excitatory regions, back cross-hatching inhibitory regions. The orientation in space–time means it has a preferred velocity, both direction and speed. Spatio-temporal operators of this sort (inferred from all the filter-based motion models of the mid ‘80s) go a long way towards explaining many phenomena, such as integrating to path of sampled motion (indicated by the series of dots) so it is perceived as smooth, and “spatio-temporal 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.

3.1. Second-order motion

Second-order motion was first demonstrated by Andrew Derrington and colleagues (Badcock & Derrington, 1985; Derrington & Badcock, 1985; Derrington & Henning, 1987). Derrington’s examples were complex gratings, comprising two drifting harmonics that caused “beats”, as they come in and out of phase. The apparent direction of motion of these patterns could vary, either in the physical direction of motion, as predicted by energy models, or in the direction of the beats (that contain no energy in Fourier space that would excite the energy models). The phenomenon could not be explained by trivial non-linearities, 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 that has prevailed), higher-order motion and sometimes “feature motion”. Zanker (1990), Zanker (1993) devised another motion stimulus that he coined “theta motion” (see demo: URL, movie 6), motion of motion-defined forms: for example leftward drifting dots confined to a rectangular region that was itself drifting rightwards. Zanker proposed a “two-layer” model to account for “theta motion”, where the second layer took the output of a motion energy operator (first layer) as input, and extracted the motion of the motion-defined object.

The phenomenon of second-order motion was brought forcefully to the attention of the vision community by Chubb and Sperling (1988), who devised a clever series of “drift-balanced” stimuli, which even on a fine scale, have no directed motion energy. Yet these stimuli are perceived clearly to move in one direction or another (see demo: URL, movies 4 and 5). In this paper, Chubb and Sperling provide a recipe for generating second-order motion stimuli, prove rigorously that standard Reichardt-like models will not detect these stimuli, and go on to develop a model that will detect them. The major feature in the model is the non-linear rectifying stage after the linear filters, which renders the output visible to an energy-extraction stage.

Chubb and Sperling (1988, p. 2004) point out that although “the existence non-Fourier mechanisms is hardly surprising, such

mechanisms have, however, received no thorough investigation”. Not then they hadn’t! But their publication initiated a cottage industry of second-order motion research, dominating the vision sessions at ARVO and ECVF, and generating some hundreds of papers (well beyond the scope of this brief review). The debate revolved principally around whether the two forms of motion really comprised functionally distinct systems, or whether both could be subserved by the same system. For example, Taub, Victor, and Conte (1997) claim, with supporting evidence, that the most parsimonious explanation is that both types of motion are detected by a common mechanism, with a simple rectifying non-linearity at the front end to convert the “non-Fourier” into “Fourier” motion energy. Cavanagh and Mather (1989) also make a strong case for a single motion system, with different styles of front-end detectors.

Ample evidence also exists for the opposing thesis. 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). And there are qualitative differences between the two types of motion: for second-order motion, thresholds for identifying motion direction are higher (relative to detection threshold) than for first-order motion (Smith, Snowden, & Milne, 1994), and the temporal acuity for second-order motion is lower than for first-order (Derrington, Badcock, & Henning, 1993; Smith & Ledgeway, 1998). While first-order motion seems to show a lower limit for speed, the limit for second-order motion seems to be defined by a minimal displacement rather than a minimum speed (Seiffert & Cavanagh, 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, Cowey, & Kennedy, 1999; Vaina, Makris, Kennedy, & Cowey, 1998; Vaina & Soloviev, 2004).

The evidence from imaging is less clear. Smith, Greenlee, Singh, Kraemer, and Hennig (1998) report that the various motion areas respond to the two types of motion differentially, with area V3 and its ventral counterpart VP responding more strongly to second-order than to first-order motion, raising the possibility that these areas represent explicitly second-order motion. However, the difference in responsiveness was not large, showing considerable overlap

across areas. TMS studies failed to disrupt selectively first- and second-order motion (Cowey, Campana, Walsh, & Vaina, 2006). There are also several psychophysical studies less consistent with the existence of two separate systems, such as cross adaptation between first- and second-order stimuli (Ledgeway, 1994; Turano, 1991), although later studies suggested that the cross-system adaptation was weaker and less specific (Nishida, Ledgeway, & Edwards, 1997).

Of course evidence for interactions and cross-talk between the two putative systems cannot be taken as evidence that all motion is subserved by a single system. Even if functionally distinct systems do exist, one would expect that their output would be combined at some stage to yield a common motion signal. At present the bulk of evidence points to independent mechanisms at low levels, combining to contribute to the sense of motion. Whether the mechanisms are anatomically distinct remains a moot point.

3.2. Third-order or attentional motion

As the battle raged between adherents of the single and dual systems, the issue became further complicated by the introduction of yet another class of motion, variously termed “third-order” (Lu & Sperling, 1995a, 1995b, 2001) or “attentional” motion (Cavanagh, 1992; Verstraten, Cavanagh, & Labianca, 2000). While first- and second-order motion were distinguished on strictly defined physical characteristics – the absence of modulation of average luminance over time – third-order motion results from psychological attributes of the stimuli, such as “saliency” or “attention”, neither particularly amenable to tight definition. Lu and Sperling (2001) operationally defined saliency as the probability that a part of the image will be perceived as “figure” rather than “ground”. The motion is therefore that of the perceptually salient figure, 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 its defining quality, say between orientation, contrast and chromaticity. Many other examples exist, such as equiluminant gratings, where one colour is more salient than the other.

Attention² has also been implicated in describing higher-order motion. Attention was first linked to motion perception by Wertheimer (1912) some 100 years ago, particularly in disambiguating ambiguous motion. More recently it has been shown that attention affects considerably adaptation of motion mechanisms (Alais & Blake, 1999; Chaudhuri, 1990, see also Section 9), and disambiguating cleverly designed stimuli (Lu & Sperling, 1995a). Patrick Cavanagh went further and suggested that a whole class of motion stimuli, not altogether dissimilar from the third order motion stimuli of Lu and Sperling, can be defined as *attentional motion stimuli*. A typical example of such a stimulus could be a luminance-modulated grating drifting in one direction with a superimposed chromatic-modulated grating 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. For further elucidation, the interested reader is referred to Cavanagh's (2011) review in this issue.

3.3. Feature tracking

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, during our normal dealings with the world,

may we expect to encounter a second-order motion stimulus, modulated, say, in contrast but not luminance or anything else? The whole field may seem somewhat academic, remote from real world situations. 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 of course is the stated aim of Lu and Sperling's third-order motion, but may in fact be a more general goal of some motion mechanisms.

The early motion models of the Marr group were designed to track edges in two-dimensional motion (Hildreth, 1984; Marr & Ullman, 1981). Although much experimental evidence is consistent with edge-tracking, or more generally, feature-tracking (Cavanagh & Mather, 1989; Derrington & Ukkonen, 1999; Morgan, 1992a; Morgan & Mather, 1994; Seiffert & Cavanagh, 1998), this approach has not dominated in recent years. One possible exception is Del Viva and Morrone (1998, 2006) who developed a feature-tracking algorithm, based on the highly successful “local energy” feature detection algorithm (Morrone & Burr, 1988; see also in this issue Morgan, 2011). They first apply the energy model to reveal salient features in scenes, then search 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 non-linearity 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 most other motion models. In particular, they show the importance of “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 (and hence Reichardt detectors), but is fundamental in the formation of visually salient features. The feature-tracking algorithm provides a good account of the phase dependence.

The field of first- and higher-order motion systems is not for the faint-hearted, as it is easy to lose one's way in the maze of confusing terminology, fine distinctions and even technical imperfections (such as failure to drift-balance stimuli). Lu and Sperling (2001) made a sterling effort to homogenize the field with a lengthy review, complete with axioms, definitions and mathematical proofs. But not all accept their demarcation zones or explanations, so it is fair to say that there is no consensus in this sub-field of motion perception, whose popularity rose so rapidly in the 1990s, and fell with almost equal rapidity a few years ago.

3.4. Low- and high-level motion

As mentioned earlier, since the formal study of motion perception began, many different criteria have been used to classify motion stimuli. Besides the *i*th order type of motion, another useful criterion to survive is the distinction between *low-* and *high-level* motion. This is, of course, a somewhat imprecise and ambivalent distinction: whereas the second and third order stimuli are defined by their physical properties (in relation to the precise energy models of motion detection), low- and high-level stimuli refer to the presumed site of analysis in the vision system of those particular system. But despite this caveat, the distinction has proven to be useful. As will be discussed in the following two sections, measuring contrast thresholds of motion stimuli (often, but not necessarily, of sine-wave gratings) seems to tap early neural levels like V1. The assumption is that contrast-thresholding occurs largely in V1, as the physiology suggests (Boynton, Demb, Glover, & Heeger, 1999; Sclar, Maunsell, & Lennie, 1990). Coherence thresholds for random-dot kinematograms, on the other hand, seem to tap higher-order processes, with much greater spatial and temporal integration (Burr, Morrone, & Vaina, 1998; Santoro & Burr,

² Aptly termed by Vincent Walsh (2003) “the psychologist's weapon of mass explanation”.

1999). Motion aftereffects measured by motion coherence show complete interocular transfer (suggesting higher-level analysis) whereas tests with static stimuli showed very little transfer (Raymond, 1993, see Section 9).

Although the theoretical basis of low- and high-level motion stimuli is certainly questionable, the distinction has proven to be useful, in the most unlikely circumstances. For example, schizophrenic patients show impairment of motion coherence but not contrast sensitivity thresholds (Chen, Nakayama, Levy, Matthysse, & Holzman, 1999), implying compromise in higher level but not low-level motion mechanisms. A similar result has been demonstrated with infusion of the serotonergic hallucinogen psilocybin (Carter et al., 2004), suggesting that, like schizophrenia, psilocybin affects high-level motion processes. Interestingly, schizophrenic patients also show weakened centre-surround processing of motion mechanisms (Tadin et al., 2006), presumably a higher-level property (see further discussion of this technique in following section).

4. Segmentation and integration of motion signals

Reliable motion perception requires integration of signals over large regions – to improve signal-to-noise levels – but also, in some circumstances, not to integrate, but to segregate (see Braddick, 1993, for an excellent discussion of this issue). One obvious example of this is the well known “aperture problem”, discussed below. An analogous problem occurs over time, in what is called the “correspondence problem” (Julesz, 1971; Ullman, 1979): in a moving random-noise kinematogram, which dots go with which? Locally there exist many solutions while globally the problem becomes much more constrained.

There is a good deal of evidence for integration of motion mechanisms. One clear example is what has been termed as “motion capture”, first described by Donald MacKay (1961), and further studied by Ramachandran and Inada (1984, 1985): a field of dynamic random dots with no clear direction of motion can be “captured” by a moving frame, or low-frequency grating or even a subjective contour. Other clear examples for segregation exist, such as the fact that shapes can be defined by motion alone (Julesz, 1971), and “pop-out” of motion against stationary backgrounds (Dick, Ullman, & Sagi, 1987).

As this review goes to press, a dramatic new demonstration of the power of motion integration has been published. Suchow and Alvarez (2011) show that objects changing in colour, luminance, size or shape appear to stop changing when they are rotated altogether (see demo on [http://www.cell.com/current-biology/abstract/S0960-9822\(10\)01650-7#suppinfo](http://www.cell.com/current-biology/abstract/S0960-9822(10)01650-7#suppinfo)). The explanation for this impressive demonstration is far from clear, but it seems plausible that this integration process subsumes all the dynamic signals within the area, not only directional motion signals but also dynamic signals associated with changes in colour, size or shape. Thus the individual colour changes of each dot are not registered, but consumed within the global motion of the dots. This demonstration points to the limits in our capacity to keep dynamic change signals segregated while global motion mechanisms are integrating over space and time (see also Burr, 2011).

