VISUAL VELOCITY AFTEREFFECTS IN RADIAL FLOW: INHERITED AND UNIQUE FEATURES

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ABSTRACT

Visual Velocity Aftereffects in Radial Flow: Inherited and Unique Features

Marta Iordanova-Maximov

A realistic radial flow field contains a range of local velocities, yet global movement is perceived at a single speed. The present experiments explore the contribution of complex motion sensors to this velocity percept, by recording changes in speed perception and speed sensitivity after adaptation to "scrambled", or to coherently expanding/contracting radial flow. A large-scale drifting concentric sine grating, conveying motion in depth, was confined to non-abutting display sectors, defining different global patterns of flow. After adapting to a flow pattern in one display region, observers compared its speed to that in a non-adapted region. Velocity aftereffects (VAEs) from continuous unchanging motion were independent of the pattern of flow: apparent speed was reduced and speed discrimination improved in inverse proportion to the speed of the test. Sensitivity to speed differences, however, was pattern specific, and superior for expansion. Also, adapted expansion recovered its apparent speed when tested against non-adapted contraction, and direction reversals of the adapter attenuated scrambled, but not coherent VAEs. No VAEs were recorded for test motions opposite to the adapted direction. It is concluded that higher-order optic flow mechanisms are not uniquely involved in velocity estimation per se, but modulate velocity judgments in response to changes in the ongoing flow. Independent expanding and contracting velocities rival and do not suppress one another when juxtaposed in space or over time. This unique motion opponency appears to be transient and depends on the 3D quality of the flow. It ensures that the speed of approaching objects is correctly perceived, regardless of stimulus history.

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1. INTRODUCTION

The experience of visual movement has two dimensions - direction and speed. Prolonged or repetitive exposure to motion distorts perception along *both* dimensions. This can be directly observed during inspection of continuous rotary motion in a small region of the peripheral visual field (Hunzelmann & Spillmann, 1984). As viewing progresses, motion *slows down* until it comes to a stop. Simultaneously, apparent contrast declines, spatial structure becomes fragmented and *direction-of-motion is lost.* After the standstill, the entire stimulus fades away. In central vision, similar processes are at work but the perceptual integrity of the ongoing motion is preserved. In this case the effects of prolonged stimulation are revealed indirectly, in the biased perception of other stimuli presented *after* the initial motion has ceased. These secondary perceptual changes are known as *aftereffects.*

The motion aftereffect (MAE) is by far the best known perceptual consequence of adaptation to motion. It is also, perhaps, the most spectacular one. After prolonged viewing of movement in a given direction a stationary pattern presented subsequently appears to move in reverse. While the illusory direction of the MAE has received much attention, there has been less interest in its speed (Wade & Verstraten, 1998). The latter has been mainly considered in attempts to measure the strength of the MAE by canceling it with real motion (Pantle, 1998). The apparent speed of moving stimuli presented at the adapted location, however, is also distorted - typically, it is reduced, but it may also increase, under certain conditions. Such shifts in perceived speed following adaptation to motion are known as velocity aftereffects (VAEs; Thompson, 1976; 1981; 1998). They are the focus of the present investigation. A related phenomenon is also of interest: as motion appears to slow down with adaptation, sensitivity to differences in speed is enhanced (Clifford & Langley, 1996; Bex, Bedingham & Hammett, 1999a).

Visual aftereffects allow psychophysicists to study the internal events, converting the retinal image into conscious perception. This tactic relies on certain assumptions about the neural representation of the stimulus dimension of interest and how this representation might change with prolonged stimulation. Over the years, much has been learned about how cells throughout the visual system signal direction-of-motion. It is now established that direction selectivity evolves in a hierarchical manner, from one processing stage to the next. Whereas cells in the primary visual cortex (V1) encode simple translation at a small scale, the highest motion processing stages are concerned with complex and behaviorally relevant patterns of motion such as large-scale radiation and rotation. A large number of studies have used the MAE to probe direction selective visual mechanisms at various levels in this hierarchy. Special combinations of adaptation and test stimuli have produced MAEs with distinct characteristics (Harris & Blake, 1992), isolating different levels of direction-of-motion encoding (Culham, Nishida, Ledgeway, Cavanagh, von Grünau, Kwas, Alais & Swanston, 1998). The stimuli used in MAE research range from contours defined by luminance, contrast, texture and disparity, to random dot fields or plaids in which several transparent motions are seen (von Grünau, 2002). Researchers have also examined higher-order complex direction-of-motion sensitivity, by recording the MAEs produced by spiral, rotary and radial motions (e.g. Bex, Metha & Makous, 1999b).

By contrast, little is known about the neural correlates of perceived speed. Accordingly, research on the VAE has been less prolific and is rarely discussed in introductory textbooks. The fundamental work on the VAE has been done exclusively with localized luminance defined sine-gratings (Thompson, 1976; 1981). In the absence of definite physiological guidelines, these studies have provided valuable data, constraining theories about how the percept of speed might emerge. The situation, however, appears to be changing. Currently, the speed-related properties of direction selective cortical cells in primates are under more intense and rigorous investigation (Perrone & Thiele, 2001; Pirebe, Castanello & Lisberger, 2003; Priebe, Lisberger & Movshon, 2006). Similarly, researchers of the MAE are taking a closer look at the temporal content of their stimuli (Alais, Verstraten & Burr, 2005).

The present work explores the effects of adaptation to large-scale radial motion on the subsequent perception of speed. Usually, such global non-uniform moving patterns reflect three-dimensional movement of the observer, objects in the environment, or both. Understanding the perception of speed in such motion is particularly important as it affects the timing of the organism's response. Indeed, physiological structures sensitive to complex flow are anatomically linked to larger systems of sensory motor control (Graziano & Cooke, 2006).

In this review of the literature we explore how primates sense velocity from local changes in the retinal image and what the behavioral utility of these signals might be. Psychophysical and physiological findings are examined in parallel, with emphasis on basic concepts and points of debate. Subsequent sections address key variables known to influence human judgments of visual speed. In particular, the discussion focuses on the effects of motion pattern and adaptation to motion on visual estimates of absolute and relative speed. These topics lead to the rationale for the present experiments and their general outline.

1.1. Visual Speed as an Important Behavioral Signal

In a natural context, the entire retinal image is in flux. Eye movements produce lateral and circular shifts, head tilts produce rotations, while linear translations of the whole body cause the image to expand or contract. These self-induced image deformations are commonly referred to as optic flow (Warren, 2004). Object motion perturbs the optic flow as well, typically, on a smaller scale. Yet sensory and motor systems make good use of this complex information.

Consider the special case of a simplified flow created by forward ego-motion, at a constant velocity, along a linear path, with gaze fixed and aligned with the direction of heading. An analogy is perceiving the world through the windshield of a car moving along a straight road. All points in such flow-field move along symmetrically arranged directions, radiating from a focus of expansion (FOE). In this case, this focal point is at fixation and coincides with the image of the heading target. Local velocity, size and texture are scaled, reflecting distances from different points in the scenery. In the periphery, larger images of close objects move faster than smaller images of distant objects around the fovea. The rate of expansion provides an estimate of the observer's own speed. Spatial and velocity gradients indicate the position of landmarks in depth. If a faster car passes by, its image will shrink at a certain rate, allowing estimation of its relative speed. If an object is on a collision course with the windshield, its image will expand at a certain rate, indicating whether and when it might hit. Thus together with other cues, visual velocity estimates allow us to time ourselves, in anticipation of future events. In fact, it may very well be that our sense of elapsed time altogether is spatially localized and locked to visual speed (Burr, Tozzi & Morrone, 2007).

James Gibson (1950) first drew attention to the fact that the visual information available to a moving observer can specify the external three-dimensional layout, as well as ego-motion trajectory and velocity. Furthermore, Gibson believed that this information is critical for various navigational tasks and enables humans to perform them with high precision. In the last two decades, the value of these ideas was finally recognized by mainstream visual science. Electro-physiological studies in the dorsal posterior parietal cortex of primates prepared this conceptual shift (Duffy, 2004). The involvement of this cortex in motion processing, visuo-spatial perception, and visuo-motor control is now well established. The existence of direct pathways between the parietal cortex and sub-cortical structures such as the colliculo-pulvinar complex and the lateral geniculate nucleus, as well as the functional specificity of parieto-frontal connections implicate visual motion signals in behavioral control (Graziano & Cooke, 2006). Furthermore, selectivity to optic-flow motion was discovered in the primate superior temporal sulcus (STS) and psychophysicists have identified similar mechanisms in the visual system of humans (Tanaka & Saito, 1989; Regan & Beverley, 1978; Freeman & Harris, 1992; Morrone, Burr & Vaina, 1995). These developments inspired investigations of the role of optic flow motion in human goal directed behavior (Regan & Gray, 2000; Warren, 2004).

Both object-based and optic-flow motion stimuli elicit motor responses in humans. Large-scale peripheral motion induces optokinetic nystagmus (OKN) and postural sway, accompanied by illusory sensation of self-motion (i.e. vection, e.g. see Howard, 1993). Object motion engages the oculo-motor pursuit system, and looming stimuli trigger defensive responses such as withdrawal, ducking and blocking. These responses are controlled both automatically and at the cortical level, and they are all strongly dependent on image speed and/or perceived speed. The velocity of smooth pursuit eye-movements, for example, is coupled with perceived speed (Ilg, 1997). The link between visual speed and motor output generalizes to more complex behaviors, such as collision avoidance and locomotion (Regan & Gray, 2000). Optic flow velocity modulates walking speed on a self-driven treadmill (Prokop, Schubert & Berger, 1997) and lateral asymmetries in velocity magnitudes can bias the perception of heading (Dyre & Andersen, 1997). In humans, however, the link between visual velocity and motor response is not simple - it is mediated by vestibular, kinesthetic and proprio-ceptive systems.

The behavior of flying insects, on the other hand, is literally driven by visual speed (Srinivasan & Zhang, 2004). Research in this area reveals important principles, governing the visual guidance of action. Bees, for example, negotiate narrow gaps by balancing image speeds in the two eyes, and control landing on a horizontal surface by holding image speed constant during approach. Most importantly, flying species maintain constant flight speed, despite changes in the contrast or the spatial structure of the visual scene (Shoemaker, O'Carroll & Straw, 2005). Such invariance in the behavioral response to the speed of motion is known as *velocity constancy.* It is a highly desirable property, as far as behavioral control is concerned. Understanding the mechanisms supporting velocity constancy is a central issue in research on visual motion. The next section examines the evidence for such mechanisms in the visual system of primates.

1.2. The Origin of Visual Speed Perception

1.2.1. Velocity, Temporal Frequency and Speed

A physical object is perceived to be moving if it changes its position in space over time. For convenience, vision researchers recreate these displacements in movies, which they present to their subjects. A simple and effective motion movie is that of a translating sine grating. The movie consists of sequential snapshots of a luminance defined sinusoidal waveform. The luminance profile of this waveform is modulated at a particular rate (*temporal frequency*). If the phase of the waveform is kept constant, clear movement is perceived, in a direction orthogonal to the orientation of the grating. The *speed* of this motion (in degrees per second) is determined by the temporal frequency modulating the grating (in cycles per second, Hz), divided by its spatial frequency (in cycles per degree). The speed and the direction of this motion together define its *velocity*.

In the literature on speed perception, the terms "speed" and "velocity" are often used as interchangeable. The main problem is that it is often impossible to determine whether observers (or neurons) base their response on the temporal frequency of the stimulus or on its velocity. This relates to the fundamental question of whether primates have mechanisms directly extracting velocity, rather than "recovering" it from the response of motion detectors, independently tuned to spatial and temporal frequency.

1.2.2. The Search for Velocity Sensors

A Signature for Velocity

To separate speed estimates based on velocity from those based on temporal frequency, both the spatial frequency and the temporal frequency must be varied in a stimulus moving in a given direction. If a speed judgment depends on velocity, it must depend on the ratio between temporal and spatial frequency (i.e. speed), rather than on their product, when each dimension is manipulated alone. This also means that the response to speed (temporal frequency/spatial frequency) will be insensitive to spatial frequency variation. Such property is essential for achieving velocity constancy. If the magnitudes of such velocity estimates are plotted as a function of spatial and temporal frequency, the strongest responses would cluster along an oriented straight line. The slope of this function would indicate the velocity at which the responses are optimal (Adelson & Bergen, 1985). If, on the other hand, the speed response is based on temporal frequency, the space-time diagram would show no evidence for a tilt. Such tests of separability have been carried out at the psychophysical and, most recently, at the physiological level. They require the use of moving sine-gratings in which spatial and temporal frequency can be independently changed.

Psychophysical Findings

McKee (1981) showed that humans are able to discriminate differences in speed as small as 5% - 7% and this limit was not much affected by random changes in temporal frequency (McKee, Silverman & Nakayama, 1986). This suggested that speed discrimination relied primarily on velocity signals and not on differences in temporal frequency. A follow-up study by Smith and Edgar (1991), however, revealed that temporal frequency discrimination in counter-phase gratings could be as good as velocity discrimination in moving gratings. Most importantly, the same study showed that differential sensitivity to temporal frequency was little affected by random perturbations of velocity. In addition, visual motion aftereffects (MAE and VAE) appear to be tuned to adapting velocity when probed with dynamic stimuli (Thompson 1981; Ashida & Osaka, 1995), but depend on adapting temporal frequency when a stationary pattern is used (Pantle, 1975). Subsequently, the findings by McKee et al. (1986) have been extended and replicated but, importantly, only for luminance defined motion (Reisbeck & Gegenfurtner, 1999).

In summary, psychophysical results indicate that perception of absolute and relative speed has direct access to velocity estimates, but can rely on temporal frequency as well, depending on stimulus context and task. While this constitutes evidence that velocity mechanisms do exist in human vision, these mechanisms appear to work in parallel with spatial and temporal frequency mechanisms. It is still unclear whether velocity sensors exist explicitly in the visual system, or are represented implicitly through some combination of signals separable in space and time (Schrater & Simoncelli, 1998). This side of the question has been tackled by physiologists, studying speed-related activity in motion sensitive areas along the dorsal visual processing stream. We review their work next, after charting the layout of motion sensitive areas in the brain.

Physiological Findings

In primates, visual motion is processed at successive levels along the retino-geniculate pathway, leading to the primary visual cortex (V1), and then dorsally, to the middle temporal (MT) and the medial superior temporal (MST) areas of the cortex. V1 provides input to MT directly, as well as indirectly, via adjacent areas V2 and V3. MST is the last strictly visual area in this hierarchy and is heavily interconnected with poly-sensory and sensory-motor areas in the posterior-parietal cortex. As one moves up through this system, neuronal receptive field size increases, and selectivity to direction-of-motion is enhanced but also becomes more complex. It is also important, that at each level, horizontal connections link neurons with similar properties and that dense feed-forward and feedback connections exist between successive processing stages. In the dorsal stream, in particular, feedback flow can be as fast as forward flow: response latencies in V1, for example, are only 5 ms shorter than in areas V3, MT and MST (≈70 ms; Bullier, 2004). This means that a neuron's response to incoming motion stimulation (i.e. forward flow) can be influenced by signals arising at a higher level (feedback), at the same time as it is being established.

Photoreceptors, retinal ganglion cells and neurons in the lateral geniculate nucleus (LGN) all respond strongly to moving stimuli. They respond, however, to the luminance change on the retina and not to the direction-of-motion. Genuine selectivity for direction-of-motion emerges in V1 and is clearly established in MT and MST cortex (e.g. Movshon, Adelson, Gizzi & Newsome, 1986). While the motion response of V1 cells changes with stimulus orientation, many MT neurons maintain their direction selectivity despite such changes. Furthermore, MT and MST neuronal activity has been directly linked to the perception of direction-of-motion (Britten, 2001).

Accordingly, neuroscientists have hypothesized that MT neurons with a strong preference for a certain motion direction will also show strong preference for a certain speed. This is to be expected from the basic properties of any Reichardt type motion detector, which integrates spatially separated sequential signals within a certain delay (Reichardt, 1961). Indeed many studies, have reported that most MT neurons respond optimally to certain speeds (reviewed by Reisbek & Gegenfurtner, 1999; Priebe et al., 2006). Typically, this has been demonstrated with broadband stimuli - i.e. moving bars or random dot fields. Speed-related tuning has been found to be quite broad, with most neurons (≈ 80%) showing peak sensitivity at some value (classified as band-pass, Krekelberg et al., 2006a). The remaining 20 % do not show a peak, but a cut-off speed, below or above which sensitivity drops. These are classified as high-pass or low-pass, respectively; with low-pass sensors (preferring low speeds) being rarely encountered in MT (4%). The distribution of preferred speeds is also broad, ranging between 7.5 deg/s and 30 deg/s, with a median of 19 deg/s (Krekelberg et al., 2006a). These statistics are generally consistent across studies. These investigations, however, do not attempt to determine whether neuronal speed preferences reflect genuine sensitivity to velocity.

Perrone and Thiele (2001) and Priebe et al. (2003) provided the first evidence for velocity tuning in direction selective MT neurons of anesthetized monkeys. They recorded the response of each cell to a sine grating moving in the preferred direction, as a function of spatial and temporal frequency. Some of these space-time response diagrams were oriented, indicative of velocity tuning. In addition to this analysis, Priebe et al. (2003) also examined directly each cell's speed tuning as a function of spatial frequency. About 25% of the cells were classified as tuned to velocity and, accordingly, maintained their speed preference despite changes in spatial frequency. For the rest of the sample, the evidence for velocity tuning was weaker and varied along a continuum, with another 25% of the cells showing separable spatio-temporal sensitivity. Remarkably, complex cells in V1 showed the same degree of velocity tuning as MT cells, with 25% of them being classified as tuned to velocity (Priebe et al., 2006). All simple cells in V1, however, showed separable responses for spatial and temporal frequency. Furthermore, in MT but not in V1, velocity tuning improved when neurons were tested with more complex gratings, in which more than one spatial frequencies were superimposed (Priebe et al., 2003, Priebe et al., 2006). The strongest improvement was seen when square-wave gratings were used, suggesting that one-dimensional sine-gratings may not provide the best stimulation, as far as extra-striate motion sensitivity is concerned.

Several conclusions can be drawn from these findings. First, velocity sensors do exist in lower, as well as in higher motion sensitive areas, but in relatively small numbers. Second, in keeping with psychophysical findings, temporal frequency sensors are prominent and operate side by side with velocity sensors, at both striate and extra-striate levels. Third, and most important, access to velocity mechanisms is determined by the nature of the stimulus. The work of Priebe et al. (2006) demonstrates that in MT, velocity tuning may be acquired or enhanced if the stimulus is enriched along one, and perhaps more dimensions. Somehow, extra-striate velocity mechanisms[1] take advantage of the natural variability in moving objects and scenes.

Several motion models demonstrate how a biologically plausible velocity sensor can be constructed from separable local responses to spatial and temporal frequency (Heeger, 1987; Schrater & Simoncelli, 1998; Perrone, 2004, 2005). Others, however, have questioned the need for such an intermediate step. It has been shown that an

---

[1] From now on, I will use the term "velocity" sparingly as it only applies to cases when there is some certainty about the mechanism involved. Otherwise, I will use the more liberal concept of "speed".

unambiguous local velocity estimate can be derived if the responses of several spatio-temporally separable mechanisms, receiving input from the same retinal region, are combined in a certain way (Grzywacz & Yuille, 1990). All theoretical proposals rely on the common assumption that the analysis of visual speed proceeds in two stages. The first stage concerns the extraction of local velocity signals from retinal image sequences. In the second stage, local velocity estimates are being integrated and interpreted, resulting in a conscious perception of speed. There is no consensus, however, about which velocity extraction algorithm is implemented by the visual system and what is the specific contribution of area MT. Some authors propose that area MT integrates the output from the specialized velocity sensors, and is critical for speed perception (e.g. Heeger, 1987). Others have suggested that both V1 and MT are primarily involved in local velocity estimation, whereas velocity integration takes place in subsequent extra-striate levels (Grzywacz & Yuille, 1990). Detailed discussion of these proposals is beyond the scope of this paper. In general, both stages of velocity processing are seen as unfolding within a unitary sensory system (Boxtel, van Ee & Erkelens, 2006). In the next section, we review empirical evidence inconsistent with such a conjecture (see Perrone 2004; 2005).

1.2.3. One or Two Systems for Speed

So far, this review has only considered speed estimates of local motion in a single direction, presented in a small region of the visual field. This is a logical first step towards understanding how speed is perceived in moving objects and surfaces. Typically, such images take more retinal space and contain a range of local speeds and directions.

On its own, a typical V1 or MT motion sensor cannot signal the true movement of images larger than its receptive field size. This is known as the aperture problem and applies to the same extent for both direction and speed (Edwards & Grainger, 2006). Local motion direction is confounded with orientation, and local speed is confounded with motion direction. The problem can be overcome only if the afferent local signals are appropriately combined (e.g. Rust, Mante, Simoncelli & Movshon, 2006). In addition, integrative processes operate jointly with processes segregating object-relevant signals from the ones which pertain to the background. It is of interest whether the pooling of local motion signals operates in the same manner for direction-of-motion and speed.

Most of the relevant evidence comes from motion integration and segregation experiments conducted with a special class of stimuli, known as random dot kinematograms (RDK). An RDK display is a field of small dots with a limited life-time, in which different sets of dots can be assigned different local motions. In essence, these displays can generate three kinds of global motion - incoherent (dynamic noise with no net direction), coherent (unique direction and speed) and transparent (two spatially interleaved coherent motions, with distinct directions and/or speeds). RDK displays are known to be particularly effective in eliciting motion specific activation in area MT, which is known to be implicated in the integration of directional signals (Britten, 2004). In such displays, containing a single speed but a wide range of local motion directions (0°-180°), human observers perceive global motion in a direction determined by the average of all local directions, regardless of their particular distribution (Williams & Sekuler, 1984). Similarly, when all dots move in one direction but at different speeds (2.2

- 11.5 deg/sec), the perceived global speed is simply the average of all local speeds, regardless of the mode of the speed distribution (Watamaniuk & Duchon, 1992). The definition of these global percepts is strong - discrimination based on either global speed or global direction is as good as discrimination based on stimuli containing a single speed or direction, respectively (Williams, Tweten & Sekuler, 1991; Watamaniuk & Duchon, 1992).

These findings suggest that spatial pooling is prominent for both direction-of-motion and speed and that the integration of both types of signals follows similar rules. Vector averaging has been incorporated in explanations of various phenomena of direction-of-motion integration such as the one-directional MAE following bi-directional adaptation (e.g. Mather, 1980). These findings give strength to the notion that speed processing unfolds within a single system, as this seems to be the case for direction-of-motion (Boxtel et al., 2006). This idea is particularly attractive to neuro-physiologists who find a continuum of neuronal speed preferences at each level they have examined (Priebe & Lisberger, 2004). Results from many psychophysical studies, however, suggest that "slow" and "fast" speeds are treated differently.

The slow-fast dichotomy is apparent in the fundamental sensitivity of the visual system to particular ranges of temporal modulation. Psychophysical studies, have identified two primary temporal frequency channels (e.g. Anderson & Burr, 1985; Hess & Snowden, 1992). One channel is low-pass and sensitive to slow rates of temporal modulation (i.e. below ≈ 8 Hz). The other channel is band pass and optimally sensitive to higher temporal frequencies (peak at ≈ 10-15 Hz). These profiles, however, are quite broad and overlapping (see generic depiction in Figure 2A). They are derived from local measurements in the para-foveal region (i.e. within a 5°- 10° perimeter from fixation). It is also known that the relative sensitivities of the two temporal mechanisms change with eccentricity, regardless of spatial frequency (Snowden & Hess, 1992). This is especially true in the far periphery (i.e. beyond 20°) where the slow mechanism looses its sensitivity, leaving perception to be dominated by the response of the fast mechanism. Psychophysical estimates of these channels correspond closely to physiological temporal sensitivities of two types of complex neurons commonly encountered in V1 - sustained and transient (Foster, Gaska, Nagler & Pollen, 1985; Hawken, Shapley & Grosof, 1996; Perrone, 2005). Sustained V1 cells receive parvo-cellular input from LGN and transient cells receive magno-cellular input. As discussed earlier, there is strong evidence that temporal mechanisms are implicated in velocity coding and speed perception, although it is not clear exactly in what way and to what extent. It is also remarkable, that a simple model based on the ratio between the fast and the slow temporal channels explains many phenomena of speed perception (see section 1.5.7, Harris, 1980; Thompson, 1982; Smith & Edgar, 1994; Hammett, Champion, Morland & Thompson, 2005).

Converging psychophysical evidence for a general slow/fast split in the perception of speed comes from different paradigms and laboratories. First, incoherent dot motion (noise) degrades the detection of coherently moving dots (signal), only when signal and noise dots move at similar speeds (i.e. both are slow - 1-4 deg/s, or both are fast - 5-10 deg/s; Edwards, Badcock & Smith, 1998). The same was found with signal dots moving in radial and rotary directions (Khuu & Badcock, 2002). Second, local speeds are averaged in the perceived speed of outward or inward radial motion, but only within the range of the fast system (i.e. 7-13 deg/s, Khuu & Badcock, 2002). A related discontinuity is reported for speed-based transparency: speed-segmentation thresholds increase sharply for speeds above ≈ 8 deg/s (Masson, Mestre & Stone, 1999). Further evidence comes from adaptation studies. Faster motions produce their strongest MAEs on fast moving patterns, and slow motions produce their strongest MAEs on slow moving or static patterns (Verstraten, van der Smagt & van de Grind, 1998). Also, bi-directional adaptation to transparent motion does not result in a combined one-directional MAE (as it normally does), but produces a transparent slow/fast MAE, if the dynamic test contains a mixture of temporal frequencies, refresh rates or speeds (van der Smagt, Verstraten & van de Grind, 1999; Alais et al., 2005). Furthermore, there is a marked asymmetry in the VAE, with slow speeds being predominantly affected (Thompson, 1981, see 1.5.3.). Finally, slow and fast speeds do not produce rivalry when binocularly fused (van de Grind, van Hof, van der Smagt & Verstraten, 2001).

Taken together, these results suggest that motion integration, segmentation and adaptation processes operate within at least two, possibly independent speed ranges (Edwards et al., 1998). There is also evidence that faster motions are pooled more strongly, and are less likely to loose apparent speed with prolonged viewing or under conditions of reduced visibility. These findings are hard to reconcile with the notion that speed processing is unitary.

The nature of the two speed systems, however, remains elusive. Although the division seems to occur early in the visual system, it is unclear how it propagates and until what stage it is sustained. It is not obvious how perceptual discontinuities in RDK displays relate to the split in the temporal frequency domain, and whether a similar split exists in velocity mechanisms (Alais et al., 2005). The distribution of speed-related neuronal preferences in both V1 and MT appears to be continuous. There are indications, however, that a fast-slow division might exist across, rather than within levels. Physiologists report consistently that, on average, MT cells prefer faster speeds than V1 neurons, but the range of preferred speeds in the two areas is overlapping (V1, 0.3 - 43 deg/s; MT, 0.4 - 80 deg/s; Priebe et al., 2006). Also, there is clinical evidence that patients with V1 lesions are unable to perceive speeds below 6 deg/sec (Barbur, Watson, Frackowiak & Zeki, 1993), whereas patients with MT lesions are unable to perceive speed above 6 deg/sec (Zihl, von Cramon & Mai, 1983). Accordingly, dynamic MAEs transfer between the two eyes to a greater extent at high adapting velocities, suggesting that extra-striate binocular mechanisms play a dominant role at higher speeds (Tao, Lankheet, van de Grind & van Wezel, 2003). Also, one behavioral study in monkeys found that micro-stimulation of MT always increased pursuit speed (i.e. perceived speed), regardless of stimulated location, and in proportion to the total injected current (Komatsu & Wurtz, 1989). By contrast, in another study, stimulation of a cluster of MT cells preferring high speeds increased perceived speed, while stimulation of another cluster with low-speed preferences reduced perceived speed (Liu & Newsome, 2005). Thus the neural correlates of the dichotomy in speed perception remain obscure.

1.2.4. The Neural Code for Perceived Speed

Psychophysical and physiological data cannot be linked in a meaningful manner unless one knows which aspects of neuronal activity inform perception. This question is being asked at the level of single cells or populations of cells in MT - the area strongly implicated in the perception of direction-of-motion. The relation between MT neuronal responses and speed perception, however, is not yet clear.