4.1. The aperture problem – and plaids

Nowhere is the conflicting requirement for segregation and integration more apparent than in the ‘aperture problem’. Fig. 4A redrawn from Hildreth (1983) illustrates the point. As a circle moves horizontally to the right, the local changes in the image can be in a very wide range of directions. Local measurements of motion, such as must be taken by neurons with small receptive

fields can only indicate the 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 in some way. The real problem here is for the system to know when to combine motions so a global percept of a moving object emerges and when to segregate these motions so we can resolve a moving pattern from its background. Adelson and Movshon (1982) tackled this problem with a seemingly simple stimulus – two sinusoidal gratings of different orientations moving therefore in different directions. The question they asked was, under what conditions will the two gratings slide one over the other transparently and when will they cohere into a single ‘plaid’ pattern. Adelson and Movshon’s conclusions were really rather simple: seen in vector space, each grating’s motion 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’ (Fig. 4B). This point determines the single direction and speed of motion that can satisfy both components of the plaid. And this intersection of constraints appeared to predict rather well the behaviour of the plaids, even in the case where the intersection

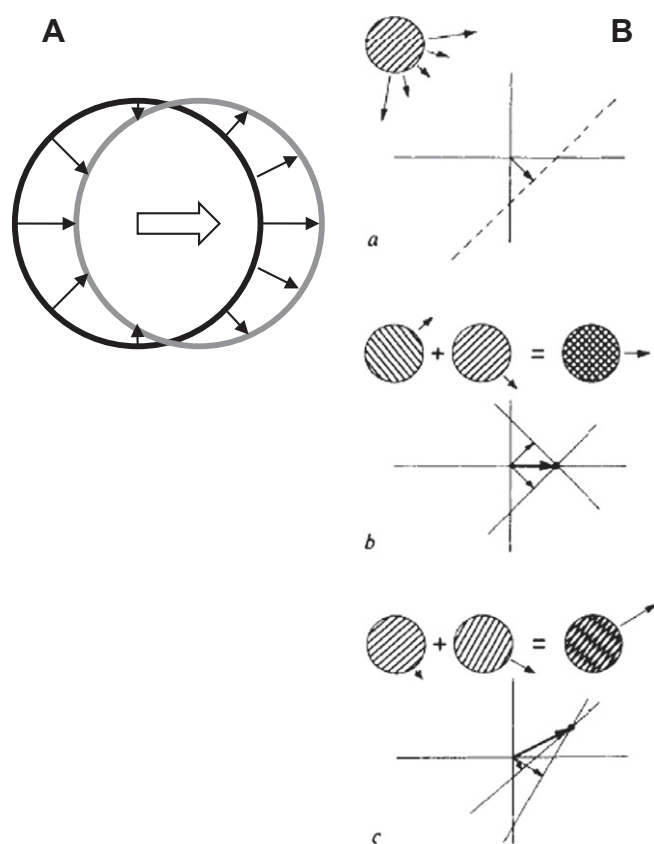


Fig. 4. (A) Illustration of the aperture problem (redrawn from Hildreth (1983)). When a circle moves horizontally, the local movement of the contours may be in a wide range of directions. If only the vector of motion perpendicular to the local edge orientation is seen, the range of motions of the circle will extend from vertically downwards through rightwards movement to vertically upwards. 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). Upper: A 45 degree 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. Middle: When added to a second grating, orthogonal to the first and moving upwards to the right, a single point marks the intersection of the two constraint lines, which predicts correctly the perceived horizontal movement of the plaid. Lower: 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.

of constraints prediction is at odds with the vector sums of the components.

The question of where in the visual system these computations are carried out has been examined at length. It might have been thought that Adelson and Movshon's paper demonstrated everything we needed to know about plaids, but not so. In the 1980s and 1990s research on plaids reached epidemic proportions (rivaling that of second-order motion!); some have questioned the intersection of constraints model suggesting that, when Fourier and non-Fourier components are combined 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), while others have suggested a role for local features 'blobs' in the plaid patterns (e.g. Alais, Wenderoth, & Burke, 1994; Bowns & Alais, 2006). Work from Derrington has supported at least two of these models; Derrington and Suero (1991) showed that reducing the perceived speed of one of the components of a plaid by adaptation (Thompson, 1982) shifts the direction of the plaid as a real reduction in the component's speed would have. This finding and others (e.g. Welch, 1989) support the notion that the plaid velocity is based on the computation of the component speeds. Derrington, Badcock, and Holroyd (1992) came to a somewhat different conclusion when they demonstrated that subjects were able to make direction discriminations on plaids even when such discriminations could not be made on the components.

Whether or not research on plaids has resolved how they are processed in the visual system, one thing is clear: plaids exemplify some of the real problems that we face in motion perception – when should we integrate components into a single motion and when should we segregate motions.

4.2. Integration and segregation mechanisms

One mechanism for integration over space is the simple linear filtering incorporated into most modern models of motion energy detection (see first section). These filters naturally blur together all signals falling within their receptive fields. Psychophysical studies suggest that the size of the receptive fields of motion detectors increase with velocity preference, and can be quite large, up to 8° for low-frequency, fast-moving gratings (Anderson & Burr, 1987, 1991). The receptive fields also extend over time, for around 100 ms (Burr, 1981). But the situation is more complex than predicted by the spatial and temporal extent of the front-end filters. There is also good evidence that motion signals from these front-end Reichardt-like detectors are combined at a later, intermediate stage of motion processing. For example, Yang and Blake (1994) used a masking paradigm to show that low and high spatial frequency information combine to mediate perception of coherent motion of random-dot patterns. Using a different paradigm, Bex and colleagues (2002) similarly showed that local-motion detectors have narrow-band spatial frequency tuning while global-motion detectors integrate across spatial frequency.

Indeed, it seems that in general, coherence thresholds for random-dot patterns 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 limit suggested by temporal summation of contrast agrees well with the temporal properties of neurones in primary visual cortex (Duyons, Orban, Cremieux, & Maes, 1985; Tolhurst & Movshon, 1975). However, 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 et al., 1998), particularly for flow motion (see next section).

It is important to note that although the motion system can summate over large regions, the summation is not obligatory, but under clear attentional control (Burr, Baldassi, Morrone, & Verghese, 2009). When regions of moving stimuli are cued, the non cued regions can be ignored, even when the cued regions are not contiguous in space. This shows that the summation does not reflect a large, inflexible 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; Verghese & Stone, 1996).

Not only is motion integration under voluntary control, but it is strongly subject to contextual influences. One of the clearest demonstrations of this is Lorceau and Alais's (2001) diamond figure orbiting behind an occluding surface (see Fig. 5 and demo: URL, movie 9). Although the local signals within the separate apertures have completely ambiguous direction, and in isolation will be seen as motion following the aperture outline, 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 but affecting the global solution, the pattern is perceived as sliding motion rather a rotating diamond. In general, the local motion components were perceived to move coherently when they define a closed configuration, but not when they define an open configuration. This demonstration provides yet another example of the resourcefulness of the system in integrating motion signals appropriately, depending on context. It 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.

It has long been known that motion summation, at least at intermediate and higher levels, cannot be obligatory, as motion can itself be a cue for scene segregation. For example, if within a given region (such as a square) all dots move in a given direction, whereas those outside the region are stationary, or oppositely drifting, the square will clearly stand out (e.g. 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, Silverman, MacLeod, & Mulligan, 1985; Regan & Hong, 1990). Watson and Eckert (1994) measured a “motion-contrast sensitivity function” by modulating spatial bandpass noise with sinusoidally varying motion, both in the direction of the edge (shear) and orthogonal to it, and determined the amplitude of the modulation that could be discriminated from dynamic noise as a function of modulation frequency. For the highest spatial frequency bandwidth, the cut-off modulation frequency was 4–6 c/deg, suggesting that, for the slow speed (1 deg/s) studied, the smallest receptive field for a motion detector was about 10', or a half-period resolution of 5': coarser than for luminance modulation, but nevertheless very fine, highlighting the capacity of the visual system to segment on the basis of velocity. Burr, McKee, and Morrone (2006) showed that motion-defined resolution varied with both filter frequency and image speed, best performance for unfiltered patterns moving at 1–4 deg/s, yielding a stripe resolution of about 3', corresponding well to estimates of smallest receptive size of motion units under these conditions, suggesting that opposing signals from units with small receptive fields (probably located in V1) are contrasted efficiently to define edges.

Tadin, Lappin, Gilroy, and Blake (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).

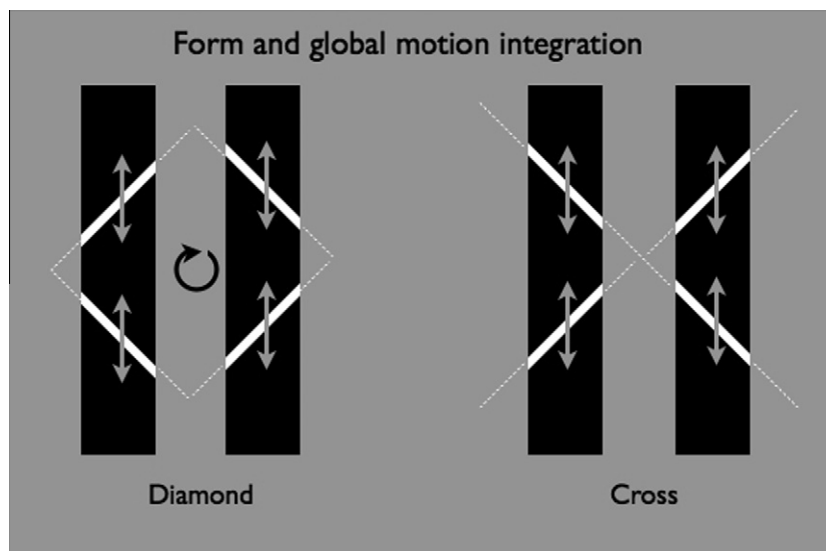


Fig. 5. Integration of local-motion signals depends on spatial form. This demonstration (that can be seen on www.xxxxxxx) is a simulation of a diamond pattern (left) or cross (right) orbiting behind two vertical apertures (illustrated by the dark stripes). At left, global motion is seen, of a diamond pattern coherently orbiting behind the apertures. At right observers perceive local vertical motion within the stripes. The only physical difference between the two stimuli is that the two stripes have been swapped. Lorenceau and Alais (2001) suggest that the diamond is perceived coherently because it is a closed, convex shape whereas the cross is not and triggers a form-based veto of global motion integration.

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 (see also Section 9). They suggest that these results reflect the action of centre-surround neural mechanisms, like those that have been described for area MT (Born, Groh, Zhao, & Lukasewycz, 2000; Born & Tootell, 1992) and MSTl (Eifuku & Wurtz, 1998): large stimuli activate the inhibitory surround, weakening the response of these units. Further studies using the reversed correlation technique reveal more about the spatial and temporal properties of these suppression mechanisms (Tadin et al., 2006).

4.3. Motion transparency

An important practical example of where motion segregation is essential is motion transparency, the capacity to see a foreground field slide over a stationary or differently moving background. This requires the visual system to represent multiple motions in the same part of the visual field. A trilogy of papers in 1994 made an important contribution to our understanding of the psychophysics, physiology and computational modelling of transparency (Qian & Andersen, 1994; Qian, Andersen, & Adelson, 1994a, 1994b). The first paper studied the psychophysics of transparency. They devised a clever but simple stimulus in which two patterns of pseudo-randomly positioned dots moved in opposite directions over the same region. When the patterns were constrained so the motion signals were *locally* opposed (paired), there was no perceptual impression of transparency (URL: [movies 7 and 8](#)). To produce transparency, it was necessary for the displays to have locally unbalanced motion signals, with some micro-regions containing motion in one direction, others in the other direction. This, more than any other example, demonstrates the incredible flexibility of the motion system to integrate or segregate. 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 the second paper, Qian and Andersen (1994) studied how cells in V1 and MT respond to these types of patterns. In general,

V1 cells do not distinguish between the stimulus conditions where the dots of opposite motion direction were constrained to fall within a local region (paired), and where the patterns contained locally unbalanced signals (unpaired). MT cells, on the other hand, reliably distinguished between the two conditions, responding well only to the non-paired 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 behaviour of V1 cells. The second stage, like the combination of Reichardt detectors illustrated in Fig. 2, introduces local inhibition between opposing directions of motion within a local region. This stage presumably has a function of noise suppression, and preventing flicker producing a sense of motion. fMRI studies have revealed 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, Boynton, Demb, Seidemann, & Newsome, 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 fulfil both requirements at the same time. Some intermediate non-linearity – 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 govern 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 (demo). To model the effect it is necessary to introduce an oriented spatio-temporal filter that operates on the output of a feature-extraction model selective to phase congruency. With this scheme, pooling of motion signals occurs between components that give rise to features, while segregation for the transparency is achieved by analysing the trajectories of the features along fixed directions.

5. Optic flow and complex motion

The flow of optical images on our retinæ produced by motion through the environment provides a rich source of visual information, fundamental for many functions such as “heading” and navigation through complex visual environments. Optic flow can be decomposed into several basic functions, including radial, circular, translation and shear (Helmholtz, 1858; Koenderink, 1986). In the early 1990s, several different groups described neurones in the dorsal portion of the medial superior temporal cortex (MSTd) of macaque monkeys that respond selectively to individual flow components (such as circular or radial motion), or combinations of them (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Orban et al., 1992; Tanaka, Fukada, & Saito, 1989; Tanaka & Saito, 1989). In the adjacent area MT neurones are also selective to motion, but respond well only to simple translational motion of appropriate velocity, not to circular or radial motion. The functional importance of MST to heading is underlined by the demonstration that micro-stimulation of MST neurones influences the direction of heading of a behaving monkey (Britten & van Wezel, 1998; see also Wurtz, 1998). Area MST is not the only area that responds to optic flow: other areas in the parietal lobe, such as the ventral intraparietal cortex (VIP) and area 7a are both sensitive to flow stimuli (Read & Siegel, 1997; Schaafsma, Duysens, & Gielen, 1997).

The single-cell physiological studies outlined above provide very clear evidence for the existence in non-human primates of specific neural mechanisms tuned to optic flow motion. These studies are reinforced by many psychophysical studies pointing to the existence of analogous neural units in humans. In the late '70s, Regan and Beverley (eg 1978, 1979) conducted a series of important studies, suggesting the existence of specialized detectors for motion in depth, or “looming detectors” as they became termed (see also Freeman & Harris, 1992). However, it is not clear that the adaptation and masking techniques that they adopted necessarily probe the higher level areas like MST, as they will also affect earlier areas like V1 and MT, which can complicate the interpretation of results.

More recently Morrone, Burr, and Vaina (1995) provided more direct evidence for mechanisms in humans that integrate local-motion signals along complex, optic-flow trajectories. They measured coherence thresholds for discriminating the direction of radial, circular and translational motion in a limited lifetime, random-dot stimulus. The stimulus dots were curtailed to a variable number of symmetrically-opposed sectors: increasing the number of exposed sectors increased the area of the motion stimulus. Thresholds increased with stimulus area, by the amount expected from ideal summation of the motion signals within the sectors. Importantly, for radial and circular motion, the local direction in the displayed sectors was maximally different, either opposite or orthogonal. Nonetheless, the system integrated optimally the local-motion signals of different directions, pointing to mechanisms – like the cells of area MSTd – that integrate local-motion signals along complex optic-flow trajectories. The integration under these conditions was obligatory, as adding noise to the non-signal sectors reduced sensitivity predictably. Interestingly, contrast sensitivity measures did not reveal the same sort of summation trends. The results were interpreted as implying two levels of analysis, a local-motion analysis limited by contrast thresholds (probably V1), followed by a system that integrates flow information (similar to MSTd). Note that although the integration in these conditions was obligatory, later studies showed that the integration was under attentional control (Burr et al., 2009), pointing to very flexible integration mechanisms.

Snowden and Milne (1996, 1997) provided further evidence for optic-flow mechanisms, showing that adapting to, say, radial mo-

tion vignetted behind a radial mask, causes a strong aftereffect when the adjacent regions (that had previously been masked) are viewed. No local detectors visible on viewing the aftereffect had been adapted, so the adaptation must be at the level of a global, integrating unit. Other evidence for a hierarchical processing of motion, from local signals to flow motion, is that radial and circular motion appears faster than translational motion (Bex, Metha, & Makous, 1998), and the aftereffects for this type of motion are stronger and longer lasting than for translation (Bex, Metha, & Makous, 1999).

In agreement with the neurophysiological studies, psychophysical summation studies suggest that these units have very large receptive fields (Burr et al., 1998), and summate information over lengthy periods, 1 or 2 s (Santoro & Burr, 1999). There is also some evidence in humans for selectivity along “cardinal directions” of optic flow – radial and circular motion – (Burr, Badcock, & Ross, 2001; Morrone, Burr, Di Pietro, & Stefanelli, 1999) although not all results point in this direction (Snowden & Milne, 1996). Imaging studies in humans also suggest that flow motion is analysed by a specialized region within the human MT complex (Huk, Dougherty, & Heeger, 2002; Morrone et al., 2000).

Finally, neuropsychological observations seem to confirm the evidence for the existence of specialized flow detectors in humans, and suggest that they are anatomically distinct from other motion areas. Lucia Vaina and colleagues (Vaina & Cowey, 1996; Vaina & Soloviev, 2004) have reported two cases with bilateral occipital-parietal lesions who present with clear deficits in optic flow perception, including heading and radial motion. Both patients performed well on other visual tasks, such as direction discrimination and perception of two-dimensional form from direction or speed differences.

During the period of this review there has accumulated a vast body of evidence from electrophysiology, psychophysics, imaging and neuropsychology studies pointing to the existence in primates of motion detectors specialized for the analysis of optic flow. This information is used by the visual system for a variety of functions, most importantly in helping us navigate through complex visual environments. How optic flow information is used for heading, and how it combines with other non-visual information is an important topic, but one that goes beyond the scope of this review. The interested reader is referred to Warren's (2004) excellent review.

6. Appearance of objects in motion: motion blur and speedlines

One of the more important consequences of the filter motion-models discussed in Section 2 was to provide a basis for an explanation of the *appearance* of objects in motion, not merely the fact that they move in a certain direction and speed. 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). While 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 that defines the form. But even for simple objects in motion, the mechanisms that analyse their form must be capable of taking into account the motion.

6.1. Motion blur

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 (Barlow, 1958), even for

objects in motion (Burr, 1981). This integration may be expected to smear the images over time, like opening the shutter of a still camera for this period. The trick is, however, that motion mechanisms are tuned to the motion and hence oriented in space–time (Fig. 3). 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 analysed not normal to the space axis (as static objects would be) but normal to the axis of slant of the spatio-temporal receptive field (see also Burr & Ross, 1986, and Fig. 3). That is, they effectively 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).

6.2. Motion streaks

It turns out that there another side to the motion-smear coin, one that has come to be known as “motion streaks”, or “speed-lines”. About 12 years ago Wilson 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 can be ambiguous as a result of the aperture problem. He pointed out that moving objects of finite size will stimulate two classes of cell: those tuned to the direction of motion, but also cells without motion tuning, oriented orthogonally (in space–space) to the direction of motion (see Fig. 6). He proposed a simple model where the broad-motion and stationary direction-selective units could be multiplied together.

Around this time, Ross and colleagues (2000) reported a new motion illusion in which random sequences of glass patterns (pairs of dots all aligned in a coherent fashion, to form global patterns) appear to move in coherent directions, following the direction of the dot pairs (URL: see movies 2 and 3). There is no actual motion

energy in this direction and it is easy to show that the motion energy is completely random. Indeed, if the motion detectors have an orientation preference orthogonal to their preferred direction of motion, then the motion should be orthogonal to the pattern, yet it is seen clearly to follow in the same direction as the spatial form, parallel, not orthogonal to the dot pairing. Ross et al. (2000) initially explained the illusion in terms of a high level interaction between form and motion channels. While this is possible, they also considered the possibility that the illusion results from the dot pairs stimulating the Geisler motion streak, or “speed-line” mechanisms. The randomly positioned dot pairs should generate a strong, but non-coherent sense of motion, equally strong in all directions, exciting many broadly tuned motion detectors of the type shown in Fig. 6. 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 favour of motion streaks. Burr and Ross (2002) showed that noise or Glass patterns oriented near the direction of motion strongly degrade motion discrimination thresholds. Furthermore, motion induced by glass patterns adds vectorially with real motion, suggesting that common mechanisms are being stimulated (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 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

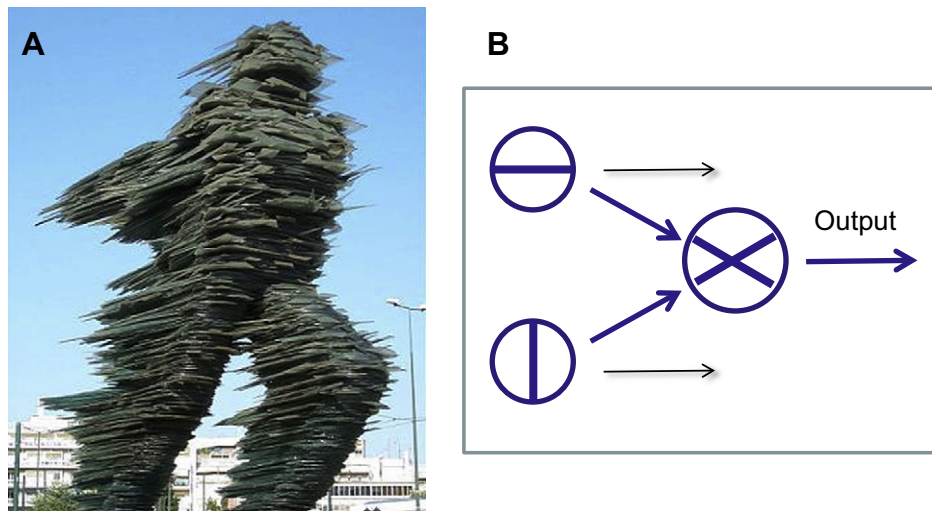


Fig. 6. “Speedlines” in human vision. (A) Cartoonists have long used the device of “speedlines” to indicate motion (introduced by Rudolph Dirks in his *Katzenjammer kids*). More recently, Greek artist Kostas Varotsos has produced three-dimensional motion streaks in this famous statue “the runner” (1988). The impression of fast motion is unmistakable. (B) Stylized illustration of Geisler’s (1999) “motion streak” model. The output of a neuron, or population of neurons, with spatially oriented receptive fields but no direction tuning (above) is combined with broadly directionally selective cells of orthogonal tuning. The spatially oriented, “non-motion” unit greatly enhances the direction selectivity of the motion detection unit. It has been suggested that mechanisms of this type lead to the sense of coherent motion from randomly draws of glass patterns.

with stimulus speed. Just as dynamic glass patterns (that contain no coherent motion energy) are seen by humans to move coherently (Ross et al., 2000), they also stimulate cells in the superior temporal sulcus (STS) 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.