There are generally two proposals. One basic assumption is that MT cells carry speed labels, reflecting their preferred speed (or velocity). Upon stimulation, each cell votes for its preferred speed, with a weight proportional to its firing rate. Perceived speed is the weighted average of all votes (Priebe & Lisberger, 2004). Recently, however, this classic place-coding scheme has been challenged. First, MT neurons seem to change their speed preference with changes in contrast (Krekelberg, 2006b). Second, Liu and Newsome (2005) reported that the response of a neuron to stimuli slower or equal to its preferred speed correlates well with perception, but the response of the same neuron to stimuli faster than its preferred speed, does not correlate with perception. This suggests that only the ascending slope of this response curve contributes to speed perception - i.e. the increase in firing rate until an optimal level is reached. Hence, it has been proposed that the speed code is based on intensity, rather than place, in that it might by carried by "the total firing rate of (possibly a subset of) MT cells" (Komatsu & Wurtz, 1989; Krekelberg. 2006b).

A complete rejection of the place-coding approach, however, may be premature. It is important to know which cells are firing to produce this mass activation. While classifying cells by their *observed* speed preference has intuitive appeal, other classification criteria may be more meaningful. Speed selective cells in MT must have retained some stable "labels", inherited from the input processes that define them. These labels, however, may be hard to unravel, because they do not seem to be attached to preferred speed. Therefore, it may be useful to classify MT speed-sensors according to their afferent connections to larger systems or processing streams. The unresolved issue about how perceived speed may be represented in neuronal responses will be revisited in relation to the VAE (see section 1.5.7.).

1.2.5. Summary

This chapter will end with its question: what are the origins of our conscious perception of speed? It certainly depends on the spatio-temporal content of the image, as well as on many other aspects of stimulation and testing (see below). Research indicates that visual speed is not extracted as an elementary feature, independent of other dimensions, yet it is little affected by them, under certain conditions. It has been shown that true velocity sensors exist in lower as well as higher levels of the visual hierarchy, but they are not numerous, and it is not known how they acquire this capacity and whether and how they might contribute to perception. It is also established that local speed estimates are pooled across space to define the movement of objects or surfaces. There is also evidence that speed estimates are more robust for faster and multidimensional motion, and that slow speeds are treated differently, but the neural substrate of these differences are unclear. Finally, it is suspected that area MT is critical for conscious speed perception, but there is no consensus about which aspects of neuronal activity carry the critical signal.

Although visual speed estimates can support velocity constancy, they are also notoriously unstable. The next section discusses a number of factors known to alter perceived speed and sensitivity to speed differences. The choice is selective, according to pertinence to the present study.

1.3. Factors Affecting Perceived Speed

1.3.1. Contrast

Besides temporal frequency, spatial frequency and velocity, stimulus contrast is the next most important variable in the perception of speed. Contrast is the normalized difference in luminance between an object and its surround and determines its visibility. At contrast levels well above threshold, slow moving gratings appear even slower if contrast is reduced (Thompson, 1982; Blakemore & Snowden, 1999). As the temporal frequency of the grating is increased, the effect of contrast lessens, until at some point (≈ 8 Hz), perceived speed is unaffected by contrast. If the grating speed is increased even further, lowering contrast increases perceived speed (Thompson, 1982; Thompson, Brooks & Hammett, 2006). The strongest effects are observed at low spatial frequencies:

at low contrast the perceived speed of slow motion may go down by as much as ≈ 50%, and the speed of fast motion may be over-estimated by up to ≈ 25%. It has been shown that contrast has a direct influence on the perception of temporal frequency, and to a lesser extent, on spatial frequency. In this manner, indirectly, contrast influences perceived speed.

Interestingly, McKee et al. (1986) showed that speed discrimination thresholds are little affected by random variations in contrast. These conflicting results have been attributed to methodological differences (sequential versus simultaneous presentation) and the minimization of contrast effects at the relatively high temporal frequencies used by McKee et al. (Johnston, Benton & Morgan, 1999). Another possible reason is that, somehow, the unique method of single stimuli used by McKee et al. allowed variation along an irrelevant dimension to be isolated from the reference velocity prior to the critical comparison. The method involves a sequential comparison between a series of variable contrast reference stimuli, and the perceived speed of a test stimulus. In this task observers rely on a global, short-term internal representation of the reference velocity, based, perhaps, on a set of independent estimates. It has been pointed out that contrast effects of different signs may cancel out when multiple independent estimates are combined (Thompson, 1993).

The contrast/speed issue is daunting at the physiological level. Response of most visual neurons increases monotonically with stimulus contrast, until a saturation point is reached (Sclar, Maunsell & Lennie, 1990). This confounds neuronal responses related to contrast with those related to speed. How could then neuronal firing rate carry the code for perceived speed? Is it possible to isolate the contrast response from the speed response? It is known, that contrast sensitivity increases from LGN through V1 to MT while the range of contrasts to which neurons respond becomes narrower (Sclar et al., 1990). The contrast response of MT neurons, in particular, saturates at much lower contrast than in LGN and V1 neurons. At first glance, this offers a solution: speed-related responses in MT might be insensitive to contrast variation, as long as contrast is not too low. Direct examination of this issue, however, has yielded mixed results. Whereas some studies indicate that the contrast dependence of the speed response is limited only to a narrow range of spatial and temporal frequency combinations (Priebe & Lisberger, 2004), recent work documents profound contrast effects on the speed tuning in MT of awake monkeys. Using RDK motion stimuli, Krekelberg et al. (2006b) found that lowering stimulus contrast not only reduced neuronal firing rate but also shifted the speed preference of most neurons towards lower speeds. Accordingly, both monkeys and humans underestimated perceived speed at low contrast.

Taken together, these results indicate that the contrast and the speed of a moving stimulus are not coded independently. Contrast affects slow and fast temporal frequencies differently, and although MT cells are generally insensitive to contrast variation at high contrast levels, their speed-related responses are not "contrast-free". Speed judgments, however, may become independent of contrast if the same motion is viewed at several contrast levels. As discussed earlier, the same conclusion was reached by Priebe et al. (2006) with respect to the dependence of MT speed responses on spatial frequency. It appears that, speed estimates are extracted more accurately from variable and multi-dimensional information.

1.3.2. Spatial and Temporal Continuity

Speed judgments are also affected by the context of stimulus presentation and testing. Speed discrimination thresholds, in particular, are very sensitive to Gestalt structures in spatial layout, temporal sequencing, and trajectory information. It is known that human observers are surprisingly insensitive to visual acceleration (e.g. Gottsdanker, 1956; Snowden & Braddick, 1991). Weber fractions for detecting speed changes in an ongoing motion are typically between 15% and 30%, values that are several times higher than speed discrimination thresholds for spatially and temporally segregated stimuli (5%-7%; e.g. McKee, 1981). Nakayama (1985) has attributed this difference to the fact that the integration of velocity signals takes some time after their initial encoding. Alternatively, it has been proposed that velocity signals that are seen as part of the same perceptual entity are grouped together in a way that obscures local speed perturbations (e.g. Verghese & Stone, 1995; 1996; 1997; Verghese & McKee, 2002, 2006).

Verghese and colleagues have examined the effect of spatial layout and grouping on the ability of human observers to detect differences in speed. They showed that increasing the number of patches containing a moving sine grating improves speed discrimination, whereas increasing the area of a single patch by the same factor - does not. Similarly, parsing a large motion patch into smaller patches facilitates speed discrimination, while fusing the segments into a larger patch has the opposite effect. As a general rule, speed discrimination is worse under conditions supporting spatial grouping, and is better under conditions favoring segmentation. These results suggest that the parsing of the retinal image into discrete entities occurs early - before or during the pooling of local speed signals across space. As a result, a single speed estimate is assigned to each visual object.

Recent work has extended these arguments to motion grouping by common trajectory (Verghese & McKee, 2002, 2006). In accord with the Gestalt principles of common fate, motions with similar directions and speeds are readily grouped together. In the presence of spatial alignment, a common motion path is perceived. Verghese and McKee (2006) demonstrated that speed differences between motions seen as continuing across a boundary are harder to detect, than those between unrelated motions, parallel to the boundary. It was suggested that local speed signals prime the integration of subsequent signals, belonging to the same motion path, thus pooling them into one common speed estimate, despite local differences in speed. Such global speed unification seems to block conscious access to the true local speeds. The neural correlates of these processes are not well understood. In general, they have been related to the formation of assemblies of neuronal responses, linked by horizontal connections. Feed-forward input may mandate certain assemblies to be formed - feed-back input, on the other hand, is likely to modulate their cohesion. At least some of these influences do not seem obligatory, as they can be overridden with practice.

Given that image parsing influences speed discrimination, does it also affect the perception of absolute speed? There is very little research bearing on this question. There is some evidence, however, that perceived speed depends on the spatial alignment of motion vectors. For example, perceived speed increases if motion elements are orthogonal or collinear to the motion path, but decreases if they are tilted relative to it (Georges, Seriès, Frégnac & Lorenceau, 2002). These effects have been attributed to horizontal interactions between orientation sensitive motion detectors in V1. They illustrate how trajectory information, consolidated at an early level, may influence the perception of speed. Higher order pattern-of-motion effects have also been found, in that radial motion (expansion, contraction) is perceived as faster than locally equivalent translation and rotation (see 1.4.5., e.g. Bex, Metha & Makous, 1998). There is also some evidence that changes in display parsing and the pattern of motion do not affect absolute and relative speed judgments in the same way, suggesting that these judgments are not necessarily constrained by the same mechanisms (Clifford, Arnolds & Wenderoth, 2000). This issue is reexamined, in part, by the present research.

1.3.3. Relative Motion

All studies reviewed so far have relied on the tacit assumption that the processing of speed information is independent of motion direction. Typically, in studies on speed perception, the direction of motion is fixed. Similarly, neuronal speed tuning is determined in a single direction-of-motion - the one eliciting the strongest response. Speed integration studies have also been limited to uniform directions-of-motion. Yet normally, the visual system is confronted with motions in different directions, segregated or overlapping in the image of the visual scene. Some of these relative motions are local, between adjacent points in the image - yet others exist on a larger scale, between regions separated in space. It is well known that in such contexts the direction of the component motions can be misperceived. A moving surround can induce strong opposite motion in the surrounded area (induced motion, Reinhardt-Rutland, 1988), or can assimilate the surrounded motion (motion capture, Nawrot & Sekuler, 1990). Also, if two different directions of motion are transparently superimposed they may appear repelled from one another (Marchak & Sekuler, 1979). A logical question arises: does relative motion exert an influence on the perception of speed? This question has been rarely asked.

Results from two studies indicate that the answer is emphatically, "yes". De Bruyn and Orban (1999) showed that in transparent displays, the relative motion between dots moving in opposite directions augments perceived speed, compared to displays in which all dots participate in one-directional motion. The speed enhancement was equally pronounced when opponent motions were spatially intermingled, as well as when they were segregated and confined to alternate bands. The effect was strong and increased linearly with physical speed: perceived speed doubled at ≈ 8 deg/s.

Recently, Edwards and Grainger (2006) have extended these findings to the perceived speed of random dot displays with varying degrees of coherence. In a completely incoherent RDK there is a large amount of local relative motion, as all dots are moving in random, different directions. On the other hand, a 100% coherent display contains no relative motion as all dots are moving in the same direction. Edwards and Grainger (2006) found that increasing coherence level decreased perceived speed, as expected from the reduction of relative motion. Intriguingly, the same manipulation enhances responses of direction selective cells in MT and, in general, increases the perceptual salience of the motion (e.g. Britten, 2004).

These results have several important implications. First, they underscore the importance of both local and global relative motion in the generation of our perception of speed. Second, they reveal a dissociation in the effects of the same manipulation on the perception of motion direction and speed. Whereas the coexistence of multiple directions may destroy the perception of motion direction, it enhances consistently the perception of speed. Conversely, a sub-optimal stimulus for direction-of-motion, elicits a salient perception of speed. It appears that speed and directional signals are not only coded differently, but are integrated differently as well. The speed enhancement effect suggests that speed signals from different directions are not simply combined in an average pool, but interact to produce the observed increase in apparent speed. Other studies also emphasize differences in the processing of direction and speed. Direction discrimination is better along the cardinal axes, while speed discrimination is isotropic (Matthews & Qian, 1999), the two tasks show different rates of learning (faster for direction) and there is no transfer of learning between them (Saffell & Matthews, 2003).

The notion of "dissociation" between the two dimensions of motion perception, however, is somewhat unsettling. Since direction and speed signals have a common origin, at some level, they must jointly represent the velocity of the same object. More studies addressing the perception of direction and speed simultaneously would be helpful in understanding the extent of these differences and their meaning.

1.3.4. Summary

In the laboratory, speed judgements are easily altered by low-level, as well as by higher-order stimulus variables. In addition to the factors discussed above, perceived speed is affected by luminance level, spatial frequency, background texture, eye-movements, as well as by the context in which the speed comparison takes place. The influence of stimulus history on perceived speed was illustrated in the very beginning. As this factor is central to the present study, a separate chapter will be devoted to it (see 1.5.).

The effect of relative motion on speed perception reiterates an important point. Speed and direction processing use image information in different ways. One distinct characteristic of speed processing is that variability along "irrelevant" stimulus dimensions, such as spatial frequency, contrast and direction-of-motion is critical for the representation of speed. In the next section we consider a class of motion stimuli comprising multiple directions, and, sometimes - multiple speeds. The perception of speed in these stimuli relates directly to the present study.

1.4. The Perception of Complex Motion

1.4.1. Complex Motion Varieties

Complex motion is a broad category - all stimuli containing relative motion are, in a sense, complex. In its current use, however, the term denotes optic-flow-like patterns of motion such as radial, circular or spiral. Mathematically, any optic flow field can be described by a combination of these simpler components and it has been assumed that the visual system performs a similar decomposition (Koenderink, 1986). Complex motion is studied with many different stimuli: e.g. square-wave and sine-wave gratings, symmetrically arranged apertures containing movement in different directions, random dot fields, and virtual reality displays. Some of these complex motion stimuli are rather "simplified", lacking a spatial gradient, a speed gradient, or both. In the commonly used random dot flow-field, for example, local speed increases linearly with eccentricity, but spatial structure remains uniform. A linear gradient, however, represents the rather special case of ego-motion towards an extended fronto-parallel plane (e.g. a wall). By contrast, the optic flow associated with most three-dimensional environments is characterized by non-linear gradients, representing observer's movement along a ground plane, through a three-dimensional cloud of elements, or a tunnel.

Structural and speed gradients do make a difference, however, in terms of both motion processing and perception. They are powerful monocular sources of depth information and support the impression of motion-in-depth, depth order and vection, in the absence of binocular disparity variation. Furthermore, there is a natural correspondence between the non-linear spatial scaling in a typical flow-field, and inhomogeneities in retinal properties and in retino-cortical mapping (Kelly, 1989; Virsu & Hari, 1996). It is known that the area of visual cortex devoted to a constant-size retinal region diminishes progressively from the fovea towards the periphery. Accordingly, performance on various perceptual tasks deteriorates towards the periphery, unless the size of the stimulus is increased according to the cortical magnification factor (a procedure known as M-scaling). Both MAE speed and the minimum detectable speed are unequal across the visual field, unless motion stimuli are M-scaled (Johnston & Wright, 1983). Thus in complex motion displays, the quality of local speed signals will vary, depending on the type of gradient used. There is growing awareness that motion mechanisms, sensitive to optic flow patterns of motion, take advantage of this information.

1.4.2. Complex Motion Sensors: Neurophysiology

A simple psychophysical study provided the first evidence for distinct sensitivity to looming motion in humans (Regan & Beverley, 1978). A square whose sides moved out-of-phase appeared to change size (i.e. to loom). The same square with sides moving in-phase appeared to slide diagonally back and forth. Adaptation to looming motion selectively raised detection thresholds for looming, but not for the otherwise equivalent translation. The authors saw in this evidence for the existence, "within the human visual pathway, of neural mechanisms (for example, classes of single neurons) preferentially sensitive to increasing or decreasing object size, respectively" (Regan & Beverley, 1978, pp. 419). Furthermore, they hypothesized, that "the neuron's special sensitivity to changing size would be revealed only by simultaneously stimulating the two regions [*of its receptive field*] with oppositely-directed motion" (Regan & Beverley, 1978, pp. 420). Later, a similar result was reported for rotary motion (Regan & Beverley, 1985). Both studies manipulated only the relative direction-of-motion. It was proposed that radial and rotary motions are processed differently from uni-directional motions, perhaps, along a separate channel, specialized for extracting relative motion information.

About a decade later, the hypothetical "changing size" neurons were found in a number of areas around the occipito-parieto-temporal junction, as well as in the frontal motor cortex of non-human primates (Duffy, 2004). Interest focused on motion sensitive areas in the STS, and on visual area MST in particular. Area MST was further subdivided in two regions - dorsal (MST-d) and ventro-lateral (MST-l). These two areas receive distinct input from MT, and contain neurons with distinct response properties, as well. Whereas MST-l seems best suited for the segregation and processing of object-motion, MSD-d has been linked to the processing of optic flow, and possibly, to the neural control of ego-motion (Tanaka, 1998; Britten, 2001). Neuronal responses in both areas, however, have many features in common, such as sensitivity to relative motion, binocular disparity and are heavily implicated in oculo-motor pursuit.

Initial studies found that MST-d neurons were triggered by moving stimuli presented over large portions of the visual field (40°- 100°), including the midline, and extending over the ipsi-lateral side (Tanaka et al., 1986, Tanaka & Saito, 1989). About half of these neurons were selective to complex patterns of motion and the other half preferred uni-directional planar motion. Most complex-motion cells responded best to symmetrical expansion / contraction of luminance defined object contours (i.e. radial or "size" neurons). A smaller group preferred rotation, and cell preferences in the rest of the sample were mixed. Furthermore, radiation and rotation neurons showed position invariance - they gave an optimal response to their preferred pattern of motion, regardless of where in the receptive field it was placed.

Subsequent investigations, using random dot fields with linear gradients, confirmed and extended these findings. Current physiological knowledge can be summarized as follows (for a complete review see Duffy, 2004; Raffi & Siegel, 2004). Directional preferences in MST-d form a continuum with two branches, with sensitivity to planar motion at one end, and sensitivity to radial and circular motion - at the other. In other words, many cells have mixed sensitivity - they respond to plano-radial, plano-circular or circulo-radial (i.e. spiral) motion, but, also, a significant number of them are uniquely tuned to a specific motion class. Out of the two branches for complex motion, the radial one is more prominent: more neurons show preference for radial than for circular motion, and, generally, preferences are better defined for radial motion than for rotation (i.e. radial motion bias). There is an asymmetry within the radial branch as well, with expansion preferences more often encountered than contraction preferences (i.e. centrifugal motion bias, e.g. Graziano, Andersen & Snowden, 1994). The functional organization of MST-d is not retinotopic, but there is some anatomical clustering of neurons with similar properties. Taken together, these response properties indicate that MST-d is well suited for optic-flow analysis during self-motion. Other areas in the parietal and the frontal cortex, however, perform similar analysis as well, and the unique contribution of MST-d remains undetermined.

1.4.3. Complex Motion Sensors: Psychophysics

Naturally, psychophysicists were intrigued by the unique neuronal properties in primate MST-d. This led to speculations that similar mechanisms might exist in the human visual system and a massive search for their perceptual correlates began. In parallel, functional imaging focused on delineating the "optic-flow" area in the human brain. Indeed, adaptation and spatial-summation studies confirmed that complex, as well as uni-directional motion signals, can be pooled over extensive regions of the visual field (Morrone et al., 1995; Burr, Morrone & Vaina, 1998). Furthermore, complex MAEs were recorded from retinal areas that were never adapted (i.e. "phantom MAEs", Snowden & Milne, 1996, 1997; Bex et al., 1999b). These psychophysical findings could be linked directly to the receptive field size and position invariance of neurons in MST-d. Furthermore, a number of studies provide evidence that fronto-parallel, radial, rotary and, possibly, spiral motion are detected by independent mechanisms, but complex patterns of motion are processed differently, and more efficiently than one-directional flow (e.g. Freeman & Harris, 1992; Meese & Harris, 2001; Burr, Badcock & Ross, 2001; Bex et al., 1999b; Iordanova & von Grünau, 2001). Overall, psychophysical results indicate that sensitivity to translating motion in MST-d is determined at previous levels, whereas complex motion sensitivity is unique to MST-d.

Some aspects of these results, however, cannot be easily mapped to neuronal properties. This will be illustrated in the context of an adaptation study, most relevant to the present research. The adaptation approach often relies on the notion that motion is processed in a hierarchical manner, and adaptation occurs at different levels, as well. By choosing appropriate adaptation conditions, test stimuli and procedures, psychophysicists can isolate global adaptation effects uniquely associated with complex motion, from those occurring locally, at lower levels. Using this logic, Bex et al. (1999b) extended the findings of Regan and Beverley (1978, 1985) to the MAEs generated by radial, rotary and translational motion.

Bex et al. (1999b) presented moving uniform sine-gratings through four apertures, arranged symmetrically in a "+" or "X " configuration around fixation. Assigning different grating orientation (i.e. direction-of-motion) to each aperture resulted in three compound patterns of motion - translation, rotation and radiation. As the local components of the three patterns were identical, any differences between their MAEs could be attributed solely to adaptation of a global mechanism, sensitive to relative motion. After prolonged viewing of each motion pattern, the strength of the MAE was measured in three different ways: i) duration of the MAE; ii) contrast required to null the MAE in counter-phase flickering gratings; and iii) threshold elevation for detecting an abrupt jump in a stationary grating. The third measure is of particular interest, because it is proportional to the apparent speed of the MAE - the faster the test grating appears to move following adaptation, the harder it becomes to detect the sudden displacement. The other two measures rely on the strength of the illusory directional signal. Regardless of method and spatial configuration ("+" or "X "), complex motion MAEs were, on average, 50% stronger than translational MAEs. There were no significant differences between the magnitudes of rotational and radial MAEs, nor between the MAEs produced by expansion and contraction (the latter data sets were collapsed).

Some trends in the detection-of-abrupt-jump data are of particular interest. First, radial MAEs were somewhat stronger than rotary MAEs, in the "+" configuration, and as measured by detecting displacement in the MAE direction, in particular. This suggests that radial MAEs may not only be directionally stronger, but also *faster* than the MAEs from translational and rotary motion. As the authors noted, detecting jumps in direction opposite to the complex MAE was also impaired, compared to translational MAEs, suggesting that this particular measure might be relatively insensitive to motion direction. In this particular case, this may be so, for reasons known to VAE researchers, who find that perceived speed is reduced in the adapted as well as contrary to the adapted direction, albeit less so in the latter case. This has been attributed to non-specific temporal frequency adaptation of mechanisms insensitive to the adapted direction (see section on VAE, below). These results hint at a possible dissociation between the effects of motion adaptation on estimates of perceived direction and speed.

The study by Bex et al. (1999b) is representative of much psychophysical data, showing enhanced sensitivity to complex patterns of motion, compared to simple translation. Accordingly, there is evidence that radial and rotary MAEs show more inter-ocular transfer than translational MAEs, consistent with the higher degree of binocularity at higher levels of the motion hierarchy (Steiner, Blake & Rose, 1994). Single cell electro-physiology in MST-d, however, indicates a stronger representation (and hence, stronger MAEs) for radial motion (radial bias), and for expansion, in particular (expansion bias). Common intuition leads to the same expectations - most of us engage sufficiently often in predominantly forward locomotion, and looming objects have behavioral priority. The psychophysical evidence for such biases, however, is mixed.

1.4.4. Directional Asymmetries in the Perception of Complex Motion

Centrifugal Bias

An asymmetry in the MAE has been observed by many nineteenth century researchers, using versions of the Plateau / Archimedes spiral, widely used at the time (Wade & Verstraten, 1998). Counterclockwise rotation of this spiral elicits a powerful perception of expanding motion, similar to that associated with approach of a three dimensional object. Conversely, clockwise rotation is perceived as contraction / retreat. In his review of early MAE research, Wohlgemuth (1911) noted that the expanding aftereffect elicited by contracting spirals is more forceful and longer lasting that the contracting aftereffect, after prolonged viewing of expanding spirals. Subsequently, this centrifugal bias in the MAE has been confirmed for spirals (Scott, Lavender, McWhirt & Powell, 1966; Reinhardt-Rutland, 1994), as well as for concentric sine-gratings (Kelly, 1989). There is also some evidence, however, that the difference may disappear with training (Scott et al., 1966).

Centrifugal biases have been found in other experimental contexts, as well. Ambiguous motion with balanced inward or outward components is perceived to have an outward direction (e.g. Georgeson & Harris, 1978; Lewis & McBeath, 2004; Giaschi, Zwicker, Au Young & Bjornson, 2007), and shorter reaction times to motion onset were reported for centrifugal random dot motion enclosed in apertures (Ball & Sekuler, 1980). Also, using sine-grating patches, Takeuchi (1997) reported that visual search times for an expanding target in a field of contracting distractors was independent of the number of irrelevant items (i.e. expansion popped out), but search times for a contracting target increased with the number of expanding distractors. Interestingly, this search asymmetry persisted in trained psychophysical observers, after extensive task-specific practice.

Most authors have attributed these centrifugal biases to a built-in, low level mechanism for looming detection and collision avoidance. Indeed, involuntary defense reactions to looming can be elicited by a wide range of structured, as well as by unstructured stimuli (e.g. expanding shadows), and are present in non-human species, as well as in newborn human infants (e.g. Ball & Tornic, 1971; Graziano & Cooke, 2002). Other researchers have suggested that environmental learning through consistent exposure to expanding flow-fields may also play a role in shaping the perceptual bias for outward motion (e.g. Georgeson & Harris, 1978). We note the duality in the interpretation of centrifugal motion as the approach of an object (looming), or the result of forward ego-motion.

Centripetal Bias

A comparable number of studies, however, have reported biases in the opposite direction, or had found no evidence for a directional bias at all (e.g. Bex et al., 1999b). Researchers had noted that the impression of motion in depth is more realistic in contracting flow-fields, possibly due to lack of several depth cues for real approach in expansion, including the lack of a terminal collision (Reinhardt-Rutland, 1994). Evidence for a centripetal bias includes: lower coherence thresholds for detection and direction discrimination of global inward motion in RDK-s (Edwards & Badcock, 1993; Raymond, 1994; Edwards & Ibbotson, 2007; Giaschi et al., 2007); shorter perceptual latencies for judging the position of targets moving in a centripetal direction (Mateeff & Hohnsbein, 1988; Mateeff, Yakimoff, Hohnsbein, Ehrenstein, Bohdanecky & Radil, 1991); and earlier development of coherence sensitivity to contracting motion in infancy (Shirai, Kanazawa & Yamaguchi, 2006). It has been speculated that the centripetal bias reflects asymmetries in the distribution of neuronal preferences in areas *other* than MST-d, such as 7a, which is involved in the precise control of arm movements towards fixation (Edwards & Badcock, 1993; Shirai et al., 2006). Another proposal is that a higher sensitivity to contracting motion may be beneficial for the control of postural sway and balance (Edwards & Ibbotson, 2007). The empirical support for these hypotheses, however, is insufficient, as the centripetal bias is not limited to the slower speeds, normally associated with body sway or manual manipulations (Edwards & Ibbotson, 2007; Giaschi et al., 2007).

In summary, perceptual asymmetries between expanding and contracting motion have been found but they have been observed in both directions. Furthermore, many of these biases can be resolved, or even reversed with small changes to the stimulus, or to the perceptual task. The conditions favoring one bias over the other in the same stimulus have not been addressed systematically, and therefore, remain poorly understood. A rarely cited study by Kelly (1989) illustrates the importance of examining the stimulus specificity of these asymmetries. His findings are also directly relevant for the present work.

In his research on contrast sensitivity, Kelly (1989) used a drifting concentric sine-wave grating (16° in diameter) whose spatial frequency decreased with eccentricity. He discovered that adaptation to this kind of motion increased contrast thresholds for motion detection in a manner that was direction specific: sensitivity loss was greater following adaptation to expanding motion, relative to the effects from adapting to contracting motion. After documenting this centrifugal bias, Kelly examined its spatio-temporal characteristics and its dependence on the spatial/speed gradient in the stimulus. He found that what he called "the forward effect" is broadly tuned to temporal frequency (1-8 Hz), but not velocity, and that it is limited to rather low spatial frequencies (0.05-0.5 cycles/degree at the fovea). Furthermore, Kelly discovered that the bias was strictly dependent on the presence of a natural, positive gradient conveying motion in depth: it was greatly reduced or abolished if the radial gradient was removed (i.e. "flat" motion) or reversed. Based on these results, the centrifugal bias was attributed to a low level motion mechanism, part of a hard-wired collision-avoidance system, responding to the common low-spatial frequency components in the images of approaching objects. The sensitivity to the gradient in the stimulus, on the other hand, could be based on a low-level match between properties of local motion detectors and the spatial/speed structure of the stimulus, as well as on global mechanisms encoding motion-in-depth. This work demonstrates how proper investigation of stimulus specificity can facilitate the interpretation of a given directional bias.

Efforts to reconcile the opposing asymmetries across studies have generated several hypotheses, awaiting empirical tests (Lewis & McBeath, 2004; Giaschi et al., 2007). Taken together, results suggest that an expansion bias is supported by supra-threshold stimuli with sufficient peripheral extent, conveying motion in depth. Also, relative motion seems to enhance the expansion bias, in the presence of stationary landmarks or motion of the opposite sign (Reinhardt-Rutland, 1988; 1994; Ball & Sekuler, 1980; Takeuchi, 1997). Similarly, in the absence of relative motion context, full-field image expansion generates much weaker or no aftereffects, suggesting that centrifugal biases may be reduced when the optic flow is attributed to self-motion (Wallach, 1987; Gurnsey, Fleet & Potechin, 1998; Durgin et al., 2005). Alternatively, they may be enhanced by the perception of objects looming relative to their background. The strongest evidence for a centripetal bias, on the other hand, concerns motion signals at threshold levels of coherence (RDK-s), presented in central vision, in the absence of limiting borders. Interestingly, the centripetal bias in perceptual latencies for target displacement (Mateeff et al, 1991) can be reversed in the presence of a stationary reference frame (Ball & Sekuler, 1980). Whether centrifugal and centripetal biases have the same or different functional roles, is a matter of debate. An important logical argument points towards a unitary interpretation (Dumoulin, Baker & Hess, 2001). As mentioned earlier, ambiguous radial motion is not directionally neutral - it appears to expand (Georgeson & Harris, 1978; Giaschi et al., 2007). Thus a radial RDK of 0% coherence is perceptually matched to a RDK containing a certain amount of coherent expansion. This would explain the higher coherence thresholds for detecting expansion, compared to contraction. From this perspective, much of the evidence for higher sensitivity to inward motion can be seen as a consequence of the built-in predisposition to perceive outward motion (e.g. Lewis & McBeath, 2004).

In conclusion, directional biases in complex motion perception do exist but their nature is not well understood. It is unlikely that they are uniquely associated with neuronal anisotropies in MST-d. The centrifugal bias, for example, appears to have a wide-spread physiological basis, as the evoked magnetic response to expanding radial motion is larger than the response to contracting radial motion over several extra-striate cortical regions (Holliday & Meese, 2005). It is also possible that optic-flow related neuronal responses in parietal cortex are not readable by perceptual systems, but are channeled directly towards systems for motor control (Britten, 2001). Certain aspects of these signals may be available to consciousness, but they are extremely sensitive to the context of testing. With these caveats in mind, the discussion will focus on the perception of absolute and relative speed in radial motion, which is central to the present study.

1.4.5. Temporal Aspects of Complex Motion Perception

Clearly, most of the work on complex motion has been concerned with the extraction of the global directional signal and its use for navigational guidance. Very little is known about the temporal properties of complex motion sensors and their contribution to the estimation of object motion or ego-motion velocity. There is sufficient evidence, however, that sensitivity to temporal change and to the speed structure of the flow-field is a defining property of these sensors and is not independent of their directional tuning.

All neurons in MST-d, MST-l and in satellite area 7a show speed tuning, although it is not known whether they respond to temporal frequency or velocity (Orban et al., 1995). Most importantly, the speed sensitivity of these cells interacts with their directional tuning - neurons that respond to one type of flow, at one speed, may respond to another type of flow, at another speed (Phinney & Siegal, 2000). It appears that direction and speed information are encoded jointly at this level - a necessary step in the construction of a behaviorally meaningful global velocity signal. As discussed earlier, however, it is unlikely that the speed processing hierarchy in the primate brain (if it exists), parallels the one for direction of motion. The speed and velocity tuning of single cells is very similar in V1 and MT, while direction selectivity evolves dramatically between these two levels. It is therefore possible that the qualitative leap in speed processing, supporting velocity constancy, occurs at levels beyond MT, or, alternatively, is not implemented in a hierarchical manner.

Sensitivity to Speed Gradients

Radial motion neurons in MST-d are also sensitive to the speed gradient in the flow-field - their direction selective responses are enhanced if their preferred pattern of motion contains their preferred gradient of speeds (Duffy & Wurtz, 1997a). Recent psychophysical work also shows that sensitivity to speed differences (Clifford, Beardsley & Vaina, 1999) and to small shifts in the directional structure of the flow field (Beardsley & Vaina, 2005) is enhanced by the presence of a positive speed gradient. It is believed that the scaling of local signals with eccentricity provides more homogenous input at the pooling stage, enhancing the precision of the global speed signal (Clifford et al., 1999). Alternatively, the processing advantage for scaled radial flow-fields may be linked to mechanisms supporting the perception of motion-in-depth. The importance of stimulus gradients is also evident in results from human functional magnetic resonance imaging (fMRI) studies in which optic-flow activation changes with the spatial distribution of local speeds (Geenlee, 2000; Orban, Fize, Peuskens, Denys, Nelissen, Sunaert, Todd & Vanduffel, 2003). Selectivity to speed gradients, as revealed by human fMRI, however, does not seem limited to higher levels of motion analysis. Area V3/V3A is strongly selective to the speed gradients in the optic flow and to the three-dimensional structure they define. Interestingly, this involvement appears to be a unique characteristic of human motion processing, as it has not been observed in the macaque brain (Orban et al., 2003). Thus the evidence for sensitivity to the local speed structure of radial motion is neither consistent, nor inconsistent with a hierarchical system.

Radial Speed Bias

Several studies, however, have documented a robust effect of optic flow pattern on perceived speed, offering some support for the hierarchical view (Geesaman & Qian, 1996, 1998; Bex & Makous, 1997; Bex et al., 1998; Clifford et al., 1999). Specifically, radial motion appears consistently faster than rotary or fronto-parallel motion, in spite of identical local speeds. The magnitude of this illusion is substantial - on average, between 30% and 40%. The largest discrepancy is between the apparent speeds of radial and rotary motion, with translation appearing somewhat faster than rotation, but still much slower than radiation. Contraction and expansion are not perceived at the same speed either, but these biases are much smaller and inconsistent across studies (contraction faster, Geesaman & Qian, 1998; expansion faster, Clifford et al., 1999). Speed enhancement of radial motion is observed with both concentric gratings and random dot fields, as well as with rather simplified stimuli, such as Gabor patches, regardless of whether a local speed gradient is present or not.

Control experiments have established that the radial bias is not restricted to particular areas of the retina, and cannot be attributed to reduced speed of fronto-parallel motion due to eye-tracking, or to subtle differences in the local trajectories defining each pattern (Bex et al., 1998). This speed illusion is not secondary to apparent differences in spatial frequency, temporal frequency and contrast, as these attributes are judged as equivalent in all patterns of motion (Bex et al., 1998). The radial speed bias, however, depends critically on the spatial arrangement of the component directions-of-motion and on their orientation bandwidth. The strength of the effect is optimal when the entire range of radial directions is visible, and requires opposition of velocity vectors along at least two differently oriented axes (Bex et al., 1998). In general, reducing the number of display sectors tends to reduce the effect, owing to the narrowing of the range of visible motion directions, rather than to loss of stimulus area. Thus the overestimation of radial speed is dependent on the dimensionality of relative motion, as motion contrast along one dimension is not sufficient to support the effect. Finally, the global speed bias persists even if subjects are instructed to make local speed estimates while ignoring the global configuration, suggesting that the effect is mandatory, and hence, pre-attentive. A satisfactory explanation of the radial speed bias does not yet exist, but there are two general hypotheses about its origin.

Geesaman and Qian (1996, 1998) suggested that the illusory difference in perceived speed of radial versus rotary/translational motion might be a perceptual correlate of the anisotropy in direction selectivity of neurons in MST-d. According to this *neural response bias hypothesis*, the perceived speed of the optic flow pattern corresponds to the strength of the neural response in MST-d, as determined by the relative number of cells tuned to each pattern of motion. These relative numbers follow the order expansion > contraction > rotation, with expansion cells outnumbering contraction cells by a ratio of about 2:1, and rotation cells - by 3:1, respectively (Duffy &

Wurtz, 1991; Graziano et al., 1994; Tanaka et al., 1986; Tanaka & Saito, 1989). The general idea is that perceived speed is encoded by the total firing rate of cells tuned to a particular pattern of motion, in comparison to the total firing rate of all other motion sensitive neurons. Although, indeed, expansion is perceived as faster than rotation, it is unclear why expansion is also judged as faster than translation, since a large number of MST-d neurons are also selective to one-directional motion. Furthermore, the apparent speeds of expansion and contraction are not consistently reported as different. Thus although the neural response bias hypothesis is attractive, it remains rather weak without an explicit model, linking cell number and total firing rate to perceived speed (Geesaman & Qian, 1998).

The second hypothesis relates the apparent speed enhancement to the perception of motion-in-depth in radial flow (Bex & Makous, 1997; Bex et al., 1998; Clifford et al., 1999). These authors propose that the radial speed estimate is based on the unique interpretation of this type of motion as approach or retreat, whereas "flat" motion is perceived in rotating and translating displays. This 3D-motion signal is likely to involve different mechanisms from those processing 2D motion. Bex and Makous (1997) speculated that for a given period of time, the perceived distance traveled in depth seems greater, compared to the apparent displacement in the fronto-parallel plane, resulting in overestimation of 3D-motion speed. If this is true, one may expect a greater radial speed enhancement in displays where the impression of motion-in-depth is more convincing. As pointed out by Clifford et al. (1999), however, the perception of motion in depth from radial motion is often ambiguous. A radial flow may be seen as a rigid environment at a changing distance from the observer, or/and as a 2D deformation of a non-rigid object (i.e. expansion/contraction) at a fixed distance from the observer. Given this ambiguity, the motion-in-depth component is rather difficult to quantify in order to predict the magnitude of the radial speed bias in a given stimulus. Paradoxically, although the RDK radial stimuli in the study by Clifford et al. (1999) contained a speed gradient, they produced a smaller speed bias than the rather impoverished "flat" gratings used by Bex and colleagues. It is also known that, in virtual environments, or with full-field stimulation, when the perception of ego-motion in depth is particularly convincing, visually perceived radial speed, as well as the MAE, are, in fact, reduced, as motion signals are being attributed to self-motion (Wallach, 1987; Durgin et al., 2005). Thus the role of motion in depth in the speed illusion remains undetermined.

Regardless of the uncertainty about its origins, the enhancement of radial motion speed is a robust phenomenon with important theoretical implications. First, together with physiological and psychophysical findings (Beardsley & Vaina, 2005), it strengthens the argument that the processing of radial motion is special, in comparison to other components of the optic flow. Second, it indicates that the pooling of local speed signals depends on the spatial organization of motion directions, implicating complex direction-of-motion mechanisms in the computation of optic flow speed. This is in keeping with the evidence for preferential pooling of faster, but not slower speeds in the context of radial motion (Khuu & Badcock, 2002). Third, the outcome of this pooling operation cannot be predicted by linear combination of local inputs (Bex & Makous, 1997; Bex et al., 1998). Because of the balanced nature of opponent vectors in the radial pattern, any linear combination would tend to reduce the global speed estimate - the opposite of what is observed. Therefore, the radial speed enhancement must involve some kind of meta-analysis that combines local signals differently, depending on the directional structure of the display. This meta-analysis should not only be sensitive to *any* relative motion, but to the *specific pattern of relative motion*, in order to produce the selective enhancement of perceived speed for radial, but not for circular flow.

Although it is often assumed that this meta-analysis is performed by pattern-of-motion analyzers at the level of MST-d, there are no empirical reasons to exclude the involvement of earlier levels, sensitive to relative motion and motion-in-depth and performing motion integration on a smaller scale (e.g. MT). It has been also proposed that the effect involves the joint analysis of global form *and* global motion in extra-striate areas of the cortex (Krekelberg, Dannenberg, Hoffman, Bremmer & Ross, 2003). Similar speed enhancement effects have been observed in rapid sequences of static images with a radial structure (i.e. the implied "static" radial flow from Glass patterns, described by Ross, 2004 and Ross & Dickinson, 2007). Furthermore, as mentioned earlier, speed enhancement effects are not restricted to radial stimuli. They occur in RDK-s containing more than one direction-of-motion (De Bruyn & Orban, 1999; Edwards & Grainger, 2006), or if local motion vectors are aligned and oriented in a certain way (Georges et al., 2002). Until more is known about how these processes might contribute to the radial speed bias, its anatomical locus remains undetermined.

Speed Discrimination in Complex Motion

Although the perception of the speed of complex motions provides some evidence for a processing hierarchy, it has been repeatedly shown that speed discrimination performance is unaffected by the global pattern of motion (Sekuler, 1992; Bex et al., 1998; Clifford et al., 1999). Speed discrimination thresholds for radial and rotary motion are identical to those for translation, and as low as those reported for spatially localized stimuli (≈ 5-7 %; McKee, 1981). These results have been interpreted as evidence against the encoding of radial / looming motion along a distinct, relative motion channel (Sekuler, 1992). Instead, it has been argued that the pooled estimate on which, presumably, speed discrimination is based, is a simple aggregate of local speed signals, regardless of their global organization. In other words, the output of the large-scale complex motion mechanisms could be fully specified by local input.

Identical sensitivity to relative speed, however, can be based on very different estimates of absolute speed, irrespective of their origin. For radial flow, speed discrimination is simply carried out on faster motions, whereas for rotary patterns its is based on slower speeds. No difference in speed discrimination thresholds necessarily follows. Thus the differential pooling of local speeds in radial motion is not in conflict with the uniform speed discrimination performance. Alternatively, in a sequential paradigm, speed discrimination could be based on point-wise comparison in a small retinal region and may not depend on a global speed signal at all. It is still an open question, however, why the information about the overall configuration of motion can be bypassed in a speed discrimination task but not in a speed-matching task. Whereas the radial speed bias has been demonstrated with both temporal and spatial comparisons, speed discrimination has been examined only sequentially. It is possible that the relative speed judgment would be forced to draw upon global speed estimates if the comparison is simultaneous, across space. Another factor allowing speed discrimination to bypass global motion mechanisms is that the comparison is between successive samples of the *same type of complex motion*, whereas in speed matching, the comparison is between the apparent speed of two *different patterns of motion*. Recent evidence strongly suggests that complex motion mechanisms are particularly sensitive to temporal changes in optic flow structure, and some of their characteristics may not be apparent with repeated exposure to the same type of flow.

Sensitivity to Temporal Change in Complex Motion

An important characteristic of the radial speed bias is its dependence on the sequence in which the comparison between optic-flow patterns is made. In a temporal two-alternative forced choice, the perceptually faster pattern (e.g. radiation) appears even faster when it is presented *after* the perceptually slower pattern (e.g. rotation). Geesaman and Qian (1998) highlighted this order effect, but remained, admittedly, puzzled by it. They attempted to explain it with rapid adaptation to the first motion, weakening its inhibitory input to the mechanisms encoding the second motion, thus boosting the apparent speed of the latter. It was reasoned, however, that this explanation would be inadequate unless unconventional assumptions were made. It is well known that, at the level of MT, strong mutual inhibition exists between opposite directions of motion (e.g. Snowden, Treue, Erickson & Andersen, 1991). No speed enhancement, however, is observed with sequential presentation of opponent complex motion (e.g. contraction/expansion; counterclockwise/clockwise rotation). For the fatigue/adaptation hypothesis to apply, one has to assume that in the cortical area responsible for the order effect, there are inhibitory connections between rotation and expansion channels (and between translation and expansion channels), but not between expansion and contraction channels (Geesaman & Qian, 1998). While this idea may seem unconventional, it is worth exploring, in the context of recent findings about neuronal responses to sequential stimulation with different types of optic flow.

Recent work indicates that MST-d neurons are exquisitely sensitive to temporal changes in the directional structure of the flow, such as morphing of one type of flow into another, or shifting the focus of expansion, for example (Paolini, Distler, Bremmer, Lappe & Hoffmann, 2000). These cells appear to be tuned to the transition itself, showing distinct response profiles (e.g. linear, stepwise or peaked). The neuron's response to the transition between optic flow patterns cannot be predicted by the sensitivity of the cell to each component presented in isolation. In keeping with these findings, recent fMRI evidence strongly suggests that the response to the spatial or temporal merging between complex motion patterns seems to be a defining characteristic of optic flow sensitive areas in the human brain (Morrone, Tosetti, Montanaro, Fiorentini, Cioni & Burr, 2000; Smith, Wall, Williams & Singh, 2006). Morrone et al. (2000), for example, identified two distinct regions within the V5/MT complex - one selective to radiation and rotation - and another, selective to translation. Anatomically separate activation was obtained, however, only when the optic flow stimulation reversed direction (i.e. contraction alternated with expansion, and rightward translation alternated with leftward translation). Stimulation with continuous (non-inverting) flow produced inseparable activation, for translating, radial and circular flow. The change in flow direction produced consistently strong and selective fMRI activation, regardless of whether the transition was gradual or abrupt, suggesting that the results were specific to the direction inversion and not to the local transients associated with it. Furthermore, the activation produced by translation was not only anatomically, but also functionally different from that produced by radiation or rotation. Whereas a clear response to translation was obtained with both continuous and alternating motion, a response to complex motion could be obtained only if the direction of flow was periodically changed.

These findings challenge the notion that optic flow sensitive mechanisms perform a linear decomposition of the flow field into simpler components. It appears that the temporal interaction between different complex flow patterns is constructive, rather than destructive, enhancing direction selectivity, and possibly, speed selectivity, as well. Complex motion neurons do not seem inhibited by opponent patterns of complex motion, or, at least, the inhibition is not of the same type as the one documented for tanslational RDK-s in MT. Thus it appears that optic flow sensitive areas in parietal cortex are specifically encoding temporal and structural changes in the optic flow, and are less responsive to its stable components.

Understanding the unique response of complex motion detectors to changing flow requires investigation of their temporal properties, which are, currently, largely unknown. There are just a few pieces of evidence relevant to this question. Single-cell recordings from macaque MST-d reveal at least two components in the temporal response to optic flow - a transient, non-linear response, both to motion onset, offset, and to change in flow trajectory (Paolini et al., 2000), and a strong, sustained component that remains invariant for up to 25 seconds (Duffy & Wurtz, 1997b). Furthermore, a psychophysical study has shown that coherence thresholds improve with exposure duration for up to 3 seconds for radial and rotary motion, whereas temporal integration for translational motion is complete within 1 second (Burr & Santoro, 2001). Contrast sensitivity for complex motion, on the other hand, is believed to be limited at earlier levels of analysis, as it becomes optimal over much shorter exposures (200-300 ms), regardless of the pattern of motion. The significance of the temporal persistence in complex motion processing is not understood. It is unclear whether it is specific to RDK stimuli, or generalizes to flow-fields defined by luminance borders. While prolonged temporal integration typically increases the signal to noise ratio and thus enhances the directional signal, it is unknown whether it is also beneficial for the encoding of speed. On the other hand, a sluggish temporal response seems incompatible with the rapidly changing demands of behavioral systems. Distinguishing the sustained from the transient components of the optic flow response is critical for understanding what information is carried by each component. Studying the dynamics of these two components with prolonged stimulation might be especially useful in separating their functional roles.

1.4.6. Summary

As apparent from this overview, research on complex motion is primarily data-driven and relies heavily on physiological findings. The rapid accumulation of empirical evidence in different stimulus contexts frustrates attempts for conceptual integration. Despite the consensus that complex motion sensitivity must arise through converging input from previous levels (e.g. Ross, Mante, Simoncelli & Movshon, 2006), there is a strong tendency to attribute various effects to neuronal properties in MST-d, exclusively. As pointed out by Perrone (2004), existing models of optic flow processing operate on ready-made image velocity estimates. There is a general trend to ignore the problems associated with obtaining those estimates in the first place, in areas such as V1 and MT. The discontinuous thinking of MST-d processing will persist, until more attention is given to the front-end input to these higher-level sensors.

Another obstacle to conceptual progress is the general lack of systematic research on the dynamic aspects of complex motion perception. Clearly, complex motion mechanisms are sensitive to the global and local speed content of the stimulus, as well as to its temporal dynamics. The outstanding question is, however, whether the speed-related responses of these mechanisms are unique or inherited from previous levels. Are local speed signals integrated in a distinct manner at these higher levels and is such integration mandatory? Are velocity mechanisms different, or better established in MST-d than in MT?

Adaptation studies have been instrumental in targeting the unique sensitivity to complex motion direction at these higher levels of analysis (Regan & Beverley, 1978; Bex et al.,1999b, Kelly, 1989). None of these studies, however, has examined the selective effects of such adaptation on the perception of global speed. The rest of this introduction reviews what is known about the effects of motion adaptation on the perception of absolute and relative speed in spatially localized moving gratings. This line of research has provided important information about the nature of local velocity mechanisms and can be extended to the study of global velocity mechanisms in complex motion.

1.5. Changes in Perceived Speed Following Adaptation to Motion

1.5.1. Early VAE Studies

The first report of reduction in perceived speed, following adaptation to motion comes from Wohlgemuth (1911). In one of his experiments, observers fixated between two vertical belts of horizontal black-and-white stripes. The left-hand belt was stationary, while the right-hand belt was set in motion at a constant velocity. After about 30 seconds of viewing, the left-hand belt was set in motion, at the same speed as the right-hand belt. Observers, however, judged the apparent speed of the previously adapted right-hand belt to be slower than that of the un-adapted left-hand belt, although both belts moved at the same physical speed. Subsequently, this effect was "rediscovered" by Gibson (1937) and confirmed by Goldstein (1959). These initial studies only examined the effects of prior adaptation to movement upon the perceived speed of a test stimulus moving at the same speed and in the same direction.

Subsequent investigators examined the effect of adapting to one speed of motion on the perception of a range of test speeds, both in the same and in the opposite direction to that of the adaptation motion (Carlson,1962; Rapoport,1964; Clymer, 1973). These studies measured perceived speed before and after adaptation, using different stimuli and techniques: estimation of the time it would take for a line to travel a particular distance (Carlson, 1962), magnitude estimation of the apparent speed of rotary motion (Rapoport, 1964) and speed matching of moving random dot patterns (Clymer, 1973). These studies established that test motion moving in the same direction as the adapter, are perceptually slowed down, with the greatest reduction found for test motions moving slower than the one used during adaptation. The perceived speed of test motions moving faster than the adapter, was either unaffected, only slightly reduced or increased (Rapoport, 1964). If test motion was opposite to the adapted direction, however, no evidence for speed overestimation was found: perceived speed was either unaffected (Rapoport, 1964), variably affected, or somewhat reduced (Clymer, 1973).

1.5.2. Selective Adaptation and Perceptual Aftereffects

Results from these early studies suggested that the VAE has distinct tuning in that its magnitude depends on the parameters of the test motion, relative to those of the adapting motion. This is to be expected, as all visual aftereffects show some tuning - a maximum effect is observed with some combination between the adaptation and test conditions. The tuning of an aftereffect is important because it provides information about the underlying perceptual mechanisms. Such inference is based on certain assumptions about the nature of these mechanisms and how adaptation might affect them (Thompson, 1998).

Prolonged exposure to a given stimulus, imaged on the same retinal surface, would deactivate (i.e. fatigue) a set of neurons, implicated in processing that stimulus. The extent of this deactivation would be proportional to the initial response of these neurons to that stimulus. In other words, adaptation is expected to be selective - the responses of the neurons most sensitive to a given stimulus attribute would be most attenuated, following adaptation, whereas neurons with different preferences would be little affected. The test stimulus is then used as a "microelectrode", probing the perceptual consequences of such selective deactivation along the dimension of interest. Therefore, as a general rule, the greatest effects are observed when the test stimulus most closely resembles the adaptation stimulus, as, presumably, the perception of both stimuli is mediated by the same mechanisms.

The tuning of a given aftereffect would depend on the neural representation of the dimension of interest. To illustrate how a typical aftereffect might arise, a classic example from the spatial domain will be useful. It is known that neurons in the primary visual cortex are narrowly tuned to specific spatial frequency ranges, densely covering the spatial frequency spectrum. A collection of such spatial frequency filters is schematically depicted in Figure 1A. Following adaptation to a grating of a particular spatial frequency (see arrow), the sensitivity of the neurons selective to that spatial frequency would be reduced the most, while neurons tuned to spatial frequencies lower or higher that the adapted value, would retain their responsiveness (see Figure 1B). Accordingly, a strong and selective decline in contrast sensitivity occurs for a sine grating at the adapted spatial frequency, but no such impairment is observed for frequencies below or above the adapted value (Blakemore & Campbell, 1969). Hence, if one examines the spatial frequency aftereffect (i.e. the shift in perceived spatial frequency, following adaptation), the generic outcome shown in Figure 1C is found (e.g. Blakemore, Nachmias & Sutton, 1970). While perception of a test spatial frequency at the adapted value remains veridical, spatial frequencies slightly lower and slightly higher than the adapted value, are underestimated and overestimated, respectively. These shifts are often described as repulsive, as test stimuli different from the adapter, appear more different from it than they actually are. The largest perceptual shifts are observed slightly below and above the desensitized (i.e. adapted) spatial frequency channel, because at these points the relative contributions of neighboring channels are unbalanced. By contrast, there is no perceptual distortion of the adapted spatial frequency itself, or for spatial frequencies very different from the adapter, because at these points the output of neighboring channels is balanced. Thus, the tuning of an aftereffect depends on the number, the particular shape, the degree or overlap and the sensitivity band-width of the channels sampling the dimension of interest, as well as on the extent to which each channel is susceptible to adaptation. In the case of spatial frequency, orientation, and direction-of-motion, the corresponding aftereffects are symmetrical, as these dimensions

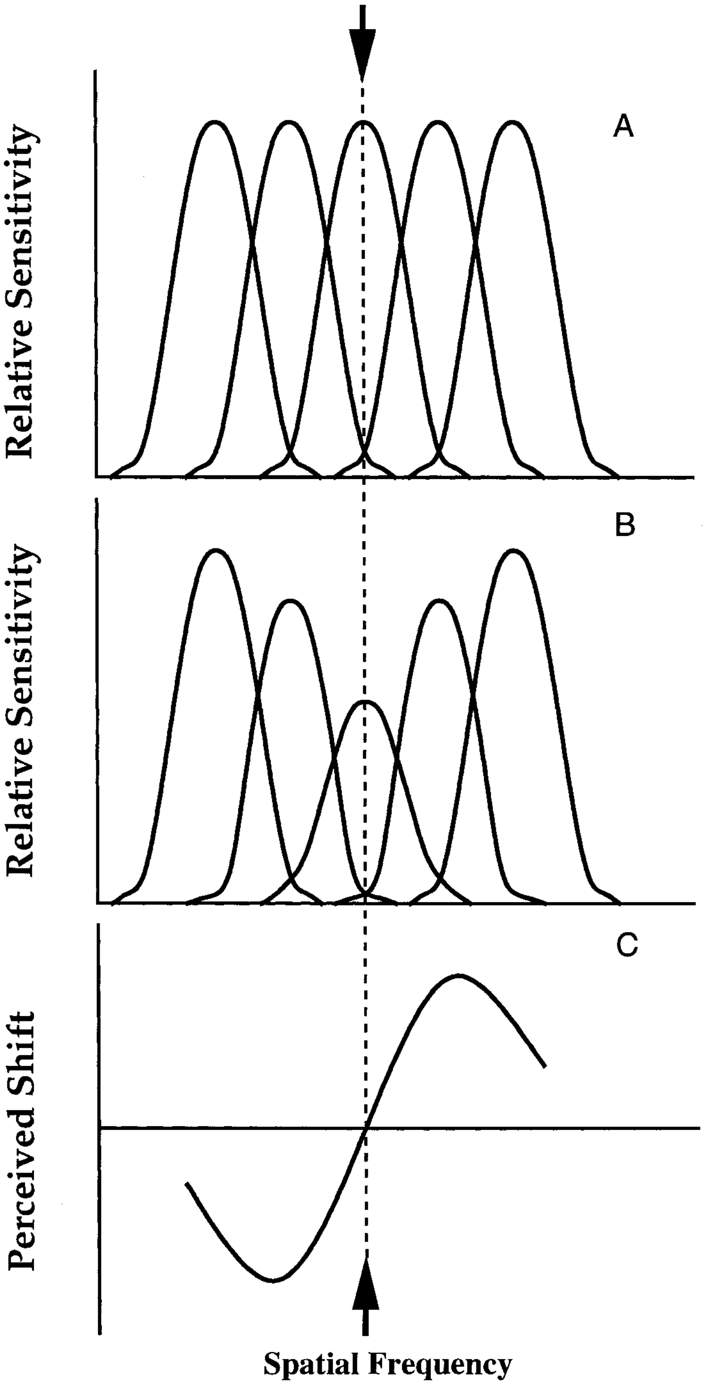


Figure 1. Generation of a typical spatial frequency aftereffect.