Evidence from imaging studies suggests that implied motion from dynamic random glass patterns stimulates human motion areas (Krekelberg, Vatakis, & Kourtzi, 2005). Furthermore, adaptation to implied motion transferred to real motion in dorsal motion areas, suggesting that the same sub-population of neurons is selective to both real and implied motion. Other areas, such as the lateral occipital complex, did distinguish between real and implied motion. Apthorp and colleagues (Apthorp et al., 2010) have reported direct imaging evidence for encoding of motion streaks in human visual cortex. They trained a multivariate classifier on stationary oriented stimuli. This classifier was then able to detect reliably the direction of fast (“streaky”) motion, but not slow motion, in many early visual areas, including V1. All the evidence suggests that the streaks are real, and aid in encoding motion direction.

If nothing else, the studies on motion streaks have illustrated the resourcefulness of the visual motion system, to use all available information – even a cue that might normally be thought of as a hindrance to motion perception rather than a feature – to help it uncover the direction of moving objects and solve the aperture problem.

7. Influence of motion on position and space

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

7.1. The “flash-lag” illusion

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 be advanced compared with the position of a briefly flashed light. It is one of the more robust visual illusions, easily demonstrated in the classroom under almost any lighting conditions (demo). For example, you can mount a translucent card in front of a photographic flash and move it around in normal lighting, periodically setting off the flash: the flash seems to lag 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, largely because the neural mechanisms of motion perception are now much better understood, and we have more robust basic models to build on. Nijhawan's original explanation was interesting, couched in terms of a solution to an inherent problem of using dynamic perception to guide action. Given the various delays in processing visual stimuli, from photo-transduction onwards, the system is always working with information that is at least 100 ms old. Therefore, in order to judge the position at the present

time it is necessary to extrapolate the motion trajectory and this, he claimed, was why a moving target seems to lead a flashed stationary one. Certainly a good idea, but it has not stood up to rigorous testing. Perhaps the most direct test of extrapolation was to measure the effect when the moving stimulus stopped abruptly or changed direction or speed: an extrapolated trajectory goes beyond the reversal point, but this was not observed experimentally (Brenner & Smeets, 2000; Whitney, Cavanagh, & Murakami, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000). Further evidence against the extrapolation hypothesis is that in order to compensate for neural latencies, the magnitude of the effect should scale with latency. For example, at low luminance (which increases latency), the effect should increase, but in practice it diminishes (Krekelberg & Lappe, 1999) or even reverses (Purushothaman, Patel, Bedell, & Ogmen, 1998).

The failure of the extrapolation hypothesis led Whitney and coworkers to suggest another simpler explanation, the “differential latency hypothesis”. Put simply, they claim that the lag of the flash occurs because the visual system responds with shorter latency to moving than to flashed stimuli, providing good evidence that the magnitude of the effect was determined by time, rather than distance. While 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 colour or luminance (Sheth, Nijhawan, & Shimojo, 2000), and even works for streams of changing letters (Bachmann, Luiga, Poder, & Kalev, 2003; Bachmann & Poder, 2001).

Murakami (2001) devised a particularly clever adaptation of the flash-lag effect. Rather than using continuous motion, bars were presented 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. These results were difficult to reconcile with theories such as interpolation or spatial averaging, but did seem reasonably consistent with differential latencies. Whatever the explanation 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 off-sides are consistent with the flash-lag effect influencing their decisions.

The flash-lag illusion is not restricted to vision. Analogous phenomena occur in audition, both for moving sound sources and “chirps”, sounds that increase or decrease in pitch over time (Alais & Burr, 2003). Indeed the magnitude of the effect is much greater than in vision, 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.

Despite the enormous research effort expended on the flash-lag effect, no single clear explanation has emerged. Most agree that neural latencies per se are not the explanation, but it is still far from clear what mechanisms lead to the perceived delay. The debate about whether the flash-lag illusion is one of space or time is probably misconceived. When objects are in motion, space and time become inseparable (see Fig. 3). The complete explanation of the flash-lag effect almost certainly needs to be couched in

terms of space–time, rather than trying to treat the two dimensions separately.

In the end the flash-lag effect has probably opened more problems than it has solved. In particular it has raised the general question of how time and temporal order is encoded in the brain, which has proven to be an extremely profitable line of research: but unfortunately well outside of the scope of this review.

7.2. Effect of motion on perceived position

Observe a grating drift behind a stationary window, and 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 (URL: [movie 10](#)). A similar effect had been described by Matin, Boff, and Pola (1976), who showed that two opposed line segments rotating around a common point appear to be offset in the direction of rotation. 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. All 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 spatio-temporal receptive fields of the type shown in Fig. 3 give about the location in space of objects stimulating them.

About the same time, Snowden (1998) and Nishida and Johnston (1999) went on to show 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 to stationary objects (Goodale, 2011; Whitney, 2002; Whitney, Westwood, & Goodale, 2003; Yamagishi, Anderson, & Ashida, 2001). 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: while the motion aftereffect is chromatically selective, not transferring from one colour to another, or from colour to luminance, 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.

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. Although the debate often stagnates on issues like whether the effects result from distortions to space or to time, it should be now clear that space and time are not neatly separable for motion, so the distinction is moot.

8. Perception of speed

8.1. Models of speed perception

This review started by discussing several models of motion perception that heralded the era we are reviewing. These models proved very successful in detecting the direction of motion, with much more limited success in judging speed. A key element of these models is a low-level motion filter, selective for spatial frequency, orientation and direction of motion could be constructed from non-selective components. As discussed earlier these models were basically very similar, but subtly different, particularly in how they might encode speed information. Watson and Ahumada showed that a collection of their linear filters might be combined into a ‘vector motion sensor’ that can estimate speed and direction while Adelson and Bergen combined the linear filters to compute motion energy.

The Adelson and Bergen spatio-temporal energy model, in its simplest incarnation, suffers from the fact that changes in velocity cannot be discriminated from changes in contrast. This issue was addressed directly by them in a following paper where they noted that “at a given spatial frequency, the value of an energy measure is a function of both the velocity and the contrast of the stimulus pattern” (Adelson & Bergen, 1986). They proposed that one solution to this problem might be to compare the relative outputs of a set of spatio-temporal energy detectors with different broad temporal frequency tuning. Specifically a group of three detectors, one tuned to leftward (L), one to rightward (R) and one for static (S) energy might be compared as $(R - L)/S$ to give a monotonic change in response with velocity. This normalisation scheme has many attractions, not least that the opponent energy measure $(R - L)$ has a long history of being a convenient mechanism to explain the movement aftereffect, stretching back to Sutherland (1961) if not Exner (1888). And, as noted by Adelson and Bergen (1986) such an opponent energy measure can be extracted by Reichardt detectors (Fig. 2).

The Watson and Ahumada (1985) model achieves a contrast invariant measure of velocity in a somewhat different way; their scalar sensors are combined into groups that share location and spatial frequency, but which differ in preferred direction. By reading out the temporal frequency response of these vector motion sensors, an unambiguous measure of velocity may be derived, as velocity is merely temporal frequency divided by spatial frequency.

8.2. Effect of contrast on perceived speed

It is now known that the perception of velocity is not entirely independent of contrast; this was reported by Thompson (1976, 1982) and has been confirmed on many occasions since (Blake-more & Snowden, 1999; Brooks, 2001; Hurlimann, Kiper, & Carandini, 2002; Muller & Greenlee, 1994; Stocker & Simoncelli, 2006; Stone & Thompson, 1992). Even reaction times to motion onset, long known to depend on stimulus speed (Tynan & Sekuler, 1982), are influenced by stimulus contrast so they depend on perceived, not physical speed (Burr, Fiorentini, & Morrone, 1998).

Any model of motion perception must make a comparison between elements tuned to different aspect of the stimulus, to generate motion invariance. The earliest models, now termed ‘ratio models’ were originally invoked to explain the motion aftereffect (Barlow & Hill, 1963; Exner, 1894; Sutherland, 1961) but ratio models have also been suggested in a slightly different form as a model of speed coding. Tolhurst, Sharpe, and Hart (1973) suggested that speed might be determined by taking the ratio of the movement-analysing and pattern-analysing channels and this idea was echoed by Thompson (1982) to account for the dependence of

speed on contrast. A more rigorously defined version of a ratio model was outlined by Harris (1986) who refined the motion detector proposed by Marr and Ullman (1981). Essentially Harris takes the ratio of putative pattern and flicker channels to derive a signal that varies linearly with speed.

More recently Heeger (1987) developed the models based on spatio-temporal filtering to tackle the problem of extracting velocity information in a range of moving stimuli from sine-grating plaids (Adelson & Movshon, 1982), moving random dot fields to a computer-generated flight through Yosemite valley. Heeger exploited the fact that in the spatio-temporal frequency domain the power spectrum of a one-dimensional signal velocity is represented a straight line whose slope corresponds to velocity. Extending this to two dimensions the velocity of a 2-D texture will be represented by a tilted plane. Heeger's model uses a 'family' of motion-energy filters; in the particular implementation in the 1987 paper he envisages twelve energy filters, eight of which are most sensitive to a particular direction of motion and four of which are most sensitive to stationary patterns of different spatial orientations.

Heeger's model performs impressively in extracting image velocity as well simulating some well-established psychophysical findings, and has physiological plausibility with velocity-tuned units envisaged at the level of MT. A slightly different approach was taken by Grzywacz and Yuille (1990) in their computational model of velocity coding in the visual cortex. Like Heeger (1987) they took as their starting point the computation of motion energies. However they identified a number of weaknesses in Heeger's model including the assumption of a flat power spectrum which limits the range of stimuli for which the Heeger model estimates velocity correctly, and the biological plausibility of Heeger's computational requirements. Grzywacz and Yuille show that a population of spatio-temporal filters needs to be decoded simultaneously to measure local velocity and that 'pattern' cells in MT are suitable candidates for this task. Thus, they argue, the role of MT is more likely to be velocity estimation with motion coherence taking place later in the visual pathway.

The models of Heeger (1987) and Grzywacz and Yuille (1990) were further developed by Simoncelli and Heeger (1998). Again this is a two-stage model with V1 seen as the site of direction tuning while MT extracts velocity information. A further refinement of this model is described in Rust, Mante, Simoncelli, and Movshon (2006). These computational models appeal to existing neuro-physiological and psychophysical findings and a full description of them is beyond the scope of this review. An excellent summary of velocity computation in the primate visual system is to be found in Bradley and Goyal (2008).

8.3. The Bayesian approach

Any model of speed processing uses departures from veridical perception to inform the model. A very different approach to interpret these departures has emerged that appeals to Bayesian statistics. Ascher and Grzywacz (2000) proposed one such model that the authors felt was more realistic than the motion-energy models that used non-causal temporal filters and flat spatial spectra – both properties that Ascher and Grzywacz felt were 'unrealistic'. Key to this model and others developed around the same time was the belief that the prior distribution of velocities in the natural world is not flat, but biased towards slow speeds (Ullman & Yuille, 1989). Weiss and Adelson (1998) and Weiss, Simoncelli, and Adelson (2002) extended the Bayesian model to provide a more rigorous instantiation of Helmholtz's dictum that given the inherent ambiguity of visual information, it is the job of our perceptual system to make the best guess about the visual world (see also Stocker & Simoncelli, 2006). Thus if objects are more likely to be moving

slowly rather than fast, then a 'slow prior' should apply. And the noisier the signal the more influence the prior should have. Indeed the authors propose that "in the absence of any image data the most probable velocity is zero" (Weiss et al., 2002, p. 599). Intriguingly there is good evidence that increasing noise in the visual system by means of repetitive transcranial magnetic stimulation (rTMS) of areas V3A and MT+ has the effect of decreasing perceived speed (McKeefry, Burton, Vakrou, Barrett, & Morland, 2008).