(A) Un-adapted state of a set of band-pass spatial frequency filters; (B) Adapted state of the filters; (C) Change in perceived spatial frequency, following adaptation. Diagram modeled after Thompson (1998).

are sampled by multiple, narrowly tuned, independent sets of neurons (i.e. channels) which are, presumably, equally adaptable. As pointed out earlier, the mechanisms encoding image speed, or velocity, are very different, and, so is the tuning of the VAE (see schematic depiction in Figure 2).

1.5.3. Tuning of the VAE

The tuning of the VAE has been extensively studied by Thompson (1976, 1981), and further elaborated by Smith (1985), Smith and Edgar (1994), Ledgeway and Smith, (1997), Müller and Greenlee (1994); Müller, Göpfert, Leineweber and Greenlee, (2004) and Hammett, Champion, Morland and Thompson (2005), among others. All these studies have used comparable stimuli and methods. They employ moving sine-wave or square-wave gratings confined to small apertures, presented bilaterally, in para-foveal vision. Perceived speed before and after adaptation is measured by means of spatial speed-matching. Since the VAE is most prominent with iso-directional adaptation (i.e. when the test motion is in the adapted direction), tuning investigations have focused on this condition.

In an extensive series of experiments, Thompson (1976, 1981) characterized the tuning of the iso-directional VAE as a function of the spatial and temporal frequency of the adapting and test motion. His fundamental findings were confirmed by subsequent investigations. First, the magnitude of the iso-directional VAE varies with adapting velocity, rather than with the spatial and temporal frequency defining this velocity.

Accordingly, the aftereffect has been referred to as the velocity aftereffect (VAE, Thompson, 1976). Notably, whereas the dynamic MAE, assessed with flickering test patterns, shows similar velocity tuning (Ashida & Osaka, 1995), the static MAE is clearly tuned to the temporal frequency of the adapting motion (Pantle, 1974). Second, in comparison to other spatially based aftereffects (i.e. the spatial-frequency aftereffect, the tilt aftereffect -TAE, and the direction-of-motion aftereffect - DAE), the iso-directional VAE shows a marked asymmetry. Although, as in other aftereffects, the shifts in perceived speed could be characterized as repulsive, a large reduction in perceived speed (up to ≈ 80%) is observed for *all test speeds slower than the adapting velocity.* Overall, *test speeds faster than the adapter* are little affected, although they may be overestimated under certain conditions (Hammett et al., 2005). In all reports, the negative VAE (speed underestimation of slower tests) is consistently stronger than the positive VAE (speed overestimation of faster tests). Another distinct characteristic of the iso-directional VAE is that the reduction in apparent speed is not limited to test speeds different from the adapting velocity, as *tests at the adapting velocity* are also significantly affected (attenuated by ≈ 30%). Finally, as for the MAE, there is an inverse-U relation between adaptation velocity and the magnitude of the VAE, and the shift in perceived speed remains a constant fraction of the adapting velocity.

An important requirement in the measurement of the VAE is to separate the contribution of concomitant contrast adaptation from the overall reduction in perceived speed (Thompson, 1981; 1982). Apparent contrast declines with prolonged exposure, and, as previously discussed, lower contrast stimuli appear to move more slowly than higher contrast stimuli of the same physical speed (see1.3.1.). Thus in part, the observed VAE could be attributed simply to loss of apparent contrast. Studies addressing this issue estimate that contrast adaptation accounts for up to about 15% of the overall reduction in perceived speed (Bex et al., 1999a). Some VAE studies have controlled for contrast attenuation by equating the perceived contrasts of the adapted and the un-adapted motions used in the speed-matching task (Bex et al., 1999a). Others have shown that adaptation to gratings of low Michelson contrast (0.11) has no effect on the perceived contrast of high contrast tests (0.33), and have therefore, adopted this protocol in the measurement of the VAE (Thompson, 1976; 1981).

The effect of contrast on perceived speed may also account for some of the positive VAEs reported for tests faster than the adapter. As explained earlier, faster speeds (> 8 Hz) may appear even faster when apparent contrast is reduced, physically, or following adaptation (see 1.3.1). This indicates that genuine speed overestimation is relatively uncommon. Positive VAEs, however, have been documented for faster tests (> 8 deg/s), even when contrast fading has been effectively controlled (Hammett et al., 2005), but only at rather low adapting velocities (≈ 2-3 deg/s). Therefore, it cannot be assumed that speed overestimation is always an artifact of contrast adaptation.

Taken together, results indicate that the tuning of the iso-directional VAE retains its basic characteristics after the confounding influence of concomitant contrast adaptation has been taken into account. A marked reduction in perceived speed is observed at the adapting velocity, with an asymmetry between the perceptual shifts for test speeds different from the adapter. There is a pervasive negative VAE at slower speed, about twice as strong as the positive VAE for faster speeds, with the latter effect limited only to specific adapt/test speed combinations.

It should be noted, that empirical estimates of the VAE tuning may be sensitive to variations in the experimental context. The general VAE pattern, described above, is based on studies using very similar stimuli and procedures (moving gratings and spatial speed matching). Following adaptation to RDK motion, however, Schrater and Simoncelli (1998) reported a more symmetrical, repulsive VAE, inseparable from the DAE obtained with the same stimuli. This result was taken as evidence for adaptation of velocity mechanisms, encoding jointly the speed and the direction-of-motion. In this study, however, observers compared the speed of stimuli that were separated in both space and time. In addition, a stationary comparison stimulus remained present during adaptation, and was set in motion during the test. Adaptation to a stationary stimulus is not a neutral condition, as it can increase the perceived speed of subsequently viewed motion (Thompson, 1981, 1993). Owing to these important procedural differences, the results from this study are not directly comparable to the bulk of VAE findings, collected with uniform methods. Thus the extent to which the VAE tuning generalizes to stimuli other than gratings remains unknown.

1.5.4. Direction Specificity of the VAE

As mentioned earlier, prior motion adaptation may also alter the apparent speed of gratings moving in the direction opposite to the one adapted. Counter-directional VAEs are less pronounced than iso-directional VAEs, and, consequently, have not received much attention. Typically, contra-directional adaptation causes about half as much velocity reduction as iso-directional adaptation (Smith, 1985; Smith & Edgar, 1994). The magnitude of this effect is generally independent of the combination between adapting and test speeds (Müller et al, 2004), showing little, or inconsistent tuning (Thompson, 1981, Smith, 1985).

Although the term "velocity" implies direction specificity, discussions of the difference between iso- and counter-directional VAEs have been sporadic. Researchers have linked *both* effects to changes in temporal sensitivities of neurons in the primary visual cortex, a large proportion of which are not direction selective. Most studies have focused on the stronger and more reliable VAE, produced by iso-directional adaptation. Other studies, have emphasized the similarity between the two effects, concluding that speed reduction occurs to the same extent, after adaptation to flicker or motion, and regardless of motion direction (Clifford & Wenderoth, 1999). Yet it has been shown, that the effects of flicker and motion adaptation are far from equivalent, with the latter showing twice as much inter-ocular transfer (70%) than the former (35%)[Hunzelmann & Spillmann, 1984; Schieting & Spillmann, 1987]. In other words, the neuronal populations processing directionless and directed motion are only partially overlapping.

A similar argument applies to the neuronal activity triggered by stimuli moving in opposite directions. A grating moving in a particular direction would stimulate a large set of units sensitive to temporal change. One set of these units would be isotropic (i.e. insensitive to motion direction), yet another set would be direction selective. Furthermore, the direction selective set would not only contain cells tuned to the target direction, but also cells tuned to the opposite motion, as well as cells with preference for other directions. As mentioned earlier, the common assumption is that since cells preferring the target direction would respond most vigorously, they would also be most susceptible to adaptation (Giaschi, Douglas, Marlin & Cynader, 1993). A related assumption is that the responses of these cells would be most relevant to perception. Yet the other cells in the activated set would also respond in some manner, and those "irrelevant" responses would also adapt. In other words, the neuronal activity associated with a moving stimulus has a direction specific, as well as a non-specific component, and the relative weight between these two components seems to depend on the particular brain region stimulated and studied (Huk, Ress & Heeger, 2001).

The apparent slow down of motion opposite to the adapted direction is believed to reflect only the general (non-specific) neuronal adaptation (Müller et al., 2004). On the other hand, the apparent slow down of motion in the adapted direction is believed to reflect both components - the non-specific one (including flicker and null responses), as well as the one that is direction-specific. Presumably, the summation of these two components is what makes the iso-directional VAE stronger. In this context, the extent to which the iso-directional VAE exceeds the contra-directional VAE would reflect the degree to which speed perception is direction specific. A related inference is that the extent to which the VAE transfers to the opposite direction of motion would reflect the degree of independence between mechanisms tuned to opposite directions of motion (Thompson, 1981).

Although the term "velocity" implies complete direction specificity, the consistent reports of negative counter-directional VAEs suggest that velocity adaptation and subsequent velocity perception are only partially direction specific. Similarly, this can be taken as evidence that responses to opposite directions of motion are only partially independent (Thompson, 1981). It is important to note that negative counter-directional VAEs have been documented only with spatially localized sine-gratings. Interestingly, in the only study of the VAE with complex motion, central viewing of a rotating pattern did not produce any measurable counter-directional VAE (Rapoport, 1964). Although the generality of this early finding has not been examined, it suggests that the degree of direction-specificity, and perhaps other characteristics of the VAE, may depend on the nature of the moving stimulus.

1.5.5. Pattern Specificity of the VAE

The issue of direction-specificity is part of the broader question about the extent to which adaptation to one moving pattern can affect the perceived speed of another moving pattern. To our knowledge, only one study has addressed this question explicitly (Smith & Hammond, 1985). This study examined the VAE produced by adaptation to a coarse, moving square-wave grating on fine-textured moving tests, and vice versa. The VAE was also investigated over a range of test motion directions, with adaptation and test stimuli of the same type. A comparable reduction in the apparent speed of the test motion was observed, whether or not the adaptation and test patterns were of the same or different types. Furthermore, both cross-pattern and same-pattern VAEs showed the same, moderate degree of interocular transfer (i.e. on average, about 50%). The direction tuning of the VAE for both types of stimuli was found to be quite broad, with the effect declining gradually as the angular separation between the adaptation and test directions increased. The VAE reached a minimum only at 90° separation, and never disappeared altogether, confirming the presence of a counter-directional VAE (i.e. at angular separation of 180°). The shape of the directional tuning, however, was different for moving bars and textures. Whereas adaptation to moving bars produced maximum VAEs when the test was in the same direction as the adapter (0° angular separation), texture adaptation produced VAEs which were optimal between 0° and 30°, with a peak at an angular separation of 15°.

In view of these findings, Smith and Hammond (1985) refrained from a simple conclusion about the pattern specificity of the VAE. Instead, they suggested that pattern-specificity is evident in some cases but not in others, because, presumably, the VAE is mediated, at least in part, by neurons sensitive to both bars and textures. Clearly, the conclusion that the VAE is only partially, or very broadly selective to the pattern or direction of motion is tenuous, as it is based on very limited data. This issue, however, is conceptually important and deserves careful study. As discussed earlier (sections 1.1;

1.2.2), a mechanism sensitive to image velocity and supporting velocity constancy should be independent of the spatial pattern carrying the motion, but is expected to be selective to the direction of motion. On the other hand, the transfer of velocity adaptation between different spatial patterns, would seem disadvantageous, from a functional standpoint (see discussion to follow, below).

1.5.6. Temporal Course of the VAE

Several psychophysical studies have examined the time-course of the VAE (Clifford & Langley, 1996; Bex et al., 1999a; Hammett, Thompson & Bedingham, 2000; Hammet et al., 2005). In general, results indicate that the decline in perceived speed with prolonged exposure to motion, parallels the decline in spike-rate in motion sensitive ganglion cells of the rabbit (Barlow & Hill, 1963), in area 17 of the cat (Gaischi et al., 1993), and in H-1 neurons in insects (Maddess & Laughlin, 1985). It has been found that both the decay and the recovery of apparent velocity are exponential, but the build-up of the VAE is much faster (e.g. 5 s) than the recovery from it (e.g. 22 s, Bex et al., 1999a). Psychophysical estimates of the time-course of the VAE, however, are more variable across studies than the changes in neuronal response rate, and the time constants of these effects vary considerably across species (Bex et al., 1999a; Hammett et al., 2000; Clifford & Ibbotson, 2003; Hammett et al., 2005). Furthermore, the physiological correlates of the increases in perceived speed, following adaptation to motion have not been identified yet (Hammett et al., 2005). Nevertheless, the broad correspondence between the effects of motion adaptation on perceptual and neuronal responses is at the heart of the oldest and most popular accounts of the MAE and the VAE, which will be considered below.

1.5.7. Accounts for the VAE

Early Ideas and Opponent Response Frequency Approaches

Initial attempts to explain the VAE were directly linked to accounts of the MAE. Gibson (1937) proposed that adaptation shifts the "null point" of the motion dimension (i.e. zero speed and zero direction) in the direction opposite to the adapted quality. Hence, a stationary stimulus, at the physical “null point”, would appear to move in a direction opposite to the adapted one (i.e. the MAE), at a given speed. Similarly, after adaptation, a test stimulus moving in the adapted direction at a certain speed, will cancel the MAE velocity and will therefore, appear as stationary. The underlying assumption is that the velocity of the illusory MAE adds to the velocity of the real motion, presented at the adapted location. A straightforward prediction from Gibson's model is that, after adaptation, the apparent speed of all stimuli moving in the adapted direction will be reduced, whereas the speed of all test stimuli moving in the opposite direction will be increased. Clearly, empirical results are inconsistent with the latter prediction.

With the development of modern ideas about the nature of motion detectors (Exner, 1894 - as reviewed by Thompson, 1976; Reichardt, 1961) and the description of cells with similar properties in the primary visual cortex of mammals (Hubel & Wiesel, 1959), explanations of the MAE also evolved. In principle, a cell is capable of detecting motion if it responds optimally to sequential stimulation across its receptive field, at a particular rate (preferred temporal frequency), in a given direction (preferred direction), provided it is less responsive or fails to respond to stimulation in the opposite direction (null direction). Similarly, the response is sub-optimal if stimulation is in the preferred direction, but its temporal rate is outside of the cell's preferred range.

Barlow's work on motion sensitive ganglion cells in the rabbit retina described how the response of a motion detector might change, as its inhibitory and excitatory inputs are altered in the course of prolonged stimulation (Barlow & Hill, 1963). Regardless of the precise nature of these input dynamics, motion sensors displayed a highly regular adaptive behavior. Stimulation with a preferred motion stimulus produced a large initial response (high rate of firing), which quickly subsided and leveled off to a rate comparable with the spontaneous discharge of the cell (i.e. when stimulation was absent). Cessation of stimulus motion led to complete suppression of the cell's activity (below spontaneous levels). Slowly and gradually, after several seconds, the cell recovered its spontaneous discharge. These findings established that a pervasive consequence of prolonged exposure to motion is that relevant motion sensors are rendered unresponsive, or less responsive, immediately following adaptation.

In consideration of the above findings, Sutherland (1961) proposed a widely popular explanation of the MAE, subsequently elaborated by Mather (1980). In essence, the MAE is believed to arise from the imbalance in the relative rate of firing of populations of motion sensors tuned to opposite (or different) directions of motion. Following adaptation, say, to rightward motion, motion detectors selective to rightward motion would become less responsive than motion detectors selective to leftward motion. If perception is determined by the "direction labels" of those cells which contribute most strongly to the overall response level, then leftward motion will be seen in a stationary stimulus, following adaptation to rightward motion. A fundamental feature of Sutherland's model is that the nature of the motion percept is based on a comparison (e.g. a ratio) between the levels of activity in populations of motion sensors, tuned to opposite (or different) directions of motion. The underlying assumption is that the neural code for perceived direction-of-motion is the firing rate of cells tuned to that direction, relative to that of cells tuned to the opposite direction.

While Sutherland's framework accounts well for the illusory direction-of-motion seen in static displays, it is less applicable to the dynamic aspects of the MAE, and cannot explain the shifts in perceived speed observed in moving tests, following adaptation (Thompson, 1976). As an extension of Sutherland's model, it was hypothesized that perceived speed, by analogy with perceived direction, is also determined by the relative amount of activity in motion sensors tuned to opposite directions of motion (e.g. Sekuler & Pantle, 1967). Similarly, it was expected that within the population of cells, selective for a particular direction of motion, individual cells were tuned to a range of different speeds (Moulden, 1974). The same distribution of preferences would be found in the population of cells selective for the opposite direction of motion. The general idea behind this reasoning is that perceived speed is proportional to the relative response level in the two populations of opponent motion sensors. Essentially, a higher rate of firing would signal faster speeds, and a lower firing rate would signal slower speeds. Thus, adaptation to one direction of motion would reduce the perceived speed of test motions in that direction, and increase the perceived speed of test motions in the opposite (unadapted) direction by the same amount. Interestingly, although couched in different terms, the prediction of this model is identical to the one proposed by Gibson (1937), and, once again, implies additivity between illusory and real velocities coexisting over the adapted location. In this context, the MAE and the VAE are seen as inseparable - i.e. the stronger the MAE, the stronger the VAE will be. Similarly, since simultaneous adaptation to opponent directions of motion abolishes or greatly reduces the MAE, the same is expected for the VAE.

Empirical findings on the VAE, however, are in obvious conflict with both Gibson's proposal and extensions of Sutherland's opponent model. Indeed, as these accounts predict, the speed of test motions in the adapted direction is reduced. The speed of motions in the opposite (unadapted) direction, however, is also reduced (albeit to a lesser extent), rather than increased, in conflict with these models' predictions. Thus the VAE pattern of results argues against an algebraic addition between MAE and real motion velocities. Also, adaptation to bi-directional (opponent) motion, virtually eliminates the MAE, while the VAE is not extinguished following such adaptation (Thompson, 1976). Furthermore, an opponent response frequency scheme cannot account for the documented increases in perceived speed, following adaptation to motion in the same direction as the one tested.

Despite their inability to account for many aspects of the VAE, and the co-dependence of neuronal firing rates on contrast (see 1.3.1), response frequency models of velocity coding have unsurpassed popularity among physiologists (e.g. Krekelberg, 2006b). Alternatively, as discussed in section 1.2.4, another possibility is that perceived speed is mediated by subsets of neurons, sensitive to particular speed ranges and thus being "labeled" for speed. This strategy is not problem-free, but can be adapted to explain the VAE.

Multiple Channels Approaches

A different approach to the VAE presumes the existence of more than one channel tuned to different ranges of temporal frequency/speed/velocity, within the population of motion sensors selective to a particular direction-of-motion (Moulden, 1980). Thus, a separate estimate of perceived speed is computed for any given direction-of-motion. Again, this estimate reflects the relative activity in the set of speed sensitive channels, with each channel carrying a "speed label" and voting with its firing rate for its preferred speed. The comparison is carried out between sets of cells selective for the same direction-of-motion, rather than between cells selective for opponent directions. This hypothetical multi-channel system is analogous to the one established in the spatial domain (e.g. for spatial frequency and orientation). As discussed in section 1.5.2, within such a system, following selective adaptation of a particular speed channel, a range of speeds slower than the adaptation rate will be underestimated, whilst a range of faster speeds will appear faster still. There should be no shift in the apparent speed of test motions identical to the adapter (see Figure 1).

The asymmetrical tuning of the iso-directional VAE, however, does not match these predictions. Similarly, psychophysical data suggest that if labeled channels for temporal frequency/speed/velocity exist, they are not numerous. Instead, as reviewed in section 1.2.3, there is strong evidence for just two temporal frequency or speed channels, broadly tuned for "slow" and "fast" speeds (see Figure 2A). Such coarse sampling of the temporal frequency dimension is in sharp contrast with the fine sampling of the spatial frequency domain (see Figure 1A). This is a fundamental obstacle in the extraction of a precise velocity signal from local spatio-temporal samples of the retinal image. Although the notion of well localized temporal frequency filters is not supported by either psychophysical or physiological data, perceptual judgements have access to precise velocity estimates, as human sensitivity to velocity differences is rather high (McKee, 1981; McKee et al., 1986). To resolve this discrepancy, it has been proposed that the visual system refines sensitivity to temporal frequency through antagonistic comparison between the outputs of the two broadly tuned temporal frequency channels. This model, outlined below, accounts rather well for the nature of the iso-directional VAE tuning.

The Two-Channel Ratio Model of Perceived Speed

This model has evolved through the work of several authors (Kulikowski & Tolhurst, 1973; Harris, 1980; Thompson, 1982; Smith & Edgar, 1994; Hammett et al.,

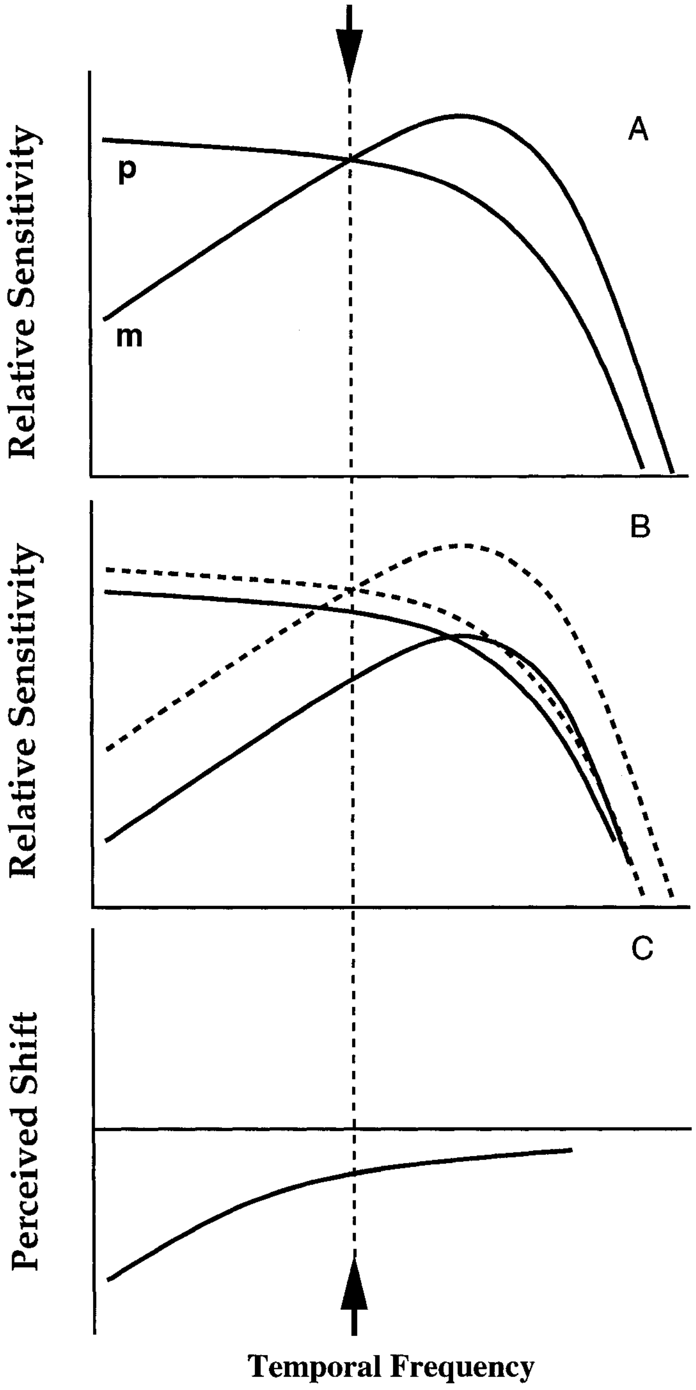


Figure 2. Generation of a typical velocity aftereffect (VAE).

(A) Un-adapted state of the low-pass (p) and the band-pass (m) temporal frequency filters; (B) Adapted state (solid lines); (C) Change in perceived speed, following adaptation. Diagram modeled after Smith & Edgar (1994), Hammett et al., (2005), and Thompson (1998).

2005). In its current form, the ratio model assumes that a moving stimulus activates two distinct mechanisms (M and P) - each broadly tuned to "fast" (M) and "slow" (P) temporal frequencies. Different authors have referred to the two mechanisms somewhat differently, such as "flicker" and "pattern", "fast" and "slow", "transient" and "sustained", "magnocellular-M" and "parvocellular-P", respectively (Hammett et al., 2005). The perceived speed of the stimulus is determined by the ratio of responses in the "fast" and the "slow" mechanisms, respectively (M/P). The sensitivity profiles of these two mechanisms (filters or channels) were described in section 1.2.3. They are depicted schematically in Figure 2A. Typically, temporal frequencies below about 3 Hz are considered "slow" as they elicit a stronger response in the "slow" channel (Edgar & Smith, 1994; Hammett et al., 2005). Similarly, temporal frequencies above 3Hz, and up to 20 Hz, are considered "fast" and would evoke a stronger response in the "fast" channel (maximum sensitivity at about 10 Hz). Speeds at the cut-off point (i.e.≈3 Hz) evoke the same response in the "slow" and the "fast" channels. At a standard spatial frequency of 1 cycle/degree (commonly used), the cut-off temporal frequency translates to a speed of 3 degrees/second (Hammett, 2005). Clearly, this cut-off value depends on the precise shapes and the degree of overlap between the two sensitivity functions.

Furthermore, based on neuro-physiological knowledge about neuronal responses in the primary visual cortex, the model assumes that: (i) adaptation reduces the sensitivities of the two temporal mechanisms in proportion to their initial response to a given stimulus (Giaschi et al., 1993); and, (ii) the "fast" mechanism is inherently more susceptible to adaptation (Solomon, Peirce, Dhruv & Lennie, 2004; Shchieting &

Spillmann, 1987; Maddess, Blakeslee & Cunningham, 1988). These two assumptions are sufficient to account for both underestimation and overestimation of perceived speed following iso-directional adaptation, as well as for the fact that speeds slower than the adapter are more profoundly affected than faster speeds.

A temporal frequency at the crossover point between the two sensitivity functions will activate equally both channels (see arrow, Figure 2A). Prolonged stimulation at that temporal frequency, however, will reduce the sensitivity of the more adaptable M-channel to a larger extent than that of the less adaptable P-channel (see Figure 2B). As a result the M/P ratio will be tipped in favor of a reduction in perceived speed, over a wide range of test speeds (see Figure 2C). Adaptation to motion, classified as "fast", would reduce the output of the M-channel, thus reducing perceived speed (i.e. M/P ratio). By contrast, adaptation to "slow" motion, would selectively reduce the P-contribution, leading to overestimation of perceived speed but *only if* the initial M-response is sufficiently strong (i.e. if test motion is sufficiently "fast"). In this manner, the ratio model accounts for the bulk of empirical data on the iso-directional VAE. It can also explain the effects of stimulus contrast on perceived speed (Thompson, 1982; 2006). The fact that a relatively simple scheme based on temporal frequency responses in V1 explains a velocity-based perceptual after-effect is in itself significant. It emphasizes the importance of temporal frequency information in the construction of velocity estimates.