One persuasive aspect of this Bayesian model is that the apparent decrease in speed of low contrast stimuli (Thompson 1982) is entirely to be expected. Furthermore the influence of contrast on perceived direction of moving plaids (especially type 2 – Fig. 4B) and lines can be accounted for. Weiss et al. (2002) conclude: "...we believe the underlying principle will continue to hold: that many motion 'illusions' are not the result of sloppy computation but rather the result of a coherent computational strategy that is optimal under reasonable assumptions". No one has given better advice to anyone studying visual 'illusions'. One note of caution might be that there are counter examples that the Bayesian model is less able to accommodate: reducing contrast does not always lead to a reduction in perceived speed. Gegenfurtner and Hawken have ample evidence that at higher rates of motion reducing contrast has little effect on perceived velocity, while Thompson, Brooks, and Hammett (2006) believe it can actually result in an increase in speed. Furthermore reducing luminance, which must surely reduce image data, can also increase perceived speed (Hammett, Champion, Thompson, & Morland, 2007).

An example of where the Bayesian approach has been applied with great success is in predicting the perceived speed from a mixture of retinal and extra-retinal movement, during pursuit eye movements. Freeman, Champion, and Warren (2010) show that combining two separate Bayes estimates at relatively early stages of visual processing, one for retinal motion and one for the pursuing speed, predicts well the perceived speed of pursued targets.

8.4. The contribution of colour to speed

During the 1980s there was increasing evidence for separate sub-systems in the primate visual pathway. The X and Y cell division in the cat (Enroth-Cugell & Robson, 1966), which became associated with the 'pattern' and 'flicker' channels in humans (1973), now became a division between the parvocellular and magno-cellular pathways. Drawing on the neuro-physiological observations of Zeki (1978), Zeki (1980) and others, Livingstone and Hubel (1987) drew clear distinctions between the properties and roles for these two visual streams. The magno-cellular pathway was identified as a colour-blind motion pathway. This conclusion was in part based on the finding that at equiluminance (also more clumsily known as iso-luminance), when the response of the magno-cellular pathway would be minimal, perceived velocity is very much reduced (Cavanagh, Tyler, & Favreau, 1984a; Ramachandran & Gregory, 1978). However, there is also evidence that motion perception is not always colour-blind. This has been demonstrated in a series of papers by Cavanagh and colleagues (e.g. Cavanagh et al., 1984a; e.g. Cavanagh, Boeglin, & Favreau, 1985) In one of these, Cavanagh and Anstis (1991) opposed a drifting luminance grating and a colour grating and, by adjusting the luminance contrast found the null point where the resulting counterphase grating appear to drift in neither direction – giving them the equivalent luminance contrast of the colour grating. Their results suggested that there was an important contribution of colour to the perception of motion.

Further evidence has come from Hawken, Gegenfurtner, and Tang (1994) who argued that if there is a single motion pathway that receives both luminance and chromatic information then the dependence of relative perceived speed on relative contrast

(Thompson, 1982) should be the same for both types of stimuli. However their results show a very different relationship, with equiluminant stimuli having a much steeper contrast dependence than the luminance stimuli. These results held only for slowly moving stimuli; at high speeds the contrast dependence was low for both stimuli suggesting the possibility of a single fast motion pathway that is not colour-blind but is largely contrast invariant. Again, reaction times to moving chromatic gratings are determined by perceived – not physical – speed, even though there is an enormous discrepancy between the two for slowly moving chromatic gratings (Burr et al., 1998).

The idea that we have more than one motion pathway was pursued further by Gegenfurtner and Hawken (1996) who measured perceived velocity as a function of contrast not just for luminance and equiluminant gratings but also for plaids, second-order, amplitude-modulated, drift-balanced stimuli. Below about 4 deg/s they again found that reducing contrast reduces perceived velocity and the dependence on contrast is greater for equiluminant gratings than for luminance gratings. This result is in line with the findings of Thompson (1982) and Stone and Thompson (1992). Interestingly the greatest effects were found with non-Fourier drift-balanced stimuli (Chubb & Sperling, 1988), but again the effects were limited to low rates of motion.

If there exist more than one motion pathway at slow speeds it is of interest to know over what range they operate. Thompson (1982) believed the upper limit for a reduction in contrast leading to a reduction in speed was about 4 Hz, that is it was a temporal frequency rather than a velocity limit. Gegenfurtner and Hawken (1996) came to a somewhat different conclusion believing that the limit was determined by a combination of both spatial and temporal frequencies. However their results were sufficiently limited to prevent them from reaching any firm conclusions.

At low velocities at least it appears that both the parvocellular and the magno-cellular pathway are involved in the computation of velocity. The obvious approach is to take some ratio of magno to parvo response to compute velocity. However some authors are rather coy about this. Hammett, Champion, Morland, and Thompson (2005) refer to the ratio of two temporal channels, one low-pass and one band pass. Clearly they have in mind magno-cells and parvocells and even label them 'm' and 'p', after Perrone (2005), but without explicitly wishing to involve both pathways in speed perception. A somewhat updated version of this ratio model by Hammett et al. (2007) again employed the low- and band-pass temporal filters proposed by Perrone (2005), this model can accommodate several findings in the literature: some velocity aftereffects (Hammett et al., 2005), decreases and increases in perceived speed at low contrast (Thompson et al., 2006) and increases in perceived speed at low luminance (Hammett et al., 2007).

8.5. Speed-tuned neural units?

Both for technical and theoretic reasons (particularly the simple Fourier description), much research into speed perception has used moving sine-wave gratings, defined by their spatial and temporal frequencies. Clearly if we have true 'speed-tuned' cells in the visual pathway then the temporal frequency tuning of cells would have to vary with the stimulus spatial frequency. Physiological reports of the tuning of cells in cat and monkey Area 17 (e.g. Foster, Gaska, Nagler, & Pollen, 1985; Tolhurst & Movshon, 1975) suggested that this was not the case and that there was separable tuning for spatial and temporal frequency. Clearly if we were to find 'velocity-tuned' units we should have to look elsewhere. The obvious candidate site was area MT.

Since 1983 it has been suspected that MT contained some real velocity-tuned cells (Newsome, Gizzi, & Movshon, 1983). The same group later reported that 'for some neurons in MT, the spatio-

temporal tuning is distinctly non-separable, with the optimal spatial frequency varying with the optimal temporal frequency to maintain a constant optimal speed for all stimulus configurations.' (Movshon, Newsome, Gizzi, & Levitt, 1988). More recent work by Perrone and Thiele (2001) has confirmed that many cells in MT can be regarded as truly velocity-tuned, although this conclusion was challenged, in part, by Priebe, Cassanello, and Lisberger (2003), who estimated that perhaps only 25% of MT cells were speed-tuned when tested with sine-wave gratings. Strikingly there appeared to be a unimodal continuum of cells from speed-tuned to spatio-temporally separable, with most cells falling somewhere between the extremes. Furthermore when stimuli comprising two sine-wave gratings were used then the tuning of cells moved towards the speed-tuned end of the continuum. In other words it may be that sine-wave gratings, for all their popularity in motion research are precisely the stimuli that the system finds it hardest to deal with. Later work by Perrone (Perrone & Thiele, 2002; Perrone, 2004) developed a plausible account of how speed-tuned MT units could be constructed from their V1 input. Meanwhile Priebe, Lisberger, and Movshon (2006) have re-examined speed tuning in V1 cells and have found that, while nearly all direction-selective simple cells have responses separable for spatial and temporal frequency, the complex cells were somewhat similar to the MT cells reported by Priebe et al. (2003). Thus over the past twenty years we have seen a shift in our understanding of speed tuning in the visual system; in the 1980s most cells seemed to have tuning separable for spatial and temporal frequencies whilst now non-separable speed tuned units seem to be ubiquitous.

The belated but nonetheless comforting finding that there exist speed tuned neurones in the visual pathway has also received support from fMRI studies. Lingnau, Ashida, Wall, and Smith (2009) have used an adaptation paradigm introduced by Grill-Spector and Malach (2001) to investigate this; following adaptation to a high contrast drifting grating, the fMRI signal change was recorded when a probe stimulus was either of the same speed or the same temporal frequency. Using the logic that if the same neuronal populations encode both the adaptation and probe stimuli the response to the latter will be attenuated, Lingnau et al. found good evidence for speed-tuning in areas MT and MST.

Evidence for the involvement of V3A as well as MT+ in motion processing in general and speed processing in particular has come from studies employing repetitive transcranial magnetic stimulation (rTMS). McKeefry et al. (2008) reported that rTMS applied to these areas reduced the perceived speed of stimuli and often impaired speed discrimination but had no effect on spatial frequency discrimination. Unfortunately the exact effect of rTMS on brain processing is unknown. It might increase neural noise (Walsh & Cowey, 2000) in which case the decrease in perceived speed would sit well with Bayesian models of speed processing (Stocker & Simoncelli, 2006) but there are also other possibilities; the effects of TMS have been shown to be state dependent: rTMS will on some occasions facilitate and on some occasions suppress activity, depending on the baseline activity of the targeted area of the brain (Silvanto, Cattaneo, Battelli, & Pascual-Leone, 2008). More specifically Cattaneo and Silvanto (2008) showed that following adaptation to motion in one direction, the application of TMS can enhance the detection of motion direction in the adapted direction relative to the unadapted direction. Thus it would appear that TMS has a similar effect as micro-stimulation of the adapted population. Burton, McKeefry, Barrett, Vakrou, and Morland (2009) have built on this finding to investigate the effects of TMS on speed perception. The most accepted model of speed encoding would propose that we take the ratio of two speed tuned channels, one low-pass, tuned to slow speeds, the other band pass and tuned to higher speeds (e.g. Hammett et al., 2005). Following adaptation to a fast

speed, the band-pass channel is adapted, the ratio drops and perceived speed is reduced. Adaptation to the slow speed should adapt the low-pass channel more and perceived speed increases. This is what Burton et al. found. But they also found that TMS combined with this adaptation reduced the perceived speed after either adaptation, a result not expected if TMS boosts the adapted neurons. Burton et al. interpret their findings as showing that TMS suppresses the most responsive neurons to a stimulus, rather than boosting the most adapted.

8.6. Speed perception during pursuit eye movements

Much research on our perception of speed has sought to simplify the problem by carrying out observations with the head in a fixed position and with the subject fixating a stationary point. Furthermore stimuli are often of short duration to restrict eye movements. The goal in most experiments here is to examine motion across the retina. However, when faced with motion in the real world we generally track the stimulus with our eyes, so in order to compute speed we must combine both eye movement and retinal movement. (We shall leave aside the problem of head movement in the perception of speed as relatively little research has looked at it). There has been a general assumption that two motion illusions arise because of errors associated with estimating eye velocity from extra-retinal signals; the Filehne illusion and the Aubert–Fleischl phenomenon. By ascribing these illusions to the gain of the eye-velocity signal being less than unity, the tacit assumption is that the retinal motion signal is error free. However, as pointed out by Freeman and colleagues (Freeman, 2001; Freeman & Banks, 1998; Sumnall, Freeman, & Snowden, 2003), this seems an unlikely state of affairs as it is well known that retinal speed is affected by contrast (Thompson, 1982), spatial frequency (Diener, Wist, Dichgans, & Brandt, 1976) and colour (Cavanagh, Tyler, & Favreau, 1984b). Freeman and Banks (1998) proposed that estimates of ‘head-centric’ velocity errors arise both from our estimates of eye velocity and in retinal motion, and this model accurately predicted the magnitude of the Filehne and Aubert–Fleischl illusions.

In the Filehne illusion (Filehne, 1922) a smooth pursuit eye movement made across a stationary background will result in the background appearing to move in a direction opposite to the eye movement. In the related Aubert–Fleischl effect (Aubert, 1886; Fleischl, 1882) the perceived speed of a tracked moving target is lower than a target that moves across the stationary retina. In both these cases, changes in spatial frequency and/or contrast affect the size of the illusions but it is only the perceived retinal speed and not the extra-retinal signal that is spatial frequency and contrast dependent (Freeman & Banks, 1998; Sumnall et al., 2003). This convincingly suggests that both extra-retinal errors and retinal speed estimate errors are responsible for misperceptions of speed when eye movements are involved. Murakami (2007) has provided some support for this approach by showing that the Filehne illusion at equiluminance can be reduced or reversed as the input gain of retinal velocity is lowered under these conditions. See Freeman et al. (2010) for a discussion of how these errors come about.

Smooth pursuits are not the only class of eye movement to affect motion perception. Saccades also impact heavily on motion perception, principally in reducing sensitivity to fast motion of low spatial frequencies (Burr, Holt, Johnstone, & Ross, 1982; Burr, Morgan, & Morrone, 1999; Burr, Morrone, & Ross, 1994; Shiori & Cavanagh, 1989), but also by affecting the motion selectivity of MT neurons in interesting and unexpected ways. Unfortunately, we cannot extend our review to cover this interesting line of research, but the interested reader is referred to Kowler's (2011) review in this series.

If the problems involved in computing head-centric speed have been taxing, then matters can only get worse if the observer moves through the world. The field of optic flow has a long history stretching back to Gibson and beyond (see Mollon, 1997) and a full discussion of it is outside the scope of this review. However recent developments which address the knotty problem of how we assess the motion of objects during our self-motion are particularly exciting. Work by Warren and Rushton (e.g. Rushton & Warren, 2005; Warren & Rushton, 2009) has spawned the ‘flow parsing hypothesis’. In essence this proposes that there is a global subtraction process that cancels the overall expanding radial flow that results from our movement forward in the world. The key is the global nature of the mechanism that discounts the retinal motion that may be attributed to the observer's motion. It would appear that local motion mechanisms make very little contribution to the process. For more discussion on these issues, the reader is referred to specific reviews, such as Warren (2004).

9. Adaptation to movement and the motion aftereffect (MAE)

A question that has occupied almost more attention than *how* do we encode motion in the visual pathway is *where* we do so. The motion aftereffect (MAE) has played a key role in this line of inquiry. At one time it appeared that the partial interocular transfer of the MAE and its immunity from the effects of attention located much motion processing around primary visual cortex and, a little later, in MT, but certainly before higher levels of processing where attention might be expected to have an effect. However research in the past 25 years has radically altered our views of the MAE or perhaps MAEs and of the influence of attention on early motion processing.

9.1. The effect of attention of the motion aftereffect

Wohlgemuth (1911), whose review of the MAE remains the single most important work on the subject, asked, in one of his experiments, the question of whether or not the size of the aftereffect was affected by the attentional state of the subject. His experiment suggested that the MAE was unaffected by attention and that position was not challenged for many years. Indeed, Blake and Fox (1974) and He, Cavanagh, and Intriligator (1996) seemed to support the low level nature of adaptation in that rendering an adapting stimulus ‘invisible’ by binocular rivalry or crowding did not affect its efficacy in inducing an aftereffect. These conclusions support the idea that sensory adaptation is a low-level process that precedes conscious perception and the effects of attention. The single contrary voice was Chaudhuri (1990) who claimed that the MAE was indeed modulated by attention. Clearly Chaudhuri was unaware of Wohlgemuth's findings – which goes to show that sometimes one is better off not knowing the literature. When Gandhi, Heeger, and Boynton (1999) reported that spatial attention *did* affect the fMRI response in V1 they listed no fewer than nine previous studies using functional neuroimaging and ERPs that had found no effect of selective spatial attention in human V1.

Chaudhuri, once a lone voice crying in the wilderness, soon attracted many converts and disciples. Shulman (1993) confirmed Chaudhuri's results and Lankheet and Verstraten (1995) demonstrated that attention could modulate the strength of the motion signals that gave rise to the MAE. Alais and Blake (1999), in an elegant experiment, showed how a ‘bivectorial’ motion stimulus – comprising two sets of dots moving in different directions – would produce an MAE whose direction depends on the attention devoted to one of the component motions. This result clearly sits uncomfortably with Blake's earlier work and he has since recanted his former position. He now has evidence that the MAE is substantially

reduced during binocular rivalry and crowding (Blake, Tadin, Sobel, Raissian, & Chong, 2006). The seeming contradiction between these findings and his previous position was reconciled by considering the contrast of the adapting pattern. It is widely believed that as adaptation contrast increases, so does the strength of the aftereffect, but that there is a compressive non-linearity in the aftereffect such that when the adaptation contrast exceeds about 2–3% contrast, the aftereffect strength remains nearly constant (Keck, Palella, & Pantle, 1976). Blake et al. (2006) note that previous reports that show no effect of suppression on aftereffect strength have all used high adaptation contrasts, contrasts that might produce saturated aftereffects. Therefore it could be the case that the effects of suppression by rivalry or crowding could be masked by this saturation. By adapting to lower contrasts on the rising part of the contrast-response curve Blake et al. were able to show that binocular rivalry and crowding can indeed affect the strength of the aftereffect.

9.2. Neuroimaging the motion aftereffect

Since the early 1990s much evidence from neuro-imaging has supported this general premise that attention can influence visual processing, even at early stages (as early as the LGN: O'Connor, Fukui, Pinsk & Kastner, 2002). An early study by Corbetta, Miezin, Dobmeyer, Shulman, and Peterson (1991) obtained psychophysical evidence that speed discrimination was better when subjects attended to one attribute of the stimulus rather than dividing their attention and that PET measurements of extra-striate visual areas during these tasks were modulated by selective attention. Further support for the effects of attention has come from Rees, Frith, and Lavie (1997) who demonstrated that both activity in MT and the duration of the MAE were reduced when a high-load irrelevant linguistic task was carried out simultaneously. This finding was taken to support Lavie's theory (Lavie & Tsai, 1994) that, given finite attentional resources, we will be less able to attend to the motion stimulus when more attentional demands are made by the high-load task.

The past ten to fifteen years have seen many imaging studies that have confirmed the involvement of human MT+ in motion adaptation (e.g. Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Corbetta et al., 1991; e.g. Beauchamp, Cox, & DeYoe, 1997; Buchel et al., 1998; Chawla et al., 1999; Huk & Heeger, 2000; O'Craven, Rosen, Kwong, Treisman & Savoy, 1997; Treue & Martinez Trujillo, 1999). One note of caution was sounded by Huk, Ress, and Heeger (2001) who pointed out that because the MAE was such an 'engaging' illusion, subjects might attend more to the illusory motion than to a control stimulus. Thus studies which compared the BOLD response in MT+ while experiencing an MAE compared to a stationary pattern might be confounding the effects of attention with the illusory motion. Huk et al.'s suspicions were well-founded; their results showed that the effects of attention on MT+ activity can be large, comparable in size with the activity produced by the MAE. However, when controlling for the effects of attention they did confirm that direction-selective adaptation does produce direction-selective imbalances in MT+ responses.

The floodgates were now open for anyone with access to fMRI to investigate in humans what had only been demonstrated previously in the macaque monkey. Huk and Heeger (2001) saw the opportunity to see if the human visual system had the same 'component-motion' and 'pattern-motion' cells reported in MT (Movshon, Adelson, Gizzi, & Newsome, 1985). Area V1 appeared to have only component-motion cells – cells that respond to motion orthogonal to local contour orientation – while MT appear to have both component-motion and pattern-motion cells; the latter responding to the direction of motion of whole patterns irrespective of the orientation of their components. The distinction in these

two cell types had been revealed in experiments using plaid stimuli and Huk and Heeger (2000) too used adaptation to plaids to separate pattern from component motions. In a cunning design, they combined pairs of component gratings into plaids that either all moved in the same direction or different directions. Thus an area of the brain that only responded to component motion would see no difference between the two sets of stimuli but an area with pattern-component cells would treat the two sets differently. In line with previous expectations area MT+ showed much greater adaptation to the coherent pattern motion. The authors also reported pattern-motion adaptation to a lesser degree in areas V2, V3, V3A and V4v.

9.3. Multiple sites for the motion aftereffect?

If it now seems well-established that motion is processed in multiple sites along the visual pathway and now it appears that we can reveal different stages of this processing with suitable psychophysical tasks. If motion is processed in many parts of the visual system (V1, V3, and MT+ for example), and if there is good evidence that these areas appear to be susceptible to adaptation, shouldn't we be able to discriminate between adaptation at one site rather than the other? There is increasing evidence that the answer to this question is 'yes'.

In 1986 von Grunau demonstrated that long range apparent motion was capable of generating an aftereffect on a flickering test pattern but not on a static one. At the time this seemed to suggest that the dynamic test was just a more sensitive way of measuring the effect. However Hiris and Blake (1992) reported that following adaptation to motion the aftereffect seen is markedly different depending upon whether the test pattern is a static or dynamic display. Hiris & Blake reasoned that testing on a stationary pattern would not optimally test those motion mechanisms involved in the adaptation, whereas a test pattern of dynamic visual noise might. They found that the MAE on the dynamic display could be confused for real motion, but the MAE on the static display never was. Raymond (1993), noting that it is generally assumed that the degree of interocular transfer of an aftereffect is an index of the proportion of binocularly driven cells involved with the effect (Moulden, 1980; Movshon, Chambers, & Blakemore, 1972), reported that when tested with a dynamic test pattern the MAE showed nearly 100% interocular transfer. This, she suggested, arose because of the total binocularity of cells in MT (Zeki, 1978), an area that does not respond to stationary stimuli (Albright, Desimone, & Gross, 1984) but does to dynamic stimuli. Nishida, Ashida, and Sato (1994) showed further differences between the two types of MAE, the static aftereffect showed partial interocular transfer following adaptation to first-order motion whereas what they called the 'flicker MAE' (tested on a counterphase modulated grating) showed complete interocular transfer with adaptation to either first- or second-order motion. Nishida and Sato (1995) went on to pit the two aftereffects against each other; adapting to first-order motion in one direction and second-order motion in the opposite direction. This led to a static MAE predominantly induced by the first-order motion and a flicker MAE in the opposite direction produced by the second-order motion. This gave further support to the idea that the static MAE reflects activity in lower-level motion mechanisms, perhaps in V1, while the flicker MAE reveals higher-level motion processing, perhaps in MT. Intriguingly Ashida and Osaka (1995) found that the flicker MAE seemed to depend on the adaptation velocity and not, as is the case with the static MAE (Pantle, 1974), on the adaptation temporal frequency. A dependence on adaptation velocity was exactly what was reported for the velocity aftereffect by Thompson (1981).

Further evidence for two aftereffects, one in originating in V1 and the other in MT has come from Aghdaee and Zandvakili

(2005) who used a logarithmic spiral as the adaptation stimulus. They tested the MAE with both the stationary adapt stimulus and with its mirror image. One property of the mirror-image test stimulus is that all contours in the pattern lie orthogonal to those of the adaptation pattern. Thus given the orientation tuning of V1 cells, there should be no contribution to any aftereffect from V1 activity. The authors found significantly longer MAEs when testing with the original rather than the mirror-image test pattern, suggesting that V1 is indeed implicated in the MAE, though not as the only site.