The ratio model of perceived speed, however, has several limitations. First, it is concerned exclusively with the temporal frequency component of speed perception, and makes only vague predictions about the direction specificity of the VAE. It has been acknowledged that "the degree of direction-selectivity existing within the "pattern" and the "flicker" channels is unclear" (Thompson, 1976; Smith, 1985). Accounts of the counter-directional VAE are sporadic and variable. It has been suggested that the more adaptable, "fast"-M temporal mechanism is *only partially* (Smith, 1985) or *not at all direction selective* (Smith & Edgar, 1994). A related suggestion is that responses to opposite directions of motion are only *partially independent* (Thompson, 1981). The general assumption of *partial* direction selectivity is consistent with reports that test motions opposite to the adapted direction are somewhat slowed down, following adaptation, but the model is unable to generate quantitative predictions.

Furthermore, in its present form the model is limited to the operation of the two temporal filters within a given spatial frequency channel, in central vision. Yet there is evidence, that the shape of the temporal filters is not entirely independent of spatial frequency and it certainly changes with eccentricity (see 1.2.3). Therefore, the extent to which the model generalizes to stimuli with different spatial characteristics remains unknown.

Several authors have also questioned the biological plausibility of the ratio model. Perrone (2004) has pointed out that the ratio model produces output proportional to the image speed. This property is quite desirable in explaining perception, but is incompatible with the non-linear (tuned) responses of motion sensitive neurons. Since a ratio operation could not be meaningfully inserted along the V1-MT response chain, Perrone (2004) suggests that if it takes place at all, it would be at a site beyond MT. This implies that the ratio may be taken on speed or velocity estimates, rather than on raw temporal frequency outputs. This hypothesis is intriguing, given that the ratio principle has emerged from psychophysical data, targeting the initial steps of motion analysis in area V1.

Recent work has attempted to assess this idea directly by testing the ratio model on speed-related neuronal responses in area MT. Krekelberg et al. (2006b) investigated the contrast response of speed-tuned MT cells in behaving monkeys. In parallel, speed perception was measured in monkey and humans at different contrast levels. In agreement with the reduction of perceived speed at lower contrasts, most cells responded less at low contrast. The authors divided their cell sample into two groups according to speed preference ("fast "> 8 deg/s and "slow"< 8 deg/s). With "fast" and "slow" channels defined by the total firing rate of cells in each group, the ratio principle erroneously predicted that low-contrast stimuli should appear faster. This was in obvious conflict with the perceptual data, where no speed overestimation was observed. The major reason behind the discrepancy was that, contrary to the original assumptions of the ratio model (Thompson, 1982, 2006), the output of the MT based "fast" mechanism was less attenuated by contrast reductions than the MT based "slow" mechanism. The authors interpreted this discrepancy as strong evidence against a labeled-line approach to speed encoding, in general, and the ratio model of speed perception, in particular.

A rejection of the ratio model based on such evidence, however, may be premature. A mechanical application of the ratio operation to a subset of neuronal responses is of questionable conceptual value. There is logical circularity in passing responses relatively close to perception through models designed to explain this perception. Clearly, more caution and preliminary work is needed before testing psychophysical models with physiological data. Despite recent advances (Krekelberg, 2006a), it is still unclear how and which MT speed responses define the VAE tuning. Until a better account is suggested, the ratio principle remains a useful heuristic, supported by much psychophysical data. Its mathematical simplicity, however, may be deceiving. As the output of the two temporal mechanisms propagates throughout the visual hierarchy, it may be hard to identify the terms of the ratio. In the primate brain, the ratio operation may be carried out by means of an intricate interaction between classes of neuronal responses, within, as well as between motion processing levels. Therefore, it may be unreasonable to expect that the hypothetical "ratio sensors" would be identified at a particular neural site (Perrone, 2004).

Bayesian Accounts of the VAE

Recently, Bayesian inference has been applied to explain distortions of perceived speed under a large number of viewing conditions (see 1.3.), including the effects of sensory adaptation (e.g. Ascher & Grzywacz, 2000; Weiss, Simoncelli & Adelson, 2002; Stocker & Simoncelli, 2006). Within this framework, perception reflects the product of two probability distributions - one, determined by prior experience and expectations, and the other - corresponding to the current sensory input. The lower the quality of the sensory input (e.g. through contrast reduction or prolonged exposure) the more the posterior (perceptual) distribution would rely on the internal, statistical prior. In this context, perceptual errors are regarded as the best solutions of a system designed to operate in the presence of uncertainty.

The application of this approach to speed perception proposes a speed "prior", an expectation of speed, perhaps based on experience. Bayesian models assume that this prior expectation is biased towards slower speeds because such velocities are more often encountered, and because human observers tend to prefer the "shortest path", or the slowest motion consistent with a given visual input (Weiss et al., 2002). Thus, whenever the definition of the incoming speed signal is reduced (e.g. low contrast, prolonged adaptation), perceived speed will be reduced as well, reflecting the a priori likelihood that the speed encountered is slow.

The fundamental problem faced by Bayesian models is determining what the prior should be (Hammett et al., 2005; Stocker & Simoncelli, 2006; Thompson et al., 2006; Hammett et al., 2007). A prior distribution can be deduced in a number of ways - from theory, empirical measurements, or for simplicity and computational convenience. Furthermore, the sensory context and the noise characteristics of incoming signals often change abruptly, and so does their perceptual interpretation. This imposes the need to modify the prior in real time, inferring it directly from psychophysical data (Stocker & Simoncelli, 2006). For example, a slow speed prior is inconsistent with the speed enhancement of fast speeds at low contrast and following adaptation to slow motion (Hammett et al., 2005; Thompson et al., 2006), or in relative or radial motion displays (Geesaman & Qian, 1998). Thus while the flexibility of Bayesian approaches to speed perception is a definite strength, it is also their biggest weakness. Although these models can account for the pervasive reduction of apparent speed in the VAE, they are inconsistent with the illusory increases in perceived speed documented under certain conditions. Because of the arbitrary choice of the prior and noise fluctuations of the incoming signal, quantitative predictions based on these models are often inadequate (Thompson et al., 2006).

1.5.8. Summary

Studies of the VAE indicate that prior adaptation to motion profoundly distorts the perceived speed of subsequently presented moving patterns, over a wide range of test speeds. While underestimation of apparent speed is the pervasive feature of the VAE, speed overestimation also occurs for fast tests and rather slow adapting velocities. The amount of distortion depends on the velocity of the adapting motion, rather than on its temporal frequency, spatial frequency or speed. Thus, the effect could be mediated by mechanisms sensing velocity directly, as well as by separable spatio-temporal mechanisms. The nature of the VAE perceptual shifts cannot be directly inferred from processes implicated in the MAE, or from a generalized reduction of neuronal firing rate, following adaptation. This is because the observed VAEs cannot be produced by simply adding the velocity vectors of the MAE and the real test motion.

In their current versions, neither response frequency models nor Bayesian accounts of speed perception can explain the precise nature of the VAE tuning, although all these approaches account for the apparent slow down of motion with prolonged exposure. On the other hand, general motion models based on spatio-temporal filtering, extract successfully an unambiguous directional signal, but their velocity estimates depend on contrast and lack precision due to coarse sampling of the temporal frequency dimension (e.g. Adelson & Bergen, 1986). These and other models are primarily concerned with the extraction of the basic velocity signal, rather than with its adaptive dynamics (e.g. Heeger, 1987; Grzywacz & Yuille, Perrone, 2004). So far, the VAE for test stimuli moving in the adapted direction is best explained by a two-channel ratio model, based on temporal frequency mechanisms identified in the primary visual cortex of mammals. In its present form, however, this model is little concerned with the direction-specificity and the pattern specificity of the VAE. Its applicability to stimuli other than spatially localized gratings has not been examined.

The profound loss of apparent velocity with continuous exposure to motion raises questions about its functional purpose. How could a distorted perception of velocity support adequate behavior? Indeed, it is well known that prolonged exposure to monotonous motion flow, impairs driving behavior. In a driving simulator, for example, driving on a straight empty road for 5 minutes, delays the initiation of overtaking maneuvers by up to 500 ms, compared to the same amount of exposure to a static scene, or to curve driving (Gray & Regan, 2000). In this case, velocity adaptation results in misjudging headway distances and time-to-contact, increasing the risk for rear-end collisions. Fortunately, exposure to unchanging flow devoid of structure is rare, and texture cues offer considerable protection (Gray & Regan, 2000). The next section examines the possibility that the cost of adaptation to motion also comes with the benefit of improved sensitivity to changes in the ongoing stimulation.

1.6. Changes in Speed Discrimination with Adaptation to Motion

1.6.1. Adaptation as an Active and Flexible Process

General Considerations

So far, we have only considered one aspect of the adaptation process - the reduction of neuronal response rate with prolonged stimulation. There is much evidence, however, that adaptation in biological systems is not equivalent to fatigue. Many aspects of the MAE cannot be explained by simple desensitization of an isolated subset of neurons. The strong dependence of the MAE on relative motion during both adaptation and testing, the presence of "phantom" MAEs in display areas that were never adapted, the distinct expression of the MAE in static and dynamic displays, the attentional modulation of the MAE, as well as the prolonged storage of the MAE have challenged the validity of fatigue-based response frequency models (e.g. see Wade, 1994; Wade, Spillmann & Swanston, 1996). As an extreme caveat, there is evidence that spiral MAEs persist for over 24 hours after the inducing stimulation has ceased (Masland, 1969; Hersheson, 1985). Clearly, individual neurons do not remain desensitized for so long. In living organisms, sensory adaptation is a perpetual process, operating on different time-scales. If adaptation were equivalent to sensitivity loss, it would severely limit behavioral capacity.

The above examples imply that adaptation is an active and flexible process, updating the internal state of the sensory system according to recent stimulus history. It is often assumed that this internal frame of reference has a default setting, an anchor, or a neutral point, against which perceptual judgements are made. A restricted sensory diet (i.e. adaptation) may temporarily shift the position of the reference point, thus resetting or recalibrating the system (Gibson, 1937; Helson, 1947). Such shifts in the internal measurement scale lead to corresponding shifts in perception. In the case of velocity, for example, the default, un-adapted reference point may be neutral (e.g. "null velocity", Gibson, 1937; Sutherland, 1961) or, alternatively, it may be biased (e.g. the " slow-speed prior" in Bayesian models). The recent proposal that Bayesian priors may be modified in real time by recent sensory input could be regarded as an attempt to integrate the recalibration principle into the Bayesian framework (Stocker & Simoncelli, 2006). The recalibration process, however, must be constrained by the output demands of the system (Wainwright, 1999). From a functional standpoint, perceptual errors should be minimized in order to maintain perceptual constancy (Andrews, 1964; Bedford, 1999). To account for perceptual distortions, error-correcting mechanisms maintain access to the default reference point of the system. In other words, recalibration and constancy processes work together to determine perceptual outcome, so that it does not interfere with behavioral demands.

Adaptive Recalibration of Neuronal Responses

Results from adaptation studies in single neurons support the recalibration principle and reveal how it might be implemented (Kohn, 2007). With continued exposure to a given stimulus level, neurons may not only reduce their firing rate, but may also shift their preference and/or response tuning along the dimension of interest. The nature and extent of this plasticity changes from one level of the visual hierarchy to the next (Kohn & Movshon, 2004). Moreover, adaptive changes observed at a given level are not entirely independent of those occurring at preceding levels. The duration of adapting and test stimulation is also important. Brief and prolonged stimulation may affect differently the transient and the sustained components of the response. Also, there is evidence that the effects of adaptation are cumulative, regardless of whether stimulation is continuous or intermittent, as long as net duration remains the same (Henrich, Schilling & Bach, 2005). Finally, the altered response of cells that were directly adapted may affect the responses of remote cells to which the target cells are connected (Krekelberg, Boynton & Wezel, 2006c).

It has been shown that in primary motion sensitive areas of mammals, responses to preferred stimuli are reduced after adaptation with preferred, but not opposite ("null") or orthogonal stimuli (Barlow & Hill, 1963; Giaschi et al., 1993). These and other findings established that in the primary visual cortex the strongest response reduction is obtained for adapting and test stimuli that, normally, elicit the maximum response from the cell. In other words, the more a neuron fires, the more it is being desensitized, or fatigued. A sub-optimal adapter, however, presented on the flank of the tuning curve would cause a local reduction in responsiveness and may produce a *repulsive shift* in the cell's preference (i.e. away from the adapter). Such repulsive shifts have been described in V1 neurons tuned for spatial frequency (Saul & Cynader, 1989a), temporal frequency (Saul & Cynader, 1989b), and orientation (Dragoi, Sharma & Sur, 2000). At this level, however, shifts in neuronal preference are relatively uncommon, compared to the consistent response reduction to an unchanging optimal stimulus. Motion adaptation effects in primate MT neurons, however, seem to be very different from those observed in V1.

First, in MT, but not in V1, adaptation to motion in the null (anti-preferred) direction can strongly enhance the subsequent response of the cell to the preferred direction (Petersen et al., 1985; Krekelberg et al., 2006c). This has been attributed to the prominent motion opponency in MT, where neurons tuned to opposite directions of motion are known to inhibit each other (Snowden et al., 1991). In such a network, adaptation of one neuron can reduce the inhibitory input to other neurons and thereby increase their response. Physiologists refer to this secondary adaptation effect as *disinhibition.* The likelihood of disinhibition following adaptation depends on stimulus context and on the property of the activated network. Increased response, following adaptation is more likely to occur with compound stimuli, containing opponent or different directions of motion (Krekelberg et al., 2006c). The effects of adaptation in the null direction of motion have been rarely examined, but they appear to be more important than previously believed, especially in extrastriate cortex.

Second, MT neuronal responses to motion are *least* affected after adaptation to the preferred direction of motion, and are attenuated the *most*, following adaptation to nearby directions of motion, "missing" the preference of the cell (Kohn & Movshon, 2004). As a result, after adaptation to near-preferred directions, direction tuning becomes significantly narrower. In addition, by contrast with V1, adaptation on the flank of the tuning curve causes an *attractive lateral shift* in tuning, towards the adapted direction. Similar post-adaptive narrowing of the tuning curve has been reported in the responses of MT neurons to speed. Speed-tuning changes, however, are less pronounced than changes in directional tuning, and lateral shifts in the speed preference of MT neurons have not yet been found (Krekelberg et al., 2006a). To our knowledge, adaptation effects in MST-d neurons have not been examined. One study, however, reports response reduction and altered direction selectivity in the posteromedial lateral suprasylvian area (PMLS) of the cat, following prolonged exposure to optic flow (Xu, Li, Li & Diao, 2001). Also, these effects were direction-specific for radiation/rotation, but independent of the direction of the test stimulus for translation (Xu et al., 2001). Taken together, these recent findings suggest that neuronal plasticity induced by adaptation to motion is more profound and multifaceted in extra-striate areas of the cortex, than in V1. In these higher motion-sensitive areas, one important consequence of prolonged motion exposure is the narrowing of neuronal sensitivity around the adapted direction and (possibly) speed.

1.6.2. Functional Aspects of Neuronal Adaptation

Several authors have attempted to link adaptation-induced shifts in neuronal tuning to repulsive phenomena in the perception of orientation (TAE, Clifford, 2002) and direction-of-motion (DAE, Kohn & Movshon, 2004). These links, however, remain tentative, at the moment. First, it is unclear whether neurons retain their pre-adapted perceptual labels after shifting their preference, or change their labels accordingly. Third, perceptual after-effects are mediated by the altered responses of populations of cells, and how adaptive changes in individual cells might transfer to the grouped response is unknown. Finally, the nature and prevalence of these tuning changes across motion processing levels has not yet been fully examined. The functional significance of repulsive and attractive shifts in neuronal tuning is not clear either, but several interesting hypotheses have been advanced.

The main suggestion has been that adaptive changes in neuronal tuning improve the efficiency of signal encoding and transmission. This can be accomplished by reducing the influence of redundant signals and/or noise (Wainwright, 1999). One way to reduce redundancy is to de-correlate neuronal responses to a repetitive stimulus from those of cells tuned to different stimulus levels (Barlow, 1990). De-correlation may be achieved by suppressing the response to the prevailing signal, by repelling the preference of the activated neurons away from it, or by narrowing of their tuning. Hence, following adaptation, there will be fewer neurons responding to the persistent stimulus, and their responses will be much weaker, leading to significant metabolic savings. As a result, responses to novel stimuli will be relatively enhanced (Sharpee, Sugihara, Kurgansky, Rebrik, Stryker & Miller, 2006).

These ideas find support in recent motion adaptation studies in flying insects, using stimuli recreating the environment in which these animals live. Heithwerth, Kern, van Hateren and Egelhaaf (2005) reconstructed optic flow perceived by a blowfly in free flight and examined the response of the H1 neuron with prolonged exposure to this behaviorally generated stimulus. Detailed analysis of changes in the H1 spike pattern revealed that, as the number of spikes drops during adaptation, the information per spike increases. As a result, the total amount of information conveyed remains constant despite the reduced overall activity of the cell. These results suggest that adaptation does not interfere with the reliable encoding of behaviorally relevant signals but increases the efficiency of this process. In another study, researchers habituated a pair of visual interneurons in the locust, by repeated presentation of looming stimuli, resembling other locusts or birds on a direct collision course (Gray, 2005). Interestingly, strongly habituated cells remained responsive to the same object approaching along a new trajectory, or to a new larger object, approaching along the same trajectory. These results suggest that if adaptation is limited to localized synapses, sensitivity to multiple and novel objects in the animal's environment is maintained (or enhanced).

Another potential benefit from changes in neuronal response tuning is that it may re-center the cell's operating range over the most recently encountered range of stimulus values. As the adapting stimulus maps onto the steepest part of the re-centered response curve, discrimination of nearby values improves. In this manner, the cell becomes more sensitive to subtle variation in the stimulus level to which it has been recently exposed. The clearest example is light adaptation in the retina (Shapley & Enroth Cugel, 1984). Retinal ganglion cells shift their luminance sensitivity (i.e. luminance response function) to match the prevailing range of light intensities. This adaptive mechanism allows humans to discriminate small changes in luminance, under very different lighting conditions. Cortical neurons (V1), shift their contrast response function in a remarkably similar manner, largely inheriting these adjustments from retinal and sub-cortical (LGN) levels (Solomon et al., 2004). Again, adaptation re-centers the sensitivity function over the prevailing contrast range.

A common feature of all these proposals is that adaptation takes into account regularities in the environment in order to improve sensitivity to novel stimuli, or to changes in the ongoing stimulation. Hence, prolonged exposure is expected to enhance the detection and discrimination of various visual attributes, similar to the known benefits of light adaptation.

The overall psychophysical evidence for post-adaptive enhancement in visual performance, however, is relatively weak. Whereas improvements in the discrimination of contrast, orientation and direction of motion have been found, following adaptation, these effects are variable across studies or small (Abbonizio, Langley & Clifford, 2002; Clifford, 2002; Kohn, 2007). This is largely because adaptation effects, as revealed in perception, do not depend exclusively on the feature of interest, but are contingent on the stimulus context in which this feature occurs. They are also heavily influenced by the degree of similarity between adapter and test.

1.6.3. Adaptation Facilitates Speed Discrimination

Despite the above reservations, a number of studies report that sensitivity to speed differences around the adapted speed improves with prolonged exposure to motion. Led by motion adaptation experiments in insect vision (Maddess & Laughlin, 1985), Clifford (1976), and Clifford and Langley (1996) measured human sensitivity to velocity changes in a maintained sinusoidal grating as a function of adaptation duration. Using a yes-no detection task, it was found that after only a few seconds of adaptation, subjects were able to detect speed oscillations that they were unable to detect at the beginning of adaptation. This result was replicated by Bex et al. (1999a), showing that detection thresholds for speed increments and decrements decrease exponentially as adaptation progresses and increase back to pre-adapted levels after removal of the adapter. Facilitation of speed discrimination with prolonged viewing was also reported by Kristjánsson (2000), but only for luminance defined (first-order), and not for contrast defined (second-order) motion. It was suggested that the enhancement in speed sensitivity is mediated by luminance based motion mechanisms capable of sensing velocity and does not extend to second-order speed estimates based, presumably, on feature tracking.

Magnitude of the Effect

Most published results do not report standard measures of sensitivity such as just-noticeable-differences or Weber fractions based on stimulus speed. Although it is hard to estimate the magnitude of the speed discrimination enhancement from detection probabilities, a closer look across studies reveals an overall threshold reduction of 20% or less, with considerable measurement error (Clifford, 2002). This estimate also includes the unknown contribution of contrast adaptation, which has been rarely taken into account (Bex et al.,1999a).

Spatial Extent

As mentioned earlier, human sensitivity to velocity differences in contiguous motion is relatively poor (e.g. Snowden & Braddick, 1991), compared to that for stimuli separated in space or time (McKee, 1981). Hence, the consolidation of the velocity signal over time may facilitate the detection of speed fluctuations with prolonged exposure to the same ongoing motion (Nakayama, 1985). The post-adaptive speed discrimination enhancement, however, has been documented in spatial speed-matching tasks as well, regardless of whether only one or both of the motions compared have been adapted (Clifford, 1996; Clifford & Wenderoth, 1999; Krekelberg et al., 2006a). In these paradigms, baseline speed discrimination thresholds are low to start with but further improvement still occurs. The fact that facilitation can stride across adapted as well as un-adapted locations raises questions about its spatial extent. Future research needs to determine whether local adaptation at a particular speed would still facilitate speed comparisons, if both test stimuli are presented outside of the adapted region. The spatial scale of this facilitation effect would also indicate the level at which this may be taking place. This issue awaits investigation.

Motion Specificity

Although most studies attribute this facilitation effect to motion-specific adaptation, the extent to which this is true is unclear. So far, measurement of the effect has been limited to test stimuli identical to the adapter, with test speed varying around the adapted level. The motion and direction specificity of the speed discrimination enhancement has been addressed, in part, by only one study (Clifford & Wenderoth, 1999).

Clifford & Wenderoth (1999) used a spatial speed-matching task to determine perceived speed and speed discrimination performance with luminance-defined sinusoidal gratings, presented in small spatial windows (3° in diameter), on both sides of fixation. Measurements were taken before and after one-sided adaptation to motion. After establishing that perceived speed declined and speed discrimination improved for same-speed test motion in the adapted direction, the direction and the nature of the adapting signal was varied (e.g. opposite motion, parallel flicker, parallel static, upwards motion, perpendicular flicker etc.). Results indicated that adaptation to motion in the opposite direction to the test and to counter-phase flicker altered speed perception and speed discrimination performance in the same way, and to the same extent as iso-directional adaptation. Therefore, Clifford and Wenderoth (1999) concluded that these effects are not motion or direction specific but depend on temporal frequency adaptation.

The above conclusion, however, is at odds with results from many studies, showing that adaptation-induced changes in perceived speed are at least partially direction specific, as the iso-directional VAE is always stronger than the counter-directional one (see 1.5.4). It appears that for some reason, the stimuli and procedures used by Clifford and Wenderoth (1999) failed to recruit motion specific mechanisms and produced only general, temporal frequency activation. For example, the alternation of different dynamic adapters within a session may have led to blending of their unique effects. As findings from this study are discrepant from others, the issue of whether the speed discrimination enhancement arises from motion-specific or general, temporal frequency adaptation, remains unresolved.

1.6.4. Linking Improved Speed Discrimination to the VAE

A few studies have documented the speed discrimination enhancement and the reduction in perceived speed concurrently, suggesting that the two phenomena are related (Clifford & Langley, 1996; Clifford & Wenderoth, 1999; Bex et al., 1999a; Krekelberg et al., 2006a). The strongest evidence comes from results indicating that the time-courses of the facilitation effect and the VAE are correlated, during both build-up (Clifford & Langley, 1996; Bex et al., 1999a) and recovery from adaptation to motion (Bex et al., 1999a). Bex et al. (1999a) demonstrated that speed sensitivity can be well described by a Weber fraction based on apparent, rather than physical speed. Hence, as apparent speed declines during adaptation to motion, sensitivity to speed differences increases.

These dual changes in speed perception have been related to functional aspects of the adaptation process, involving tuning changes in individual neurons (see 1.6.1; 1.6.2). Correspondingly, the VAE has been linked to mechanisms minimizing redundant, background activity (e.g. decline in firing rate). On the other hand, the improvement in relative speed sensitivity is believed to reflect optimization of processing for stimuli around the adapted level. It has been suggested, for example, that shifts in the position of the tuning curve, re-centering the operating range of the cell over the prevailing speed could explain both reduction in perceived speed and increased differential sensitivity, following adaptation to motion (Clifford & Ibbotson, 2003). Shifts in neuronal preference, however, do not necessarily align the peak of the tuning curve with the adapted level. Depending on the direction of the shift, and on whether it is repulsive or attractive, perceived speed and speed sensitivity may be variably affected.

Another possibility is that the narrowing of neuronal speed-tuning, regardless of whether it is being shifted or not, enhances signal resolution and facilitates perceptual discrimination. Results from a recent adaptation study in primate MT are consistent with this proposal. Krekelberg et al. (2006a) recorded changes in the speed tuning of MT neurons, and measured speed perception and discrimination of the same stimuli, in the same animals, as well as in humans. Following adaptation to random dot motion, reduction in perceived speed and improved speed discrimination were documented for both humans and monkeys. In parallel with these perceptual changes, adaptation reduced the magnitude of the speed response in individual neurons, as well as the width of their speed tuning. On average, across test speeds, humans underestimated perceived speed by 17% and monkeys – by only 6%. The corresponding average reduction of neuronal firing rate was about 8% but varied with test speed in individual cells – it was most pronounced for test speeds offset from the adapter, suggesting narrowing of the speed response tuning. The average improvement in speed discrimination performance was just 3% in humans, and 6% in monkeys. Although this study makes an important effort to link adaptation in single cells to perceptual changes, the effects reported are subtle and should be regarded with caution. First, the confounding influence of contrast adaptation was not factored out, although in a companion paper, using similar methods, the same authors demonstrate the profound influence of this variable on speed-related responses in MT (Krekelberg et al., 2006b). Second, adaptation was rather brief (2 seconds) and neuronal responses were not measured while the animals were performing the task.

In conclusion, accounts of the facilitation effect are not fully developed. Existing hypotheses are constrained by lack of relevant data, as well as by difficulties relating responses of single cells to perceptual performance. Nevertheless, the evidence that adaptation to motion can improve speed discrimination is consistent, and, therefore, strong.

1.6.5. Summary

This last chapter paints a broader picture of sensory adaptation and draws attention to its possible functions. There is growing awareness that adaptation is an active process of recalibration, rather than a passive build up of neuronal fatigue. Accordingly, cortical neurons shift and sharpen their response tuning, based on the range of recently encountered stimuli. The nature of these neuronal adjustments suggests that the visual system takes advantage of regularities in the environment to optimize its response to stimulus change. A consistent benefit from adaptation to motion has been reported on speed discrimination tasks: as the perception of absolute speed is compromised, sensitivity to speed differences around the adapted value improves. In all published data, however, this performance enhancement is much subtler than the concurrent decline in perceived speed. This is puzzling from a functional standpoint: as information about absolute speed is essential for behavioral timing, the cost of degrading such information seems much higher than the small improvement in sensitivity to relative speed. Further explorations of the link between the VAE and the speed discrimination enhancement may shed light on this apparent paradox.

1.7. The Present Study: Purpose and Outline

The experiments described in this thesis measure changes in perceived speed and speed discrimination concurrently, after adaptation to large-scale radial motion. To our knowledge, this is the first study of radial velocity after-effects. Therefore, it follows closely the methodology of existing research on local VAEs (Thompson 1976; Thompson, 1981), and on adaptation effects in complex motion (Regan & Beverley, 1978; Kelly, 1989; Bex et al, 1999b).

The main goal of this study is to examine the nature of velocity processing at higher levels of the motion hierarchy, sensitive to the directional structure of behaviorally meaningful patterns of image flow. It is of particular interest whether these complex direction-of-motion mechanisms make a distinct contribution to the perception and discrimination of speed. So far, there is little evidence for a functional hierarchy in the representation of speed: the nature and the distribution of speed-related neuronal preferences does not change much between V1 and MT (Priebe et al., 2006). Therefore, if speed mechanisms do evolve at some level, this should occur in motion sensitive cortex beyond area MT (e.g. MSTd).

To target these higher stages of motion analysis effectively, we use large-scale radial motion, containing a natural speed gradient, simulating motion-in-depth through a tunnel. The use of concentric, luminance-defined sinusoidal gratings ensures continuity with relevant research at the local level. Depending on the sign of the temporal modulation, the flow field is perceived to approach (or expand), or to retreat (or contract). In addition to its relevance to behavior, this particular stimulus was chosen for several reasons. First, sensitivity to radial motion dominates neuronal preferences in MST-d and in adjacent sensory cortex. Hence, exposure to such motion is expected to produce a robust response at this level. Second, the stimulus matches the receptive fields' extent of MST-d neurons, as well as their selectivity to positive speed gradients in the flow. These factors also optimize psychophysical sensitivity to radial flow. Third, radial motion is perceived as faster than comparable rotation and translation, suggesting that the mechanisms selective to this type of motion may process image speed differently (Geesaman & Qian, 1998). On the other hand, speed discrimination performance seems to be independent of motion pattern, implying that no such difference exists (Sekuler, 1992; Clifford et al., 1999).

The present study uses the VAE as a tool to explore whether radial motion sensors make a significant and unique contribution to global judgments of visual velocity. It has been shown that the VAE depends on adapting velocity, rather than on temporal frequency, spatial frequency or speed (Thompson, 1976; 1981). Thus the VAE is well suited to characterize the neural response to velocity at any processing level, regardless of whether this response is based on separable spatial-temporal frequency mechanisms, on direct velocity measurements, or on both.

The tuning of the VAE has been characterized in detail for spatially localized sine-wave gratings, with tests moving at different speeds, in the adapted and opposite to the adapted direction. The present work examines the *tuning of the radial VAE* in the same manner, at a single adapting velocity, with the radial motion stimulus described above. Speed discrimination performance is recorded simultaneously and is expected to improve, following adaptation. If the VAE and the speed discrimination enhancement have a common origin, their dependence on test speed (i.e. tuning) should be correlated, as it has been shown for their temporal course (Clifford & Langley, 1996; Bex et al., 1999a).

At the local level, the iso-directional VAE shows distinct asymmetrical tuning, consistent with adaptation of two broad temporal frequency mechanisms, identified in primary visual cortex (Thompson, 1982; Smith & Edgar, 1994; Hammett et al., 2005). If velocity is represented differently at and beyond the level of MST-d, adaptation to stimuli preferentially processed at this level is expected to produce VAEs with different tuning characteristics. One can only speculate about how exactly the VAE tuning might change, because the nature of the underlying mechanisms is unclear. It is conceivable for example, that at this level the encoding of temporal signals becomes more precise and is mediated by a larger number of narrow band-pass mechanisms. If this is the case, the VAE tuning should become more symmetrical (i.e. minimal perceptual shifts at the adapted velocity, and larger repulsive shifts of comparable magnitude for test speeds different from the adapter).

The *direction specificity* of the radial VAE is also of interest. At the local level, the extent to which the VAE transfers to tests moving opposite to the adapted direction is variable, indicating partial or no direction specificity. These findings have not received much attention. They do indicate, however, that non-directional temporal frequency mechanisms contribute substantially to the local effect. The present stimulus is expected to produce stronger activation in extra-striate motion sensitive cortex than the local gratings used to study the VAE in the past. Whereas most neurons in areas MT and MST are strongly direction selective, the proportion of such motion sensors in V1 is smaller. The direction selectivity of MT neurons is further enhanced, following adaptation to motion (Kohn & Movshon, 2007). In this context, the direction specificity of the radial VAEs would indicate to what extent judgments of global velocity rely on temporal frequency signals, and to what extent opponent velocity signals affect one another at these higher motion processing stages.

The issue of *directional asymmetries in the perception of radial motion* is also relevant to our topic. Most studies using luminance-defined gratings similar to ours (e.g. Kelly, 1989), reveal a perceptual bias favoring expanding motion. This has been shown with or without prior adaptation, using direction sensitive measures (e.g. the MAE, detection thresholds). Studies using RDK displays, on the other hand, tend to find evidence for a centripetal bias. It is unclear whether similar biases exist in the perception of speed. In RDK displays contraction is judged as slightly faster than expansion (Geesaman & Qian, 1998), but an opposite bias has also been found (Clifford et al., 1999). In this study we re-examine this issue by comparing the VAEs produced by expanding and contracting flow.

To isolate adaptation effects occurring at or above the level of MST-d from those at preceding levels, we manipulate only the global directional coherence of the flow, without altering any other aspects of the stimulus. This manipulation, as well as the measurement of the VAE itself, requires partitioning of the flow field. The present stimulus is split in four large non-abutting sectors, arranged in a symmetrical "X". Flow direction is assigned independently to each sector, forming three global patterns of flow - "scrambled", expanding and contracting. In the expanding flow, outward motion is assigned to all sectors. In the contracting flow, all sectors contain inward motion. The scrambled flow contains equal amounts of expansion and contraction, with half of the sectors expanding and the other half - undergoing contraction. While all three flow patterns are expected to activate all motion processing levels, extra-striate cortex beyond MT will be more strongly engaged by the coherent patterns of flow, than by the scrambled one. To separate these effects, VAE is assessed following adaptation to each one of the three types of flow. The effects obtained in the scrambled condition are used as a baseline.

A similar strategy has isolated successfully other adaptation effects in complex motion (i.e. elevation of motion detection thresholds - Regan & Beverley, 1978; and the MAE - Bex et al., 1998). Complex motion aftereffects are known to be stronger than those produced by translational motion. Accordingly, neurons in extra-striate motion regions show a higher degree of adaptive plasticity in comparison to V1. Therefore, it is expected that adaptation to coherent flow in the present study will produce larger VAEs than adaptation to scrambled flow.

The VAE is measured in a series of related experiments by means of spatial speed-matching. After adaptation to a particular flow in two juxtaposed display sectors, observers compare motion speed in the adapted sectors to that in the other two, non-adapted sectors. The same measurements are also taken without prior adaptation. The tuning of the VAE is assessed by comparing pre-adaptation to post-adaptation speed matches, for test motions in the adapted direction and opposite to it, across a range of test speeds.

Experment 1 examines the tuning of the VAE following adaptation to scrambled flow, against non-adapted flow of the same type (i.e. scrambled). Experiment 2 measures the same effects, following adaptation to coherently expanding or contracting flow. Again, the speed comparison is between adapted and the non-adapted flow patterns of the same type (i.e. both are contracting, or both are expanding).

Experiment 3 controls for possible "phantom" adaptation, which may alter perceived speed in non-adapted display regions, confounding the measurement of the VAE. To ensure that the comparison flow remains unaffected by remote adaptation it is presented in the non-adapted direction. In this experiment, the effects of adaptation to coherent flow (expansion or contraction) are re-evaluated against a comparison stimulus of the opposite sign. In other words, the adapted speed of expansion is matched to that of non-adapted contraction and, conversely, adapted contraction is judged against non-adapted expansion.

In Experiment 4 the stimulus reverses its direction throughout adaptation, in order to optimize extra-striate activity specific to radial flow (Morrone et al., 2000). The total amount of exposure to each flow direction is the same as in the other experiments, while adaptation duration is doubled, accordingly. In this experiment, observers adapt to inverting scrambled or coherent flow and the recorded tuning of the VAE is compared to that obtained with continuous adaptation in Experiments 1 and 2.

All experiments have the same design. Their specifics are described in the sections to follow. Some aspects of the present results were communicated in an abstract form (Iordanova-Maximov & von Grünau, 2005).

2. GENERAL METHOD

2.1. Apparatus and Materials

All aspects of stimulus generation, experimental design and data collection were controlled by a Power Macintosh G4 computer (Apple OS 9.2), equipped with the VPixx software for visual psychophysics (version 2.01, VPixx Technologies Inc., www.vpixx.com). Visual stimuli were projected on a Cineperm light-gray translucent screen by means of a Proxima 6800 liquid crystal desktop projector connected to the computer. A Minolta Luminance Meter LS-100 was used for luminance measurements and calibration.

A rear projection setup was used in all experiments (see Figure 3). Experiments took place in full darkness, with the projector being the only source of light. Viewing was binocular, from behind the screen, through a circular aperture. Two side panels were attached to the edges of the aperture in order to block irrelevant context. On the screen, the visible stimulus covered a circular area with a radius $\boldsymbol{r}$ of 60 cm. Viewing distance $\boldsymbol{d}$ was 70 cm. Spatial resolution of the projector was 1024 pixels horizontally and 768 pixels vertically, with a frame refresh rate of 75 Hz. The observer's line of sight was perpendicular to the screen. Gaze was straight ahead, focused on the display's geometrical center (marked by a fixation dot). The retinal image of the stimulus had a radial extent of 40.1° in degrees of visual angle, as determined from $\tan \alpha = r / d$ (e.g. Kaiser, 2007). To maintain constant viewing distance and angle, head position was fixed with a head-and-chin rest (not shown in Figure 3). To allow response entry, the computer keyboard was placed next to the chin rest, under the observer's dominant hand (not shown in Figure 3).

A common concern with rear projected stimuli is that the observer looks directly at the light source. As a result, the area around fixation appears brighter than the rest of the display. Such spatial non-uniformity, however, is of little concern in this study. The flow fields were concentric and symmetrically placed around fixation and no stimulus was presented within a 5° radius from the center of the display. Nevertheless, care was taken to reduce the initial visibility of the "hot spot": i) the brightness setting of the projector was set to its minimum and ii) brightness was further reduced by a neutral density filter placed in front of the projector's lens. All displays in this study had the same average luminance of 0.5 cd/m^2.

2.2. Stimuli

2.2.1. Spatial Waveform

The generic stimulus is a circularly symmetric, spatially non-uniform pattern, centered at fixation. It consists of luminance defined concentric sine waves, scaled with eccentricity to represent a perspective view through a tunnel. Spatial frequency varies inversely with the squared distance from the center of this concentric stimulus, as illustrated in Figure 4. With one exception (see 5.3.1, Experiment 3), the same spatial frequency gradient was used for all stimuli throughout this study. The simulated tunnel is straight and cylindrical, of a constant diameter, with a vertical periodic sine-grating "painted" on its walls. Figures 6 and 7 represent snapshots of the spatial waveform, as it appears in the actual displays.

2.2.2. Local Velocity

Temporal modulation of the above pattern sets it in motion. Depending on the sign of the temporal modulation, the concentric waveform appears to drift either outwards or inwards, with respect to the stimulus center. At any point in the stimulus, average local speed is a function of temporal and spatial frequency, as follows:

(1) Speed = Temporal Frequency / Spatial Frequency
(deg/sec) = (cycles/sec, or Hz) / (cycles/deg)

Since spatial frequency decreases with eccentricity (denominator), local speed increases accordingly. This creates an exponential gradient of local speeds in the stimulus at each rate of temporal modulation (see Figure 5).

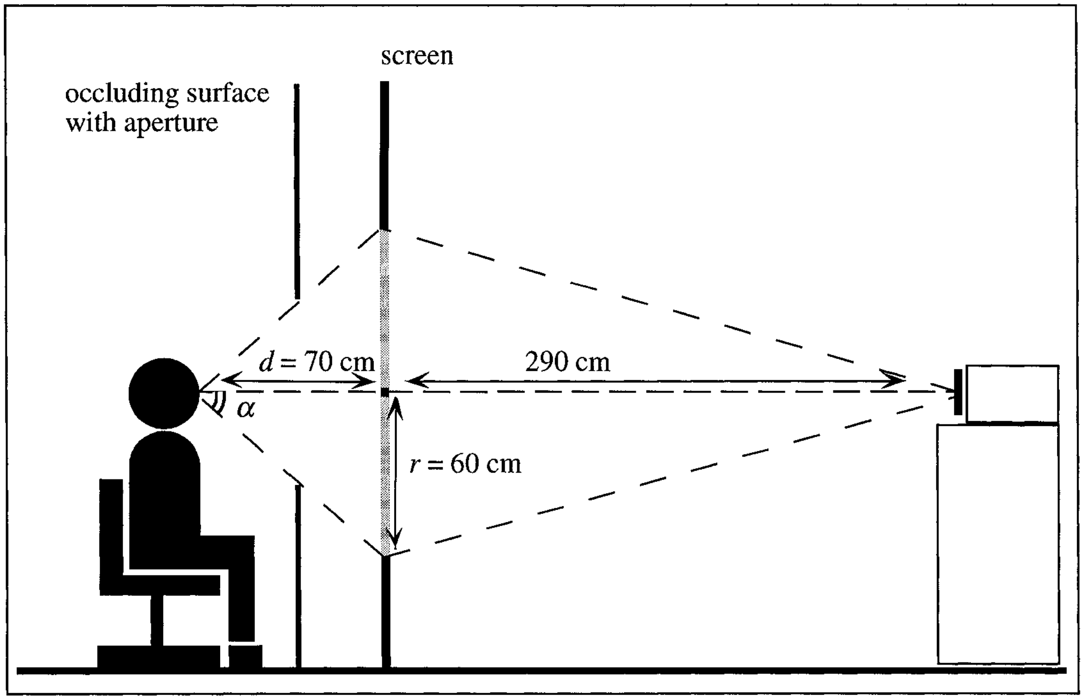


Figure 3. Rear projection set-up used for all experiments.

Stimuli were displayed within the visible area of the screen (shaded in gray). See text for details.

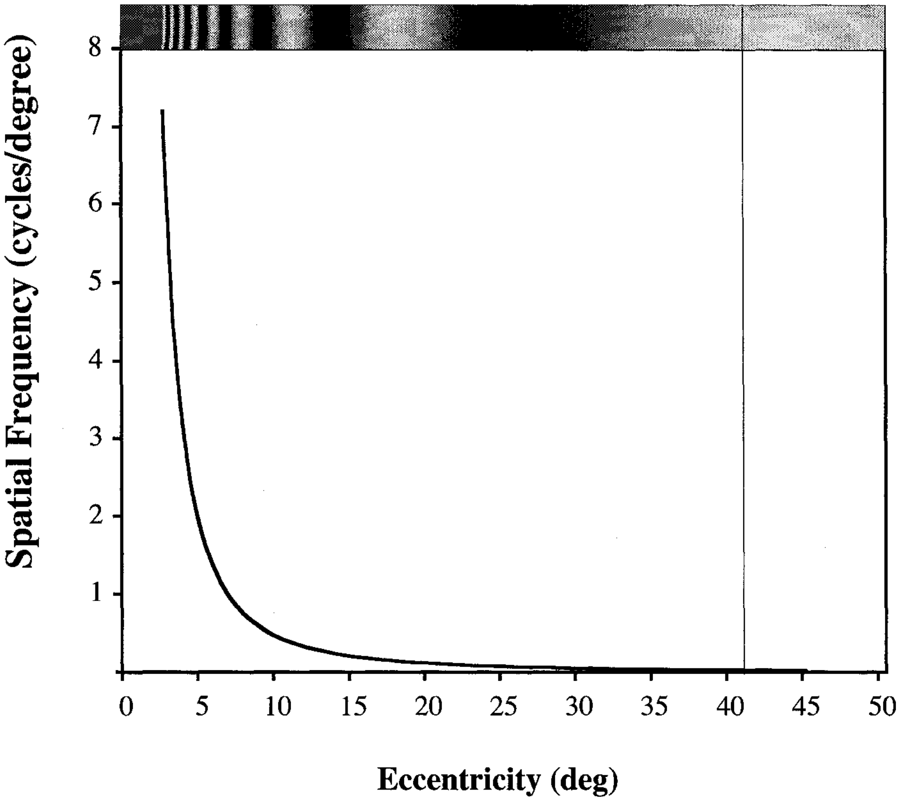


Figure 4. The spatial gradient of the flow-field.

Spatial frequency decreases with the square of eccentricity, as illustrated by a slice through the waveform (top inset). The vertical line marks the peripheral limit of the stimulus.

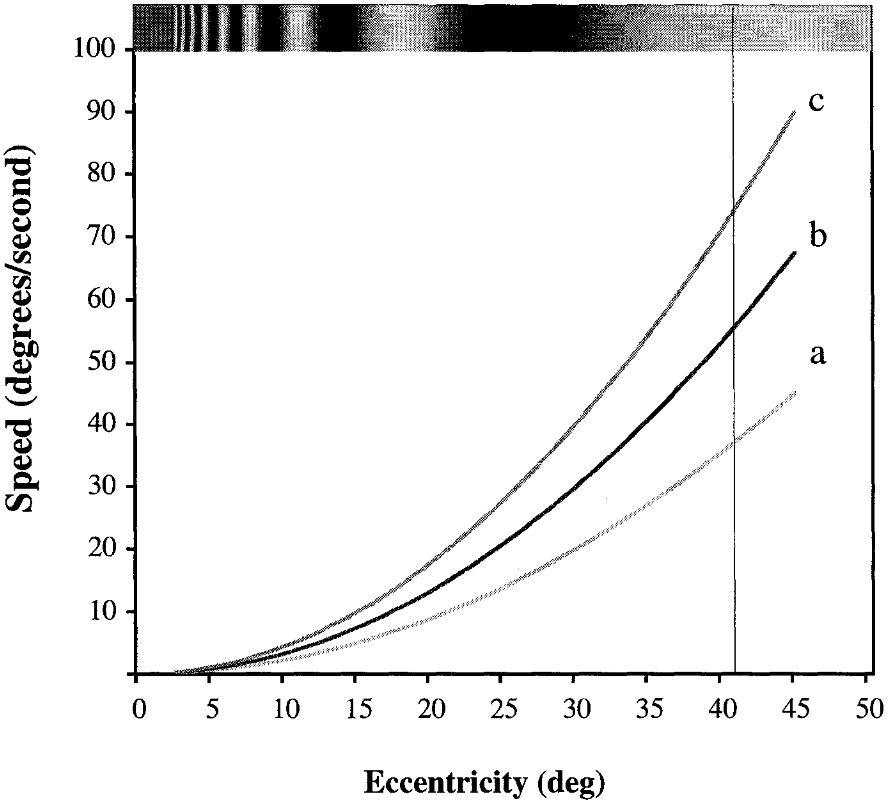


Figure 5. Local speed as a function of eccentricity.

The three curves depict the speed gradients produced at each one of the three temporal frequencies used in this study (a) 1.0 Hz, (b) 1.5 Hz and (c) 2.0 Hz. The vertical line marks the peripheral limit of the stimulus.

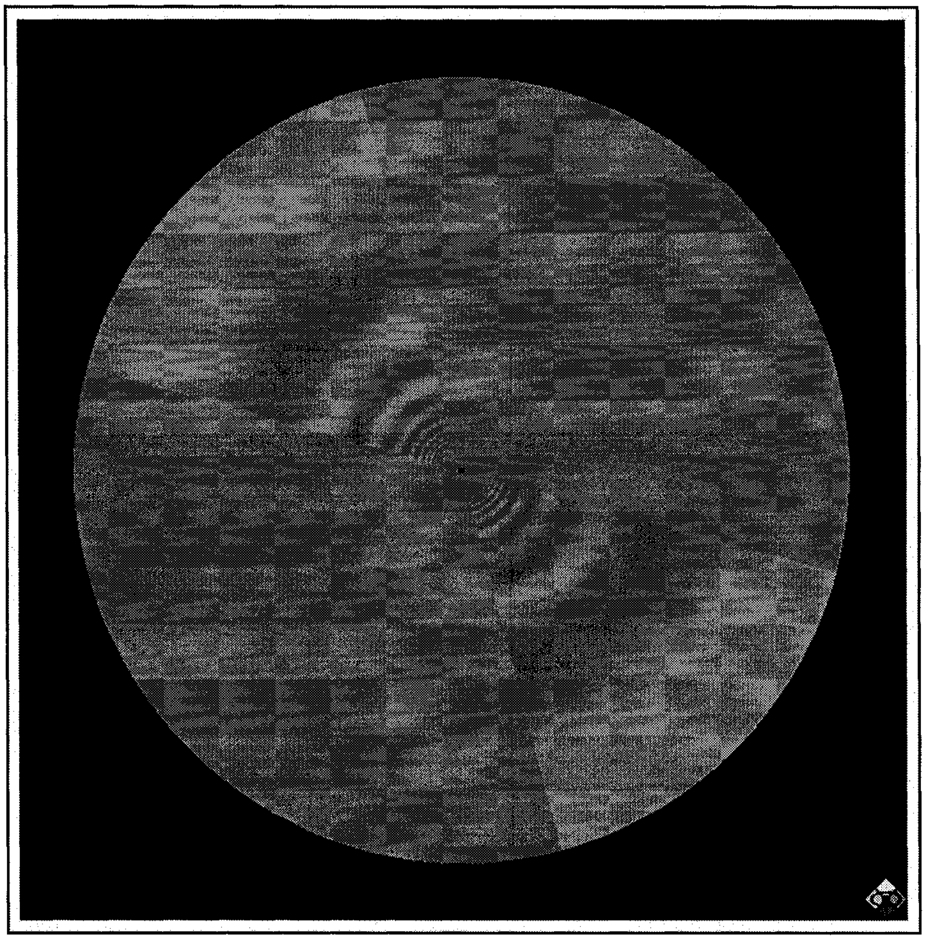


Figure 6. A single frame of the adaptation display.

The concentric waveform is confined to a pair of sectors cut from an annulus region. The inner and the outer radii of the annulus subtend 2.5° and 40.1°, respectively, in degrees of visual angle. Michelson contrast is 11% and temporal modulation frequency is 1.5Hz for all adaptation conditions.

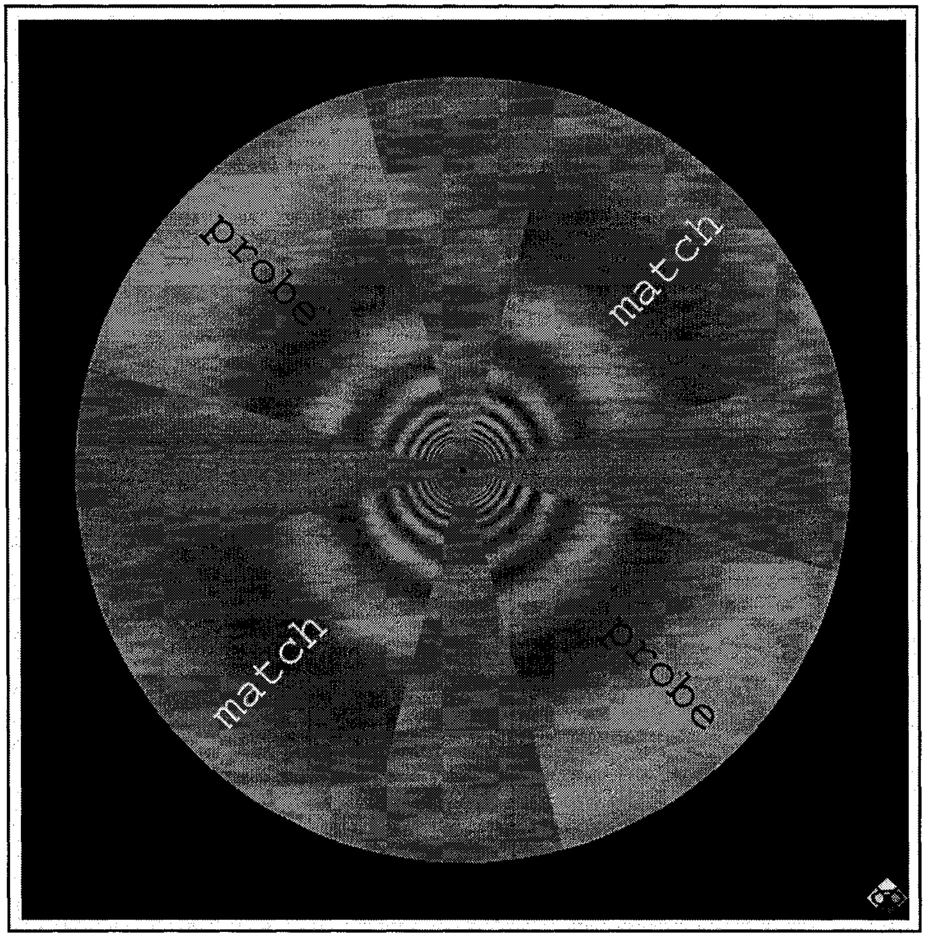


Figure 7. A single frame of the test display.

Observers compared flow speed in the two probe sectors to that in the two match sectors. Text labels are added for illustration purposes only and are not part of the actual stimulus. Michelson contrast in all sectors is 33%. Spatial extent is as described in Figure 4.

2.2.3. Global Velocity

The gradient of local speeds is not apparent unless one scans the display deliberately. Instead, with steady fixation at the geometrical center, one perceives global motion at a single velocity.

In principle, the speed of this global motion can be derived from the local speed of any display element at a given distance from the focus of motion, if viewing distance and the actual radius of the tunnel are known (Peter April, personal communication). The latter parameter, however, is unconstrained: the same flow pattern can be produced by a large number of tunnels of different widths and spatial periods of the wall grating.

Another way to characterize this global speed is to average all local speeds across the stimulus spatial extent. For example, doubling temporal frequency will double local speed, at any point in the stimulus, increasing the space-averaged speed by the same proportion (see Figure 5). Whether this manipulation will double the perceived magnitude of the global speed is an empirical question, not addressed by the present study.

The experimental paradigm in this work relies on relative rather than absolute speed judgements which allows us to bypass the above measurement issues. It is important to emphasize that i) the generic stimulus produces a unitary percept of global velocity, and, ii) the perceived magnitude of this global velocity is proportional to the rate of temporal modulation, although the precise scaling relationship remains unknown.

2.2.4. Motion-In-Depth

The global motion of this radial stimulus is readily interpreted as motion-in-depth (MID) along the observer's line of sight. This corresponds to the physical situation of moving along the center of this tunnel, at a constant speed. As the observer moves along the tunnel it is the wall texture that causes the retinal flow. The same retinal flow, however, can be produced in a motionless observer, positioned in the center of the tunnel, if the tunnel undergoes linear motion along the observer's line of sight. Thus the present stimulus may create the impression of forward or backward linear self-motion (i.e. vection) *or* of looming object motion (i.e. tunnel's approach or retreat). During debriefing, all observers reported that: i) they experienced the flow as MID which they attributed to the scene looming, rather than to their own displacement relative to the scene; and, ii) the vividness /strength of the MID impression lessened with prolonged viewing of continuous, uni-directional flow. Thus the impression of large-scale object displacement in depth dominated perception, whereas vection was weak.

2.2.5. Displays

For the purposes of this study, a segmented version of this generic flow-field was used. Display partitioning was necessary in order to compare perceived speed in adapted to non-adapted regions and to change the global organization of motion, without changing the spatial layout or local speed distributions in any way. The size and the arrangement of display sectors aimed to preserve as much as possible the direction bandwidth and the opposition of motion vectors characteristic of the full-field radial flow.

Three types of stimulus configurations were used: i) baseline adaptation display; ii) motion adaptation display; and iii) test motion display.

Baseline Adaptation Display

In the baseline adaptation display, the entire stimulus area was set to a uniform gray level (except for the presence of a central fixation mark). The uniform gray background had the same average luminance as all motion displays. There was no motion stimulation.

Motion Adaptation Display

The motion adaptation display consisted of a pair of diagonally placed; juxtaposed 60^{o} sectors of the generic stimulus, presented against the gray background described above (see Figure 6). Motion direction in each of the two sectors was set independently, according to experimental condition (centrifugal/centripetal/scrambled). A temporal frequency of 1.5 Hz was applied to stimuli in both sectors, in all adaptation displays. Spatial phase at motion onset was the same for both sectors, and was kept constant throughout.

Test Display

The test display consisted of two pairs of sectors, with four sectors, in total, separated by 30° gaps, forming a symmetrical cross-like configuration (see Figure 7). One pair replaced the adaptation stimulus and contained the probe stimulus. The other pair contained the matching stimulus and was orthogonal to the probe. Probe and match regions were spatially interleaved but non-overlapping.