Maruya, Watanabe, and Watanabe (2008) have used dynamic continuous flash suppression to present a totally unperceived moving pattern to one eye. This pattern nonetheless produced both an MAE on a static and a dynamic test field. However, intriguingly, the usually robust interocular transfer seen in the dynamic MAE was completely abolished when the adaptation pattern was invisible. This led the authors to conclude that higher level adaptation does not occur when the adapting stimulus is invisible. In contrast, Whitney and Bressler (2007), using crowding as a technique to reduce awareness of visual stimuli report that second-order motion aftereffects, assumed to arise beyond V1, persist. Clearly there is still much we have to learn about motion adaptation.

Over the past 25 years there have been dozens of papers on the MAE and it not possible to do justice to all those that have made a contribution here. Fortunately, the excellent book, "The Motion Aftereffect", edited by Mather, Verstraten, and Anstis (1998) will furnish the reader with more information about the aftereffect than, in all probability, they want.

10. Illusory motion

In 2000 Baingio Pinna published a striking new visual effect (Pinna & Brelstaff, 2000). A seemingly simple figure of small squares arranged in a circle, appeared to rotate as one moved one's eyes to and fro towards the centre of the picture, Fig. 7A.

Of course, that motion can be seen in a stationary image is nothing new – quite apart from the movement aftereffect, induced motion & the autokinetic effect, there have been artists (such as Bridget Riley) who have produced works which conjure up motion, (see Zanker & Walker, 2004). What is striking in the case of the Pinna effect is that the figure is so simple and the illusion of motion so compelling. The explanation seems to lie with the aperture problem. If direction-selective neurons are orientation selective they report movement which is in a direction orthogonal to their preferred orientation. The micro-elements of the Pinna illusion have a strong orientation once they are blurred (Fig. 7B), as they are when they fall on peripheral vision. As we move our head closer to the pattern it expands on the retina, but the interpreted motion of each micro-element is strongly dominated by its local orientation and each has its preferred direction of motion at an angle of 45° to its expansion. Taken together all the elements in one ring are grouped by common fate and a coherent rotation of the ring is observed.

This striking illusion illustrates how low-level motion detectors – of the type discussed in Section 2 – must both inform the system about local motion and contribute to computing global movement from self-motion. However this explanation is not quite the whole story, as has been pointed out by both Morgan (2002) and Gurnsey, Sally, Potechin, and Mancini (2002). In the Pinna illusion the effect is greater when we move our heads towards the figure than when we just expand the image on a screen in front of us, even though the retinal motion is identical in the two cases. When we move towards the picture it appears the visual system can 'discount' the image expansion brought about by our motion and recover the 'true' motion of objects in the world.

At about the same time that the Pinna illusion was published, Akiyoshi Kitaoka started to produce seemingly unending variants of images that contain illusory motion. Perhaps the most famous of these, entitled 'Rotating snakes', involves several components, as, perhaps, all good illusions do, Fig. 8. Kitaoka and Ashida (2003) built on an illusion first reported by Fraser and Wilcox (1979) and elaborated by Faubert and Herbert (1999). Here the illusory motion appears when the pattern is in peripheral vision and when there is a transient from eye movements or a blink. Faubert and Herbert propose that the illusion arises because of the different latencies of response for low and high luminance patterns, an effect that is enhanced by the integration of information over a large retinal area in the periphery. In the 'rotating snakes' illusion it appears that the Fraser & Wilcox illusion is optimised, and the explanation given by Kitaoka and Ashida (2003) is in terms of the faster latency of the black and white areas compared to the dark and light grey areas by virtue of their contrast with average grey of the display. This explanation was revised by Conway, Kitaoka, Yazdanbakhsh, Pack, and Livingstone (2005) who liken the illusion to a static version of Anstis and Roger's (1986) four stroke motion in which a sequence of apparent motion and reverse apparent motion (Anstis, 1970) produces seemingly unending forward motion.

The advent of fMRI has introduced a new way to examine the illusory motion seen in static displays. Kuriki, Ashida, Murakami, and Kitaoka (2008) examined the BOLD response in motion sensitive areas of the brain – V1 and human MT complex (hMT+) – to the Snakes illusion and a control pattern similar to the Snakes illusion that did not elicit spontaneous motion. They found, under three conditions, no eye movements (NEM), guided eye movements (GEM) and spontaneous eye movements (SEM), that while no difference was observed between the two stimuli in V1, there was an increased BOLD response in hMT to the Snakes illusion figure and that this effect was greatest for spontaneous eye movements and least for fixation.

In 1991 Zeki and colleagues (Zeki et al., 1991) used Positron Emission Tomography (PET) to study cerebral activity of subjects observing a monochrome version of the celebrated image by artist Isia Leviant (1996) entitled 'Enigma', Fig. 9. Observers experience rapid circular motion in the concentric circles of the image as well as a shimmering in the high-contrast radial lines. Zeki and his colleagues found an increase in their regional cerebral blood flow (rCBF) in an area largely surrounding MT. However there was no significant activity in V1 to the display, although this area shows high activity to a real motion stimulus. This result may seem to many to be somewhat unremarkable, indeed Zeki et al. felt the 'interest in this result is as much philosophical as it is physiological', but nonetheless the finding has proved controversial. There has been growing evidence that in fact an explanation in terms of microsaccades is adequate, at least for one aspect of the illusion.

Of the two illusory motions experienced in the 'Enigma' figure the shimmering on the radial lines has been exhaustively investigated by Zanker and colleagues (2010) using 'riloid' figures – computer generated stimuli that ape Bridget Riley's famous op-art painting 'The Fall' which is to be found in the Tate Britain Gallery, London. These shimmerings seem adequately explained by microsaccades that occur while viewing the pictures. Whether the illusory rapid circular motion can be explained in the same way is harder to tell. Troncoso, Macknik, Otero-Millan, and Martinez-Conde (2008) monitored eye movements while looking at the Enigma figure and found a close correlation between the strength of the illusory motion and the production of microsaccades. This they claimed, suggests that the origin of the illusion cannot be solely cortical.

The origins of the rapid circular motion is still controversial; Hamburger (2007) has demonstrated the effect persists when the

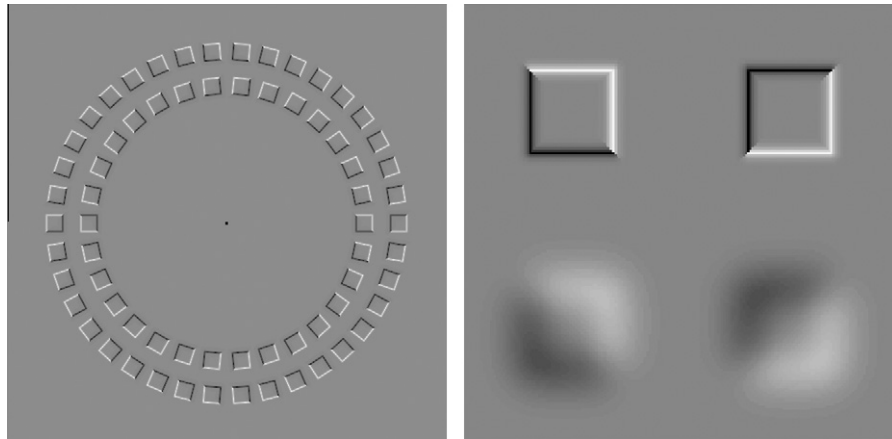


Fig. 7. (a) Pinna's illusion. While fixating the centre of the figure, movement of the head towards the figure gives a striking illusion of the inner ring rotating counterclockwise while the outer ring rotates clockwise. (b) A micro-element of the Pinna illusion seen in peripheral vision will have orientations that provide the orthogonal motion cues as the pattern expands.

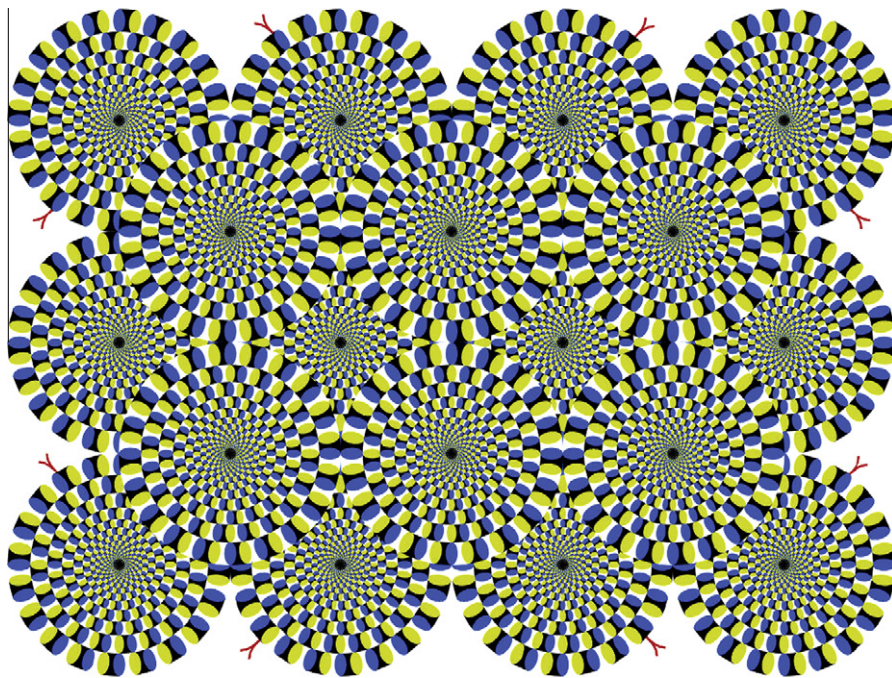


Fig. 8. Akiyoshi Kitaoka's 'rotating snakes' illusion. A complex pattern like this one may have several elements involved in the motion it generates when we move our eyes over the pattern. Visual latency to different luminances, apparent motion and reversed apparent motion have all been implicated in the effect.

ciliary muscles are paralysed to prevent accommodative responses, casting doubt on Gregory's (1993) belief that accommodation was responsible. To make doubly sure Hamburger also used a 2 mm artificial pupil which obviated the need for accommodation. The persistence of the illusion under these conditions confirmed Zeki's (1994) similar observation following the application of atropine. Furthermore, Hamburger induced the Enigma figure as a strong positive afterimage and found the motion persisted, though it was 'spurious and faster' than that seen with direct viewing. This appears to suggest that, although not necessary for the illusion, microsaccades may enhance the effect.

One final motion illusion deserves a little attention given the interest shown in it over the past 25 years. The Ouchi illusion, first described by the eponymous Japanese artist, is shown in Fig. 10. Inspection of the figure leads to relative movement between the central circle pattern and its surround. If the page is moved to

and fro along the diagonal the effect is generally enhanced. Clearly the motion signals from the centre and surround areas are providing conflicting information. The usual explanation suggests that when local-motion signals are integrated to provide a 2-D estimate of movement direction, some error arises (e.g. Hine, Cook, & Rogers, 1997). Mather (2000) took this explanation a step further and linked the explanation to the observation by Castet, Lorenceau, Shiffrar, and Bonnet (1993) that drifting lines appear to move fastest when their orientation is orthogonal to their direction of motion (see Section 8.6). When the vertical and horizontal edges of the Ouchi figure are moved obliquely, there is an integration bias towards seeing the motion as being orthogonal to the orientation of the longer edges of the elongated rectangular elements (Nakayama & Silverman, 1988) and it is this bias that gives rise to the illusion. A somewhat different explanation has been proposed by Ashida, Kitaoka, and Sakurai (2005). By using line

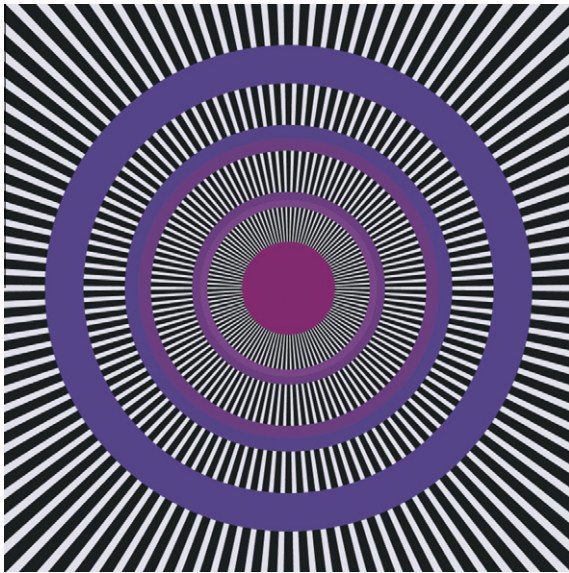


Fig. 9. Isia Leviant's 'Enigma' generates two types of illusory motion: the shimmering of the radial lines and the rapid circular motion in the concentric rings.

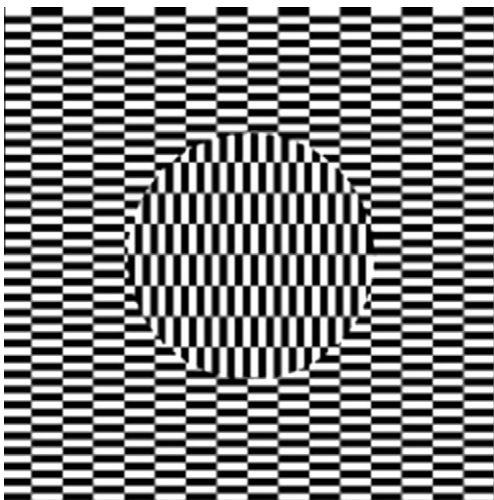


Fig. 10. The Ouchi illusion. After inspecting the figure for a short while the central area moves relative to the surrounding background. As with other motion illusions, though there may be several components to the effect, consideration of the spatio-temporal energies of the display often provides the explanation.

segments rather than rectangles as elements in the illusion, Ashida was able to show that randomising the position of the elements greatly reduced the size of the illusion. This finding, a problem for explanations in terms of the motion vectors of edges, was satisfactorily accommodated by considering the Fourier fundamentals and lower harmonics in the display rather than the edges.

It would be hard not to include one stunning illusion, not of a stationary pattern in which is seen illusory motion, but an illusion in which real motion renders stationary objects invisible. Bonneh, Cooperman, and Sagi (2001) produced a global moving pattern superimposed on high-contrast stationary dots. After a few seconds fixating the display, the stationary dots simply disappear (demo). This fascinating effect has attracted much attention without any real consensus emerging as to why the effect occurs. One intriguing possibility, proposed by New and Scholl (2008) is that when the visual system, faced with a large area of coherent movement, detects a small stationary spot, it assumes that the spot may be a scotoma and thus fills it in. Another creative suggestion is that

it relates to motion streaks: as the visual system suppresses visibility of the streaks, stationary objects falling in their track are also suppressed (Wallis & Arnold, 2009). Whatever the explanation, this effect is certainly one of the more robust illusions to be reported, and even works with physical objects: there is a version in the Exploratorium in San Francisco where rotating a transparent disk painted with small, randomly position dots above some dollar bills causes the bills to disappear intermittently!

11. Multi-sensory motion perception

One field that has expanded unexpectedly over the last quarter-century is multi-sensory perception. It is now clear that the senses do not operate independently from each other, but are closely linked, interacting at many neural levels, including very early levels. While a full survey of the advances in this field is well beyond the scope of this review, it seems opportune to remind us that the visual system is not completely isolated from the other senses, such as audition and touch. Readers interested in a more thorough coverage of the area are referred to the excellent handbooks and reviews, such as Calvert, Spence, and Stein (2004), Trommershäuser, Landy, and Körding (2012) and Stein and Stanford (2008).

Evidence for multi-sensory combination of motion signals has existed for some time. Barry Stein, one of the major pioneers in the field, demonstrated back in the 70s that neurons in the deep layers of cat superior colliculus respond to visual, auditory and tactile stimuli, but much better to the combination two or more than to single-sense stimuli (Meredith & Stein, 1985; Stein & Arigbede, 1972). More recently fMRI studies have shown that the human MT complex responds not only to visual movement, but also to tactile movement (Blake, Sobel, & James, 2004; Hagen et al., 2002). Other studies show that audio-visual motion activates clusters in the superior temporal gyrus, the supramarginal gyrus, the superior parietal lobule, and the cerebellum, much more strongly than either auditory or visual motion alone (Baumann & Greenlee, 2007).

Psychophysical evidence for functional integration of motion signals between senses is somewhat intricate. It has long been known that sight and sound interact in speech perception, best illustrated by the well known McGurk and MacDonald (1976) effect: observing lips mouthing a different sound from that played acoustically influences the perception of the heard sound. There are many examples of slight improvements of reaction times and error rates when moving stimuli are presented both visually and acoustically (see for example Driver & Spence, 1998).

Meyer and Wuerger (2001) studied the interaction of moving dot stimuli and moving sound sources: when displayed together, both near individual threshold, the two sources sum to increase sensitivity. However, the amount of summation was slight (about a root-two advantage), and not direction specific: being the same when the auditory and visual motions were in the same or opposite directions. This small non-directional advantage is readily explainable as a mere statistical advantage, as there is more information in two sensory sources than in one (akin to probability summation: Graham, 1977). Meyer, Wuerger, Rohrbein, and Zetzsche (2005) later reported direction-specific summation for co-localized object stimuli, but this was not confirmed by Alais and Burr (2004), who found non-directional summation under all conditions. More robust, functionally useful interactions have been observed for biologically relevant stimuli, such as "biological motion" (Brooks et al., 2007), and tap dancing (Arrighi, Marini, & Burr, 2009).

Interactions have also been demonstrated with haptic and visual motion. Many of the standard visual motion illusions, such as the barber-pole illusion (reflecting the aperture effect) have been reported for haptic stimuli (Bicchi, Scilingo, Ricciardi, &

Pietrini, 2008). Tactile motion also produces a strong aftereffect, perhaps not surprisingly. More surprising is the fact that it transfers to visual motion, and vice versa (Konkle, Wang, Hayward, & Moore, 2009). Given the evidence that both senses activate human MT, and that MT seems to be implied in the motion aftereffect (Tootell et al., 1995), MT seems a likely candidate to mediate this cross-sensory transfer.

Blake and colleagues have reported several interesting demonstrations showing how touch (Blake et al., 2004; James & Blake, 2004) and voluntary action (Maruya, Yang, & Blake, 2007) can disambiguate visual motion. Summation of haptic and visual motion has also been studied. As with visual and auditory motion, visual and haptic motion signals sum to increase slightly sensitivity in a non-directionally specific way, again like probability summation (Burr, Sandini, & Gori, in press). However, a related technique called *facilitation*, also termed the “pedestal effect” (Nachmias & Sansbury, 1974; see also Pelli, 1987) did reveal functionally relevant directionally specific interactions. There are differences between summation and facilitation. Whereas for summation the strengths of both stimuli are varied together to determine threshold, with facilitation an uninformative *pedestal* is always present in both intervals of the 2AFC trial. At certain values (usually just above threshold) the non-informative pedestal facilitates detection and discrimination, resulting in what is called a “dipper function” (see Solomon, 2009, for a primer on pedestal effects and the “dipper function”). At appropriate signal strengths, haptic motion acts as a pedestal for visual motion, and vice versa – but only for motion in the same direction (Burr et al., in press). When the direction was opposite (even consistently opposite and subjects aware of this), there were no facilitation effects.

So why should facilitation, but not summation, reveal functionally useful direction-specific multi-sensory interactions? The reason is not completely clear, but the evidence suggests the action of thresholding before cross-sensory combination of sensory information. In the summation paradigm, the signals from the individual senses do not reach individual threshold, and are therefore not combined in the multi-sensory percept: the small non-directional advantage is a statistical advantage expected on theoretical grounds (see Ernst & Banks, 2002). With facilitation, however, the pedestal is weak but supra-threshold. Presumably this information is relayed to other sensory motion areas, where it facilitates detection. The means by which it facilitates the motion are not entirely clear, but it is clear that real motion signals must exist: if they are consistently in the wrong direction, the subject cannot use that consistent information (“mentally inverting the direction”) to facilitate thresholds.

As we begin to have a firmer understanding of visual motion, it is natural that researchers will extend their efforts to study motion in other senses, and the combination of motion information from many senses. Ultimately perception is multisensory, a full understanding requires not only understanding of vision, but of how all our sensory apparatuses link together to provide a unique representation of the world.

12. Concluding remarks

Most readers will agree that the last quarter-century has seen spectacular advances in our understanding of motion perception. Much of this progress owes a good deal to the technical advances during the period. Hardware and software developments have permitted stimuli of almost arbitrary complexity to be generated, allowing research to be question- rather stimulus-driven. And the advent of neuroimaging techniques of increasing spatial and temporal resolution – PET, fMRI, VEPs and MEG – have not only revealed which brain areas are involved in the human brain (and

their relationship to non-human motion areas), but also furnished useful information about the underlying physiological mechanisms.

But the success of the research of the last few decades probably owes as much to the strong theoretical foundations built up in the mid '80s as to the technical innovations: there is nothing so practical as a good theory! The systems-theory approach, previously applied separately to spatial and temporal vision, led to a series of solid, filter-based models that explained many of the seeming mysteries of motion, and spawned a generation of fruitful research. These models were not just toys for the modellers: they were intuitive and accessible, and could be applied to a range of problems from speed perception to illusory motion. Some of these lessons have been forgotten, and new “mysteries” are described, without considering whether they could simply result from the spatio-temporal energy of the stimulus; but by and large the contributions of the models have been invaluable.

As to be expected, the initial models discussed proved not to be the final word: they could not account for second and higher-order motion, proved inadequate for estimating speed and ran into problems in explaining the conflicting demands of for segregation and integration. But their failure was informative, and led to a clarification of the underlying processing, and to more advanced and comprehensive models.

Not all (possibly very few) of the questions raised during this period have been solved. The surface has just been scratched on the mysteries of segregation, integration and transparency, and phenomena like the “flash-lag” and related effects still elude a full explanation. And no-one has a clue what causes “motion-induced blindness”. However, the research prompted by these discoveries has been extremely fruitful in elucidating the interactions between space and motion, and the lack of outright victory serves to dampen the smugness of those who would believe that all has been solved.

One clear conclusion to emerge from the wealth of studies is that the motion system is extremely resourceful in the face of challenging problems. 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; and 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 been learned, suggests that there may well be many other surprises around the corner.

So what will our (now) young colleagues report in the next quarter-century review of motion perception, due in 2035? Certainly our knowledge of the physiology of the human motion systems will progress, as the imaging techniques improve their spatial and temporal resolution. And it is to be hoped that, after the low-hanging fruit has been picked and digested, more ambitious studies will attempt to unravel the underlying function of these structures. There will probably be increasingly greater levels of interaction between physiologists, modellers and psychophysicists, as no one technique is sufficient. We can expect many more multi-sensory studies, trying to understand how the various senses combine to yield one unique percept. As the low-level processes become better understood, the research will probably move to higher levels of processing, such as memory and decision making. And we can be quite confident that new and fascinating illusions will be discovered, challenging our models and theories of visual

processing. But what is most certain is that those of us who choose to stay in the field will be profitably employed for at least the next quarter-century.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2011.02.008.

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