Observers were asked to compare the perceived speed of the probe flow to that of the match flow. A cross-diagonal layout was chosen to minimize the influence of known lateral visual field asymmetries in visual speed perception (Smith & Hammond, 1986) and the sensitivity advantage for motion along the cardinal axes (Gros, Blake & Harris, 1998, Giaschi et al., 2007). Furthermore, to counterbalance such anisotropic influences, half of the data were collected after inversion of the projected image along the vertical axis. In these mirror displays, the relative orientation and position of all sectors was swapped (e.g., left oblique became right oblique and probe and match stimuli reversed places).

A given temporal frequency (i.e. speed) was applied jointly to both segments within a pair. In any given block of trials, the temporal frequency of the probe motion was fixed at one of three reference values - 1Hz, 1.5Hz or 2Hz. Match temporal frequency varied around the reference point (see section 3.2.3 - Test Phase, Experiment 1). Motion direction was manipulated independently within individual sectors to form coherent or incoherent global patterns of flow. The starting phase of the probe and match flow was randomized to ensure that the speed comparison is not based on positional cues.

Test stimuli had a higher Michelson contrast (0.33), than the adaptation stimulus (0.11). This is known to counteract the loss of apparent contrast with prolonged exposure to motion and the changes in perceived speed associated with it (Thompson, 1981, 1982; Hammett et al., 2000). Thus the speed estimates obtained in this study are affected by motion adaptation alone, and are not confounded by concomitant contrast adaptation.

3. EXPERIMENT 1

3.1. Rationale and Hypotheses

This first experiment assessed the nature of the VAE elicited by the type of stimuli used in this study, with minimal engagement of extra-striate motion mechanisms, selective to large-scale radial flow. Changes in perceived speed and speed discrimination performance were recorded following continuous adaptation to a compound motion pattern with a scrambled global direction of flow. Testing was done against a scrambled matching stimulus, as well. The scrambled flow contained equal amounts of expansion and contraction distributed across sectors. The resulting MID was incongruent as well, with some parts of the display perceived as approaching, while others - as receding in depth. The overall impression was of "warped" motion flow, inconsistent with any self-motion or object-motion situation.

To facilitate comparisons with existing research, Experiment 1 follows closely the experimental protocols implemented by Thompson (1981) and Bex et al. (1999a, 1999b). The present flow-fields, however, differ in many ways from the localized gratings used in these studies (e.g., spatial scale and layout, range of motion directions, spatio-temporal gradients). Therefore, prior to addressing any other questions, it is important to evaluate the net effect of this new stimulus context in light of previous findings.

The scrambled flow-field used in Experiment 1 is expected to activate all motion sensitive levels, leading to, and including human homologues of primate extra-striate areas MT and MST, as well as neighboring parietal cortex. It is expected that this stimulus will elicit an optimal response in motion sensors with receptive fields of limited spatial extent (up to 10°), such as those found prior to and in area MT. Subsets of these motion sensors are expected to attain optimal levels of adaptation, as they will be stimulated in their preferred direction-of-motion. By contrast, the large-scale complex motion sensors such as those found in areas MST-d and beyond, are not expected to respond to the scrambled flow in an optimal manner. A typical expansion sensitive cell, for example, will receive inconsistent input in its receptive field covering large portions of the visual field, including the visual midline. As centripetal motion will be imaged in one part of this receptive field *and* centrifugal motion - in another, the hypothetical expansion sensitive cell will be stimulated in its preferred and non-preferred radial direction-of-motion at the same time. Hence, its response to the scrambled flow is expected to be inconsistent and weak. Rotation and translation sensors are unlikely to respond strongly to the scrambled flow either, because its directional structure is incongruous with the preferences of these cells. Thus while the scrambled flow in the present experiment is expected to elicit strong responses in motion sensitive areas prior to MST-d, it is expected to produce only weak or general activation at the level of MST-d and beyond.

If, as expected, the scrambled flow does not fully engage global radial-motion analyzers at higher levels in the motion processing hierarchy, the contribution of these levels to any measurable perceptual aftereffects would be minimal. Therefore, Experiment 1 is expected to produce VAEs similar to those described at the local level. Thus we hypothesize that adaptation to the present scrambled flow will generate VAEs with the following general characteristics, as reviewed in the Introduction and summarized by Thompson (1998) and Bex et al. (1999a):

1. Observers will *underestimate* the perceived speed of the scrambled flow, after adaptation to motion *in the same direction* (iso-directional adaptation). The magnitude of this negative VAE is expected to lessen progressively as test speed approaches and exceeds the adapted value. If any speed *overestimation* occurs (positive VAE), it will be confined to *probes moving faster* than the adapting motion.

2. Observers will also *underestimate* the perceived speed of the scrambled flow, after adaptation to motion *in the opposite direction* (contra-directional adaptation), but this VAE is expected to be smaller than the iso-directional one. This negative counter-directional VAE is expected to show little if any systematic dependence on test speed.

In addition to changes in perceived speed, Experiment 1 also quantifies speed-discrimination performance. Although the present speed-matching task is not designed to measure speed discrimination thresholds, it provides an index of speed discrimination ability (see Dependent Measures, below). Very few studies have measured changes in differential speed sensitivity and speed perception concurrently, in the context of the same paradigm. Such measurements are important in understanding whether perception of absolute and relative speed involves the same or different neural mechanisms - an issue which is currently under debate (Clifford et al., 2000). Although both processes must rely on the same speed estimates, they respond differently to changes in the directional structure and the spatial configuration of motion. Whereas speed perception appears to be sensitive to the global pattern of motion (Geesaman & Qian, 1996; Bex & Makous, 1997), speed discrimination is not (Sekuler, 1992; Clifford et al., 1999). Conversely, while speed discrimination thresholds are strongly affected by the spatial parsing of the motion display in discrete objects (e.g. Verghese & McKee, 2006), speed perception seems resistant to such manipulations (Clifford et al., 2000). On the other hand, adaptation to motion affects both absolute and relative judgments of speed and there is a strong correlation between the temporal courses of these two effects (Bex et al., 1999a). Several studies have found that as apparent speed declines with adaptation to motion, sensitivity to speed differences around the adapted value is increased in proportion to the loss in perceived speed (e.g. Clifford & Langley, 1996; Clifford & Wenderoth, 1999; Bex et al, 1999a, Huk et al., 2001). Based on these findings, a similar facilitation effect is expected in Experiment 1. Hence, we hypothesize that:

3. The loss of apparent speed following adaptation will be associated with *improved sensitivity* to speed differences on the speed-matching task and the magnitudes of these two effects will be correlated, as a function of reference speed.

In Experiment 1 the measurement of perceived speed and speed sensitivity is described in detail as it applies to all experiments in this study.

3.2. Method

3.2.1. Subjects

Six subjects (including the author), ages between 22 and 42 years, took part in all conditions of Experiment 1. All subjects had normal or corrected to normal visual acuity and no history of visual disorders. Except the author, all subjects were naïve with regard to the purpose and design of the present experiments. Three subjects were trained psychophysical observers, while the other three had no such experience. They all followed the same task-specific training protocol, prior to data collection. Observers not employed by this laboratory were paid for their time and effort.

3.2.2. Stimuli

The spatial characteristics of the baseline, adaptation and test stimuli were described in the previous section (see General Method, Figures 6 & 7). In Experiment 1, the global radial flow in all pairs of sectors was "scrambled" by assigning opposite flow directions to the two sectors within a pair. This manipulation was applied to all adaptation and test stimuli, as illustrated in Figures 8, 9 and 10. For example, the adaptation stimulus in Figure 9 contains inward motion in the lower right sector and outward motion in the upper left sector. Similarly, the test stimulus used for comparison contains outward motion in the lower left sector and inward motion in the upper right (e.g. Figure 9, test t1-a, white arrows). Thus both adaptation and test stimuli yield the impression of an impossible, "warped" motion flow.

3.2.3. Procedure

Trial Sequence

All trials had identical temporal structure, as illustrated in Figures 8-10. Each trial consisted of an adaptation phase, followed immediately by a test phase. A beep sound at the end of the adaptation phase alerted the subject that the test phase had begun and a response is expected. Subjects were instructed and trained to keep their gaze fixed on a central dot throughout the entire sequence of events in a trial.

(1) Adaptation Phase

Adaptation lasted for 2 minutes on the first trial of a session, and was then “topped-up” on each subsequent trial by an additional adaptation period of 5 seconds. A topping-up adaptation procedure was adopted to prevent the decay of VAE over time (Thompson, 1981). Depending on the particular session, during the adaptation phase of each trial, observers viewed an empty background (baseline sessions, Figure 8), or a continuous motion flow of an unchanging direction (motion sessions, Figures 9 and 10). The same adapting stimulus was used for all trials within a session.

(2) Test Phase

Following adaptation, the perceived speed of the scrambled flow was measured by means of *spatial speed matching*. In the test display (Figures 8-10, t-boxes), observers compared the perceived speed of the probe flow presented in the adapted pair of sectors (black arrows) to that of the same type of flow in a non-adapted pair of sectors (white arrows). On each trial, observers performed a two-alternative-forced-choice (2AFC) task, indicating whether probe speed (e.g. left oblique pair) or match speed (e.g. right oblique pair) appeared to be faster. Observers were trained to maintain steady fixation, while making a global speed comparison between the two spatially interleaved but non-overlapping display regions, regardless of the particular combination of motion directions within them. Debriefing revealed that observers adopted this strategy naturally, as it made the task easier to perform.

In this and all subsequent experiments, global radial speed was manipulated by changing temporal frequency, while spatial frequency remained the same. In separate sessions, perceived speed was measured for probes drifting at three reference rates, below (1 Hz), at (1.5 Hz), or above (2 Hz) the adapted value (1.5 Hz), respectively. While probe speed was fixed within a session at a given reference value, the speed of the match flow used for comparison was controlled by the *method of constant stimuli*. Match temporal frequency was randomly chosen on each trial, from a set of seven evenly spaced values, bracketing the temporal frequency of the probe. The comparison drift rates were as follows, with the reference temporal frequency underlined: (0.25 Hz, 0.5 Hz, 0.75 Hz, **1 Hz**, 1.25 Hz, 1.5 Hz, 1.75 Hz); (0.375 Hz, 0.75 Hz, 1.125 Hz, **1.5 Hz**, 1.875 Hz, 2.25 Hz, 2.625 Hz); and (0.5 Hz, 1 Hz, 1. 5 Hz, **2 Hz**, 2.5 Hz, 3 Hz, 3.5 Hz). To equate speed discriminability at all three reference levels, the interval width in each set was made proportional to the reference value (in keeping with Weber's law). These specific ranges of temporal frequency variation were established during pilot testing. Within these ranges, the motion signal remained clear and supported reliable speed discrimination. It was also determined that these ranges were wide enough to accommodate possible shifts in perceived speed, following adaptation.

The starting phases of the probe and match gratings were randomized across trials, to ensure that the speed comparison is not based on tracking of positional cues. Test stimuli reversed direction randomly between trials, with probe speed being measured in the adapted direction or opposite to it. As an added benefit, the change in test direction also minimized the build-up of adaptation to the comparison flow.

Test stimuli were displayed for 550±50 milliseconds, with test duration being randomly jittered on each trial. Observers could respond throughout the presentation of the test pattern or after it had been removed. Responses were recorded by a key press, which also ended the trial (i.e. scissors symbol on Figures 8-10). All trials were self-initiated, to ensure stable initial fixation and optimal readiness for the task.

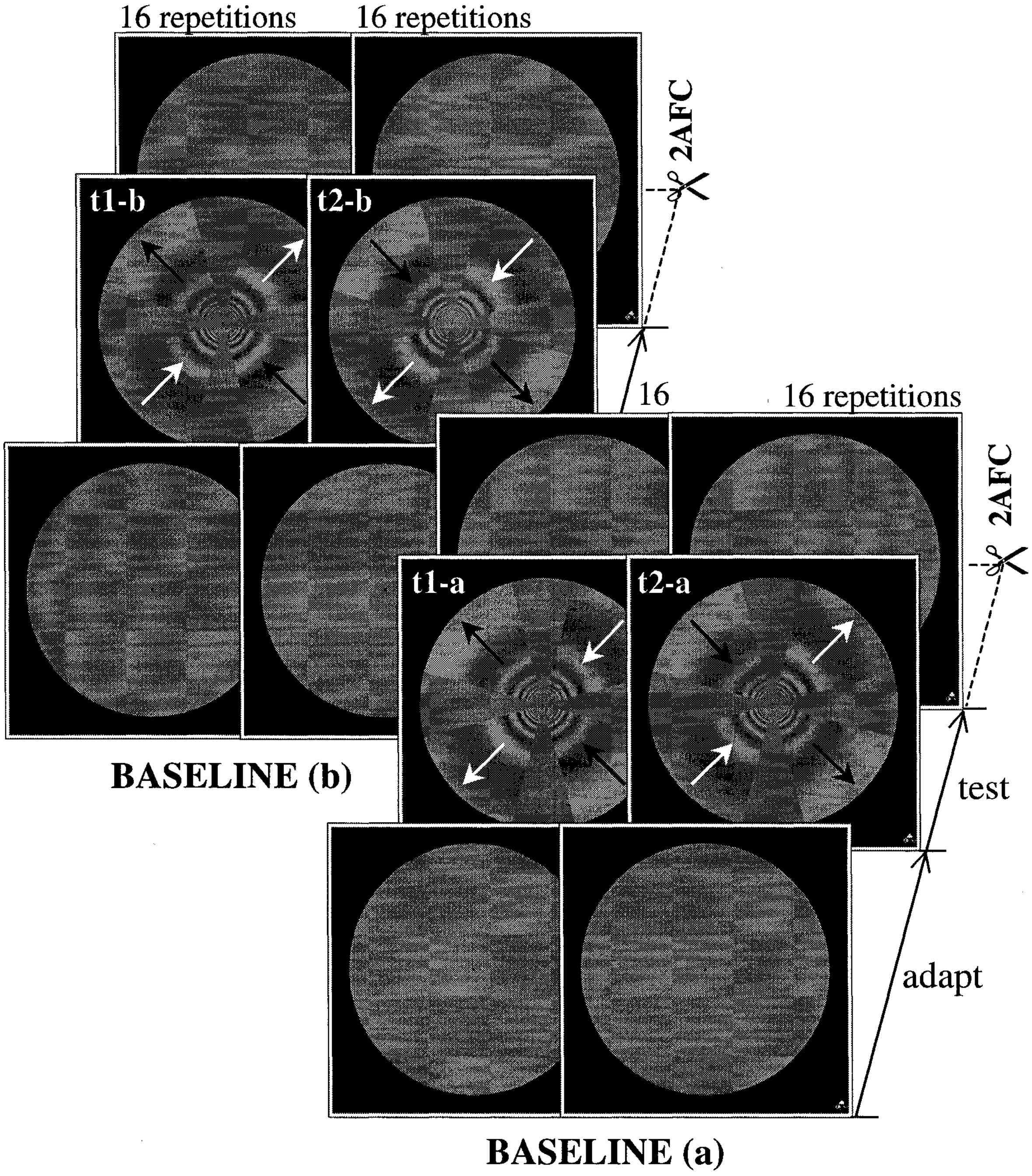


Figure 8. Baseline speed-matching in scrambled flow (Experiment 1).
Trials (a) and (b) belong to separate sessions. Arrows indicate flow direction in individual segments. Black arrows mark the probe stimulus and white arrows – the match. The same labeling is used in subsequent figures.

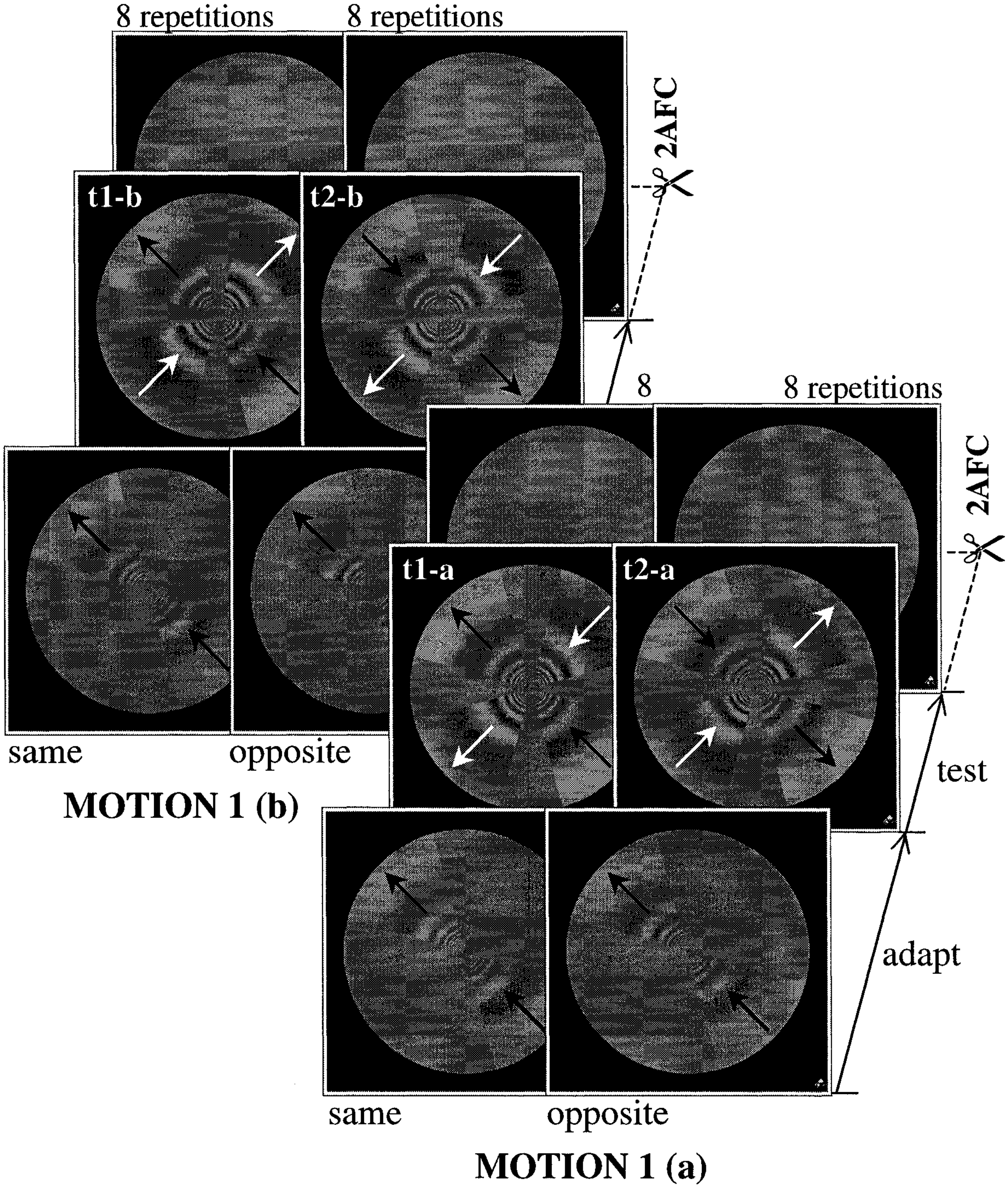


Figure 9. Speed matching after adaptation to scrambled flow of type 1 (Experiment 1). Trials (a) and (b) belong to separate sessions. The motion probe (black arrows) is in the adapted direction, or opposite to it.

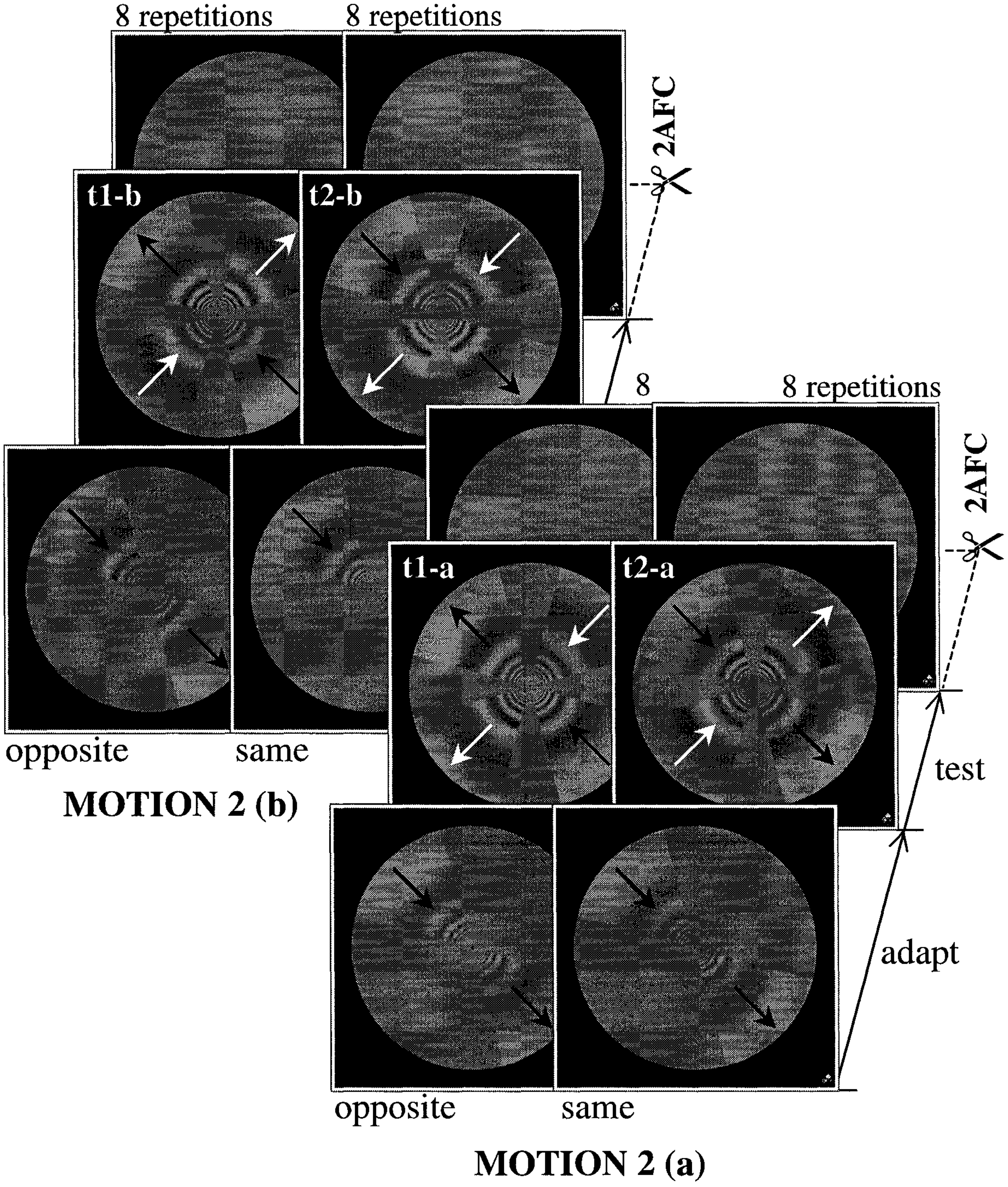


Figure 10. Speed matching after adaptation to scrambled flow of type 2 (Experiment 1). Trials (a) and (b) belong to separate sessions. The motion probe (black arrows) is in the adapted direction, or opposite to it.

Experimental Sessions

In the scrambled flow fields described above (Stimuli), the precise pairing of directions is arbitrary, with no one pattern being of more interest than the other. Therefore, several alternate versions of the adaptation and test stimuli were created and these were run in separate sessions. The grouping of trials in sessions is illustrated in Figures 8, 9 and 10.

The two types of scrambled flow used during adaptation and testing (indexed 1 and 2, black arrows) were combined with two types of match flow (indexed a and b, white arrows). This was carried out in the absence of prior motion adaptation (Figure 8, baseline sessions a and b) and following adaptation to scrambled flow of type 1 (Figure 9, motion sessions a and b) or type 2 (Figure 10, motion sessions a and b). As mentioned earlier, trials with opponent test patterns (1 and 2) alternated randomly within a session, with probe direction being the *same* as or *opposite* to the adapted direction. All sessions were also repeated with mirror inverted projection (see General Method). This resulted in a total of four (4) baseline sessions and eight (8) motion adaptation sessions, ran at each one of the three reference speeds.

Administration of sessions to subjects was distributed over days and weeks. Before actual data collection, all subjects practiced baseline speed matching. Practice level was deemed sufficient when two consecutive sessions yielded functions with asymptotic r^2 values and slopes. All subjects achieved this criterion within two to four practice runs.

Sessions from Experiment 1 were administered in a quasi-random order to each subject, mixed with sessions from Experiment 2. Throughout data collection, three important rules were respected. First, baseline sessions were always administered before adaptation sessions, if both were to be run on a given day. Second, straight and mirror inverted stimuli were always administered on separate days. Third, a minimum of 15 minutes rest period was imposed between consecutive sessions, and a longer waiting interval was respected if a different adapting stimulus with about to be used.

Experimental Conditions

As explained earlier, each subject ran four (4) baseline sessions and eight (8) motion adaptation sessions, at each one of the three reference speeds. Each session yielded two speed matching functions, one for probes in the adapted direction (iso-directional adaptation) and one for probes opposite to the adapted direction (counter-directional adaptation). In the final analysis, these functions were grouped in three conditions of interest, at each one of the three reference speeds (1Hz, 1.5Hz and 2Hz):

1) perceived non-adapted speed of the scrambled flow

   [all *baseline* data in straight (Figure 8) and reversed displays].

2) perceived speed of scrambled flow after iso-directional adaptation

   [all *same* motion data in straight (Figures 9 and 10) and reversed displays].

3) perceived speed of scrambled flow after contra-directional adaptation [all *opposite* motion data in straight (Figures 9 and 10) and reversed displays].

Therefore, data for each subject, from all relevant sessions, were collapsed across trials, to yield a single speed-matching function per condition, at each of the three standard speeds. This resulted in nine functions per subject in Experiment 1. The organization of the raw data in Experiment 1 is summarized in Table A1, Appendix A. All speed-matching functions of interest were based on the same number of trials per stimulus level (64).

3.3. Results and Discussion

3.3.1. Analysis of Psychometric Functions

Figure 11 shows a typical psychometric function describing the baseline speed matching performance of a naïve observer with no previous experience in visual psychophysics. In this example, the observer compared the perceived speed of scrambled flow drifting at 1 Hz (standard) to that of matching flow whose temporal frequency varied randomly across trials between the seven levels indicated on the X-axis. The speed comparison was repeated 64 times, at each stimulus level. Data points (open circles) indicate the proportion of times that this observer judged the speed of the match stimulus to be faster than that of the probe (measured on the Y-axis).

Setting Confidence Limits

Binomial standard errors (error bars, Figure 11) and binomial 95% confidence intervals (95% CI, dashed curves) were estimated around each data point, using the Wald asymptotic method with continuity correction (Newcombe, 1998). The upper and lower 95% CI were calculated as follows:

$$(2) \qquad p \pm \left(\left(z \right) \sqrt{pq / n} \right) + 1 / 2n \Big)$$

where p is the proportion correct responses, n is the total number of observations on which p is based (i.e. 64), $q = 1 - p$, z is the chosen critical value from the standard normal distribution (in this case, $z = 1.96$), the term $\sqrt{pq / n}$ denotes the standard error, and $1/2n$ is correction for continuity. With the present sample size, the value of the continuity correction is quite small (0.008), as the binomial distribution approximates the normal curve. To avoid the creation of meaningless CI-s with lower limits below 0 and upper limits above 1, no CI-s were formed around extreme data points, showing no variability (i.e. response probability of 0 or 1).

Fitting Logistic Functions to Data

The observed probability of "match faster" responses as a function of log stimulus level produces an S-shaped psychometric function, which is expected to be symmetrical below and above the 50% level (see top inset, Figure 11). The logistic function has similar characteristics known to represent this relationship well (Harvey, 1986):

(3)
$$p(x) = \gamma + \left[(1.0 - \gamma) . \frac{1.0}{1.0 + e^{-SL}} \right]$$

$$SL = \log_e \left[(x / \alpha)^\beta \right]$$

This function is completely specified by three parameters: α, the stimulus intensity at which the slope of the function is maximum; β, the steepness of the function; and γ, the probability of a correct response due to chance alone (i.e. 50% with the present speed-matching paradigm).

The solid curve in Figure 11 represents the logistic function fit through the raw data points (open symbols). Dashed curves represent the same function fit through the upper and lower 95% CI limits, surrounding each data point. The optimal parameters of the logistic function α and β were estimated by ordinary least squares regression (Systat 5.2). The obtained functions provided an excellent fit to the data, for all subjects and all conditions in Experiment 1. On average, the percent of variance accounted for was M=99.4% (SE=0.09) and never fell below 96.6% (see r^2 values in Appendix A, Table A1).

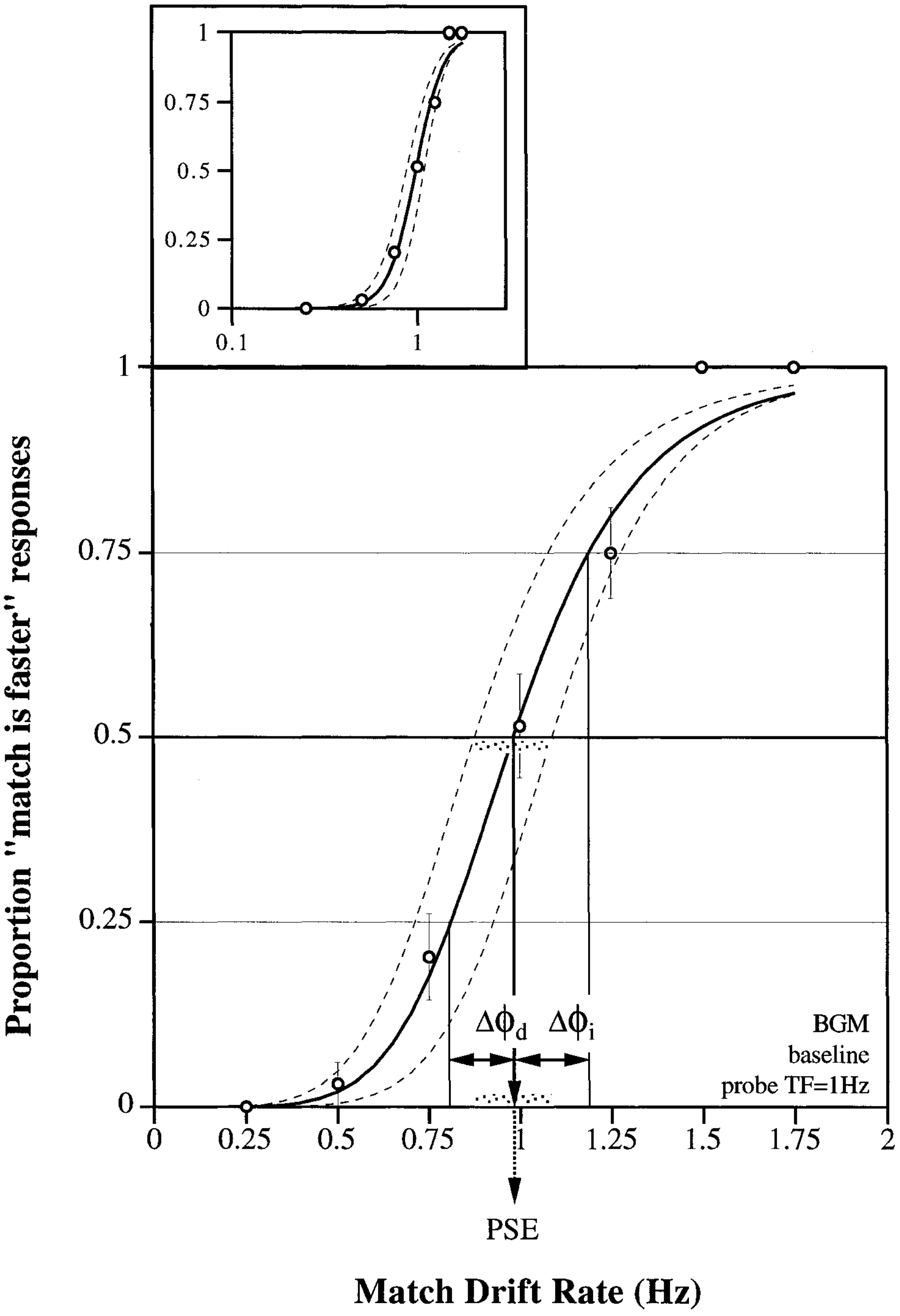


Figure 11. Typical speed matching function (Experiment 1).

Solid curve shows the best fitting logistic function (see inset for log-scaled X-axis). Dashed curves show the upper and lower 95% confidence limits to the fit. Error bars show binomial standard errors. Baseline data for an inexperienced, naïve observer (BGM). More details in the text.

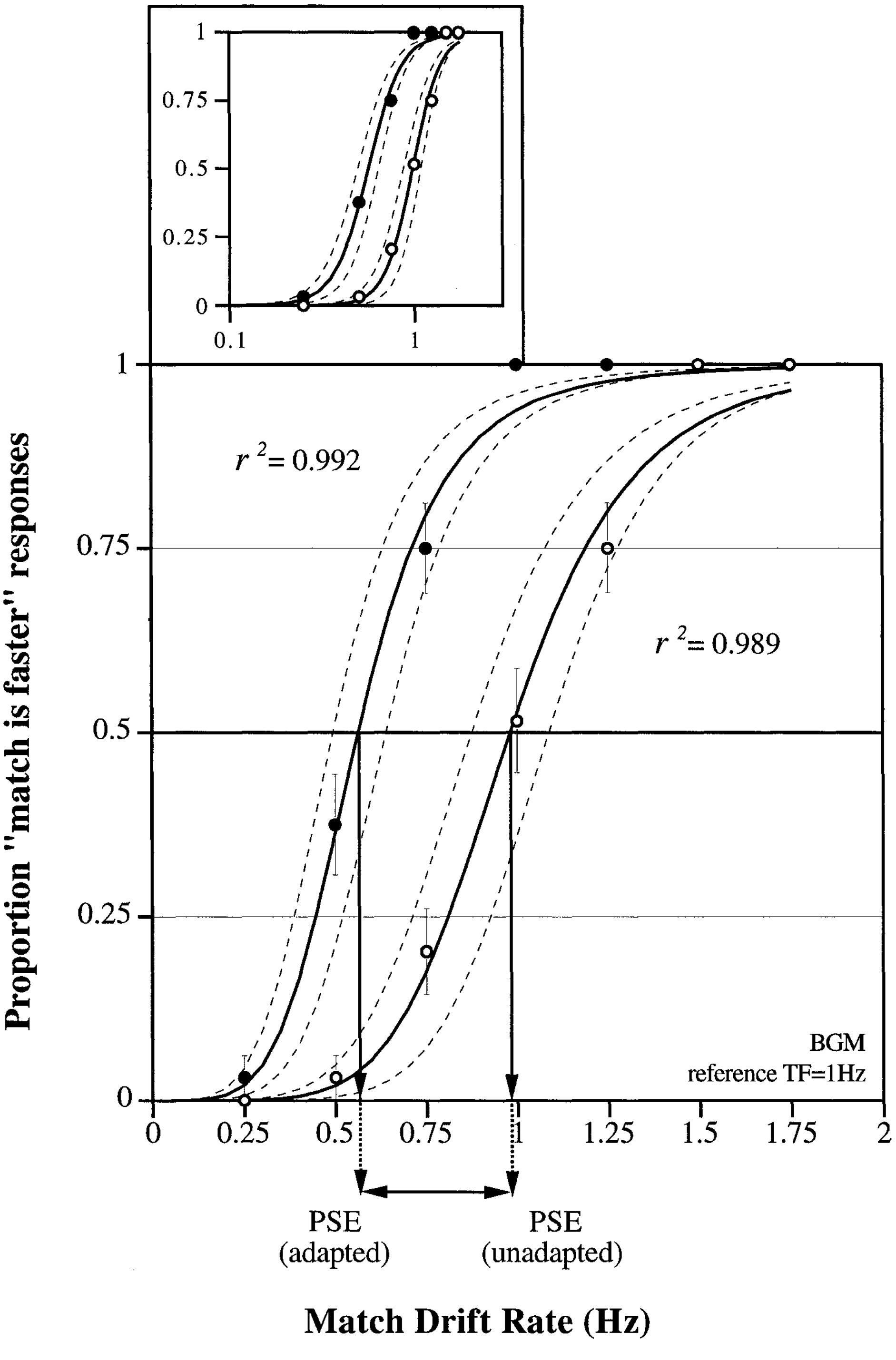


Figure 12. Measuring the change in perceived speed after adaptation (Experiment 1). An example of an iso-directional VAE (i.e. motion probe in the adapted direction). Naïve observer: BGM. More details in the text.

Dependent Measures

Two measures of interest were derived from each psychophysical function: a point estimate of perceived speed and a speed discrimination index (SDI), akin to a Weber fraction based on reference speed. The magnitude of the VAE was determined by comparing the two speed estimates obtained independently with and without prior adaptation to motion.

A. Perceived Speed

The reference temporal frequency value at which the proportion of "match is faster" responses is at chance level (i.e. 50%) indicates the point of subjective equality (PSE) – i.e. the point at which probe and match speeds are perceived as equal and hence could not be distinguished (see Figure 11). This value represents the perceived speed of the probe flow for a given subject, in a given condition. The PSE values associated with the upper and lower CI functions mark the 95% CI around the point estimate of perceived speed (shaded bar in Figure 11). It is noteworthy that the point estimate does not always lie in the middle of the CI, as the upper and lower margins of error often have different widths.

The meaning of these measurements is best illustrated in the context of Figure 11. This particular psychophysical function reveals that subject BGM matched the non-adapted speed of scrambled flow drifting at 1Hz to that of a scrambled comparison flow, drifting at 0.98Hz (PSE). The margin of error associated with this measurement is given by the confidence interval [$C\ (0.88 \leq PSE \geq 1.09)=0.95$]. It can be ascertained with 95% confidence that the true estimate of perceived speed is to be found between 0.88Hz and 1.09Hz – a range that encompasses the veridical value (i.e. 1Hz).

B. Magnitude of the VAE

The shift in perceived speed following adaptation to motion was measured by the ratio of post-adaptation to pre-adaptation PSE-s. Figure 12 shows the baseline and post-adaptation speed-matching data for subject BGM, when the motion probe was in the adapted direction (Experiment 1). The adapted function (filled circles) is clearly shifted to the left with respect to the non-adapted function (open circles, re-plotted from Figure 11), with no overlap between the corresponding 95%CI-s. Following adaptation, perceived speed is reduced to 0.56 Hz [$C(0.49 \leq PSE \geq 0.64)=0.95$], compared to the speed estimate for the same motion at baseline – i.e. 0.98 Hz, [$C\ (0.88 \leq PSE \geq 1.09)=0.95$]. The magnitude of this VAE is 0.57, indicating that the adapted speed estimate is 57% of the non-adapted one, which constitutes a 43% loss of apparent velocity relative to the baseline.

C. Differential Speed Sensitivity

The slope of the speed-matching function is an important index of task difficulty, in general, and of speed discrimination performance, in particular. It reflects the sensitivity to physical speed differences between the two types of flow being compared, with steeper slopes indicating higher sensitivity. In addition, although differential sensitivity is independent of the point estimate of perceived speed (PSE) it determines the margin of error around this estimate (i.e. steeper slopes are associated with narrower CI-s).

A readily interpretable speed discrimination index (SDI) could be derived from the psychometric function in Figure 11. It is based on the minimum speed difference between the standard and comparison stimuli needed to support reliable discrimination. As the upper and the lower parts of the logistic function are symmetrical on a log axis, the 25% and 75% on the Y-axis are taken as discrimination performance cut-offs, beyond which speed discrimination accuracy becomes better than chance. The distances between the respective X-values and the PSE indicate the just noticeable speed decrement ($\Delta\phi d$) or increment ($\Delta\phi i$) in the comparison stimulus. The SDI is defined as the average of $\Delta\phi d$ and $\Delta\phi i$, which, similar to the Weber fraction, is weighted by the reference drift rate (dr).

$$\text{SDI} = (\Delta\phi d + \Delta\phi i) / (2 \times dr) \qquad (4)$$

For the data presented in Figure 11, for example, $\Delta\phi d = 0.17$ Hz, $\Delta\phi i = 0.21$ Hz and the reference speed is 1Hz. This yields a SDI of 0.19, meaning that for subject BGM, at baseline, match temporal frequency had to differ by at least 19% from the reference temporal frequency, to support reliable discrimination.

The usefulness of the SDI can be demonstrated in Figure 12. In addition to the adaptation induced leftward shift in the psychometric function, its slope had become steeper. This increase in differential sensitivity is reflected in the reduction of the adapted SDI = 0.13, in comparison to the non-adapted SDI = 0.19. In other words, the higher the sensitivity to speed differences, the smaller the SDI and the steeper the slope.

3.3.2. Effects of Adaptation on Perceived Speed

Figure 13 presents the average speed estimates obtained in the three experimental conditions (baseline, iso-directional and contra-directional adaptation) as a function of reference speed (X-axis). The speed-matching values plotted on the Y-axis are PSE-s expressed as fractions of the reference speed. Thus a speed match of 1.0 indicates veridical perception of speed, whereas values *less than 1.0* or *greater than 1.0* indicate *under*-estimation and *over*-estimation, respectively.

The remarkable consistency between subjects is evident in Figures A1, A2 and A3 (Appendix A). In these figures, individual data are presented in the same manner as in Figure 13. The 95% confidence limit around individual speed estimates (error bars) permit independent evaluation of the effects for each subject. Correspondingly, the average standard error in the data is low (below 0.03), indicating that Figure 13 is representative of individual performance.

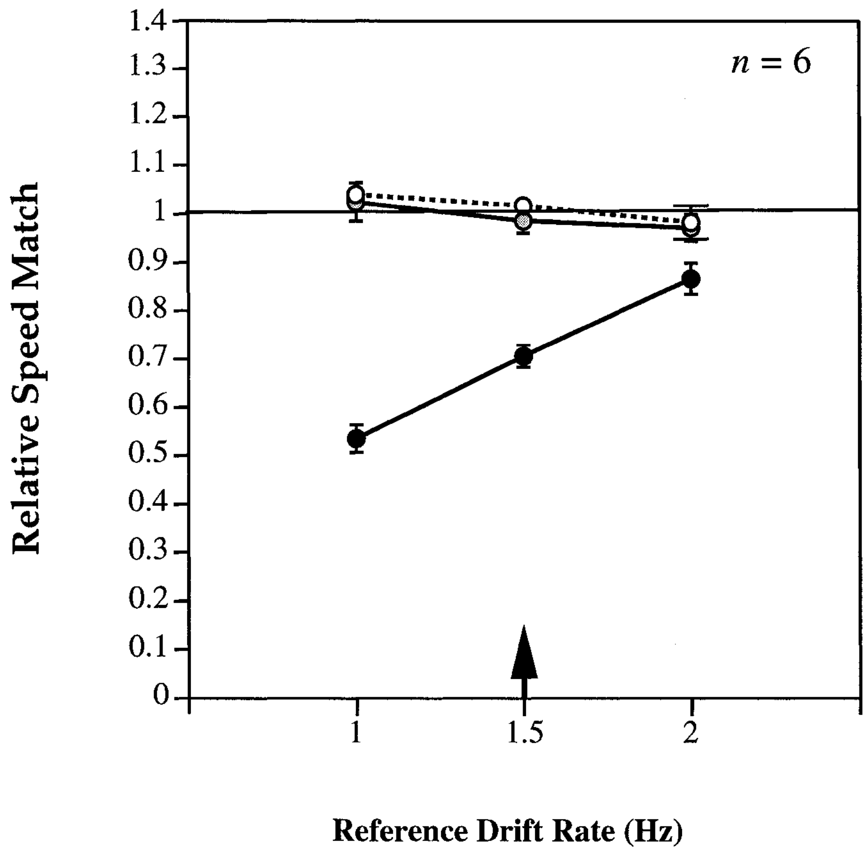


Figure 13. Changes in the perceived speed of scrambled flow following adaptation (Experiment 1).

Speed matches are expressed as fractions of the reference drift rate. Average data from all six observer at baseline (····○···), and after adaptation to iso-directional (——●——), or contra-directional (——◍——) flow. Error bars show standard errors. Black arrow indicates the drift rate of the adapting flow.

Perceived Speed at Baseline

Prior to adaptation, speed estimates were veridical (≈ 1) - deviating, on average, no more than 2% from the reference value (Figure 13). In other words, observers matched the probe flow to a comparison flow of the same physical speed.

Iso-directional VAE

As expected, the apparent speed of the "scrambled" flow was greatly reduced following adaptation to the same type of motion, in the same direction (Figure 13, filled circles). The magnitude of this negative VAE decreased monotonically as test speed increased. On average, compared to non-adapted levels, perceived speed fell down by 49% (SE=2.5%) for probes *slower* than the adapted speed (1Hz), by 31% (SE=2.4%) for probes moving *at the adapted speed* (1.5Hz) and by only 11% (SE=3.7%) for probes *faster* than the adapted motion (2Hz). Whereas the speed of 1Hz and 1.5Hz probes was reliably underestimated by all subjects (95%CI), speed estimates of 2Hz probes were not always significantly lower than baseline (see Figures A1-A3, Appendix A). No overestimation of speed was recorded, however, for these faster tests (2Hz).

As hypothesized, the *iso-directional VAEs* produced by the scrambled radial flow are very similar to those obtained with spatially localized gratings, in terms of both their magnitude and tuning (Thompson, 1976, 1981; Smith & Edgar, 1994; Müller & Greenlee, 1994; Bex et al., 1999a). The perceived speed of all test motions is reduced, following adaptation (negative VAEs), but the effect becomes progressively weaker as test motion approaches and exceeds the adapted value. While the loss of apparent velocity is greatest for test motions slower than the adapter and remains substantial for tests moving at the adapting speed, test motions faster than the adapter are not much affected.

The absence of positive iso-directional VAEs for tests moving faster than the adapter is not unusual. This effect depends on the specific parameter range in a given study and has been observed in some adaptation experiments (e.g. Rapoport, 1964; Hammett et al., 2005) but not in others (Carlson, 1962; Thompson, 1981; Smith, 1985; Müller et al, 2004). In principle, the finding of exclusively negative VAEs is consistent with the ratio model of perceived speed, reflecting, presumably, predominant adaptation of the fast (M-magno-cellular) temporal mechanism, whose response is selectively weakened relative to that of the slow (P-parvo-cellular) temporal mechanism. The adapting and test motion in the present study are likely to activate preferentially the magno-cellular processing stream, as they contain mostly peripheral motion at low spatial frequencies (i.e. high speeds). As a result, the M/P ratio would be lowered over a broad range of test speeds. In addition, in the present experiments apparent contrast loss was effectively counteracted, eliminating the possibility that as perceived contrast declines faster tests will erroneously “speed-up”, following adaptation (Thompson, 1982, 2006).

The magnitude of the present iso-directional VAEs is comparable to average published values. It may be argued that the present effects actually underestimate the true size of the VAE, if pursuit eye-movements have reduced the retinal velocity of the adaptation flow. Whereas such an influence cannot be ruled out completely, we believe it is minimal in the context of the present stimulus layout and task. Although tracking the scrambled adaptation flow is possible (e.g. from the lower right towards the upper left quadrant, see Figure 9), it is quite difficult to carry out along a diagonal axis, especially when head position is fixed. In addition, the local speed gradient in the stimulus and the impression of disjoint motion-in-depth prevents the pursuit system's from readily matching eye velocity to that of the stimulus (Howard, 1993; Ilg, 1997). Furthermore, observers were instructed and trained to keep their eyes fixed at the center, and they quickly learned that this strategy is to their advantage while performing the global speed-matching task. Finally, the absence of motion stimulation in the area around fixation decreases the likelihood of involuntary eye-deviations. The influence of eye-movements on speed estimation was of no concern in subsequent experiments, where centrifugal and centripetal directions of motion were used.

Contra-directional VAE

Contrary to expectations, results indicate that, on average, speed estimates remained unaffected by prior motion adaptation in the opposite direction (gray circles, Figure 13), as they coincided with those made at baseline (open circles, Figure 13). The small shifts observed in the individual data were insignificant and inconsistent across observers (see Figures A1-A3, Appendix A).

In the context of existing research, a complete absence of counter-directional VAEs is unusual and, therefore, noteworthy. Such results have been reported by only one other psychophysical study, using rotary motion (Rapoport, 1964). The rest of the evidence indicates that adaptation to motion reduces the perceived speed of motions moving in direction opposite to the one adapted, although stimuli moving in the adapted direction are more strongly affected. This has led to assertions that the VAE is only partially direction specific (Smith, 1985; Smith & Edgar, 1994). By contrast, the velocity adaptation in Experiment 1 can be described as *completely direction specific*, which also implies that speed responses to opposite directions of motion are *functionally independent*. In neural terms, this means that populations of cells selective for opposite directions of motion provide separate estimates of perceived speed. The direction specificity of the present VAEs is a desirable outcome, consistent with strong extra-striate involvement in the processing of the present stimuli (Huk et al., 2001, Kohn & Movshon, 2004). Direction selectivity is prominent at these levels and is enhanced by prior adaptation to motion (Kohn & Movshon, 2004). The absence of counter-directional VAEs also indicates that psychophysical judgments were based on velocity (i.e. speed *and* direction), rather than on drift rate or temporal frequency alone.

3.3.3. Effects of Adaptation on Differential Speed Sensitivity

Results presented in Figure 14 characterize speed-discrimination performance on the speed-matching task in Experiment 1. Average SDI (Y-axis) is plotted as a function of probe speed (X-axis) and adaptation condition (different bar shades).

Without prior adaptation, the average baseline SDI (across white bars) was 15 %. This value is comparable with empirically established sensitivity to velocity changes in the same ongoing motion (i.e. 15%-30%: e.g. Snowden & Braddick, 1991, Bex et al., 1999a) but is at two times higher than speed discrimination thresholds for spatially and temporally segregated stimuli (5%-7%: McKee, 1981). Such differential sensitivity loss might be attributed to the specific demands of the present speed-matching task, to the incongruent directional signal, or to both factors combined. To compare the global speed in the interleaved pairs of sectors, observers had to maintain spatial grouping for each pair, while disregarding the disjoint component directions-of-motion within them. Contrary to intuition, all subjects found the task to be effortless after only a few trials of practice. This suggests that the SDI elevation reflects a global interference due to the directional scrambling, rather than excessive cognitive effort.

Furthermore, Figure 14 indicates that speed discrimination performance improves following adaptation to motion but the effect depends on test speed. A two-way within-subjects' analysis of variance (ANOVA) confirmed that both of these factors affect the SDI, with the interaction between them being highly significant ($F(4,20)=4.232$, $p<0.01$; Table A2, Appendix A). Analyses of simple effects and paired comparisons reveal two important aspects of this interaction.

First, the main effect of test speed on speed discrimination is significant ($F(2,10)=4.549$, $p<0.05$; Table A2, Appendix A) but only at baseline ($F(2,10)=11.71$, $p<.01$, Table A3, Appendix A), with SDI-s at the fastest speed (i.e. 2.0 Hz: $M=0.13$,

$\underline{SE}$=0.01) being significantly lower than those at the slowest speed (i.e. 1.0 Hz: $\underline{M}$=0.19, $\underline{SE}$=0.02; Tukey HSD, $\underline{p}<0.01$). This is a common finding in the speed discrimination literature, indicating that faster motions have a temporal integration advantage over slower motions within a given limited exposure duration (McKee et al., 1986; Nakayama, 1985). Naturally, the advantage disappears when exposure to motion is sufficiently long (i.e. after adaptation).

The second effect is of particular interest, as it concerns an a-priori hypothesis about how speed discrimination ability might change, following adaptation to motion. As expected, prolonged viewing of the scrambled flow had an important overall impact on subsequent differential speed sensitivity ($\underline{F}(2,10)=6.243$, $\underline{p}<0.05$; Table A2, Appendix A). This effect was significant for probes slower than the adapting motion (i.e. at 1.0 Hz; $\underline{F}(2, 10)=11.81$, $\underline{p}<0.01$; Table A4, Appendix A) with faster tests being progressively less affected. Furthermore, planned comparisons between means indicated that post-adaptation SDI-s were significantly reduced compared to baseline, but only for probes moving in the adapted direction and slower than (i.e. at 1.0 Hz; $\underline{M}$base=0.19, $\underline{SE}$base=0.02 versus $\underline{M}$iso=0.11, $\underline{SE}$iso=0.01; $\underline{F}(1, 5)=38.96$, $\underline{p}<0.01$) or at the same speed as the adapting stimulus (i.e. at 1.5 Hz; $\underline{M}$base=0.14, $\underline{SE}$base=0.01 versus $\underline{M}$iso=0.10, $\underline{SE}$iso=0.02; $\underline{F}(1, 5)=28.95$, $\underline{p}<0.01$). On average, iso-directional adaptation improved differential speed sensitivity by 42% for 1.0 Hz tests and by 28% for 1.5 Hz tests. No significant change in speed sensitivity was found for tests faster than the adapter (2.0 Hz) and after adaptation to the opposite direction-of-motion.

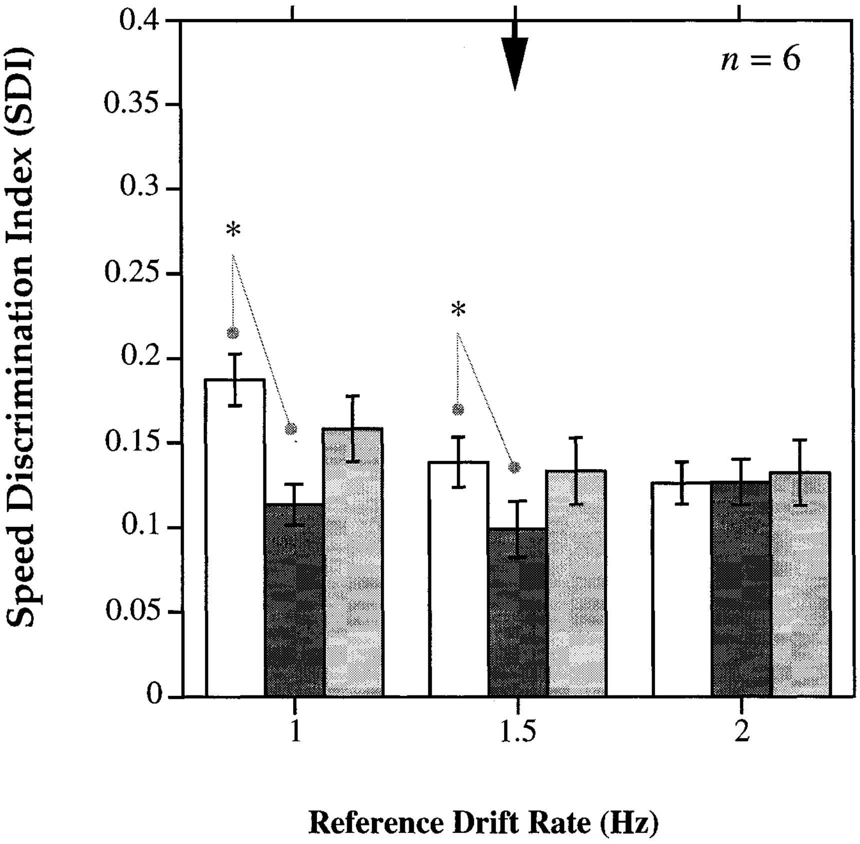


Figure 14. Effects of adaptation on sensitivity to speed differences in scrambled flow (Experiment 1).

SDI is a fraction of the reference value. Average data from all six observers at baseline (□) and after adaptation to iso-directional (■) or contra-directional (▨) flow. Error bars show standard errors. Black arrow indicates the drift rate of the adapting flow. Asterisks mark significant differences between means (p<0.01).

Figure 15 allows a direct comparison between the iso-directional speed discrimination enhancement and the iso-directional VAE recorded in Experiment 1. The facilitation effect is expressed as a ratio between post-adaptation and pre-adaptation SDI-s, quantifying the change in differential sensitivity in proportion to baseline. Similarly, the VAE is expressed as a ratio between post-adaptation and pre-adaptation PSE-s, indicating the change in perceived speed, in proportion to baseline. When plotted in this manner, the data clearly illustrate that the magnitudes of the two perceptual aftereffects change in parallel as a function of reference speed.

The present results agree with existing reports that adaptation improves sensitivity to speed differences around the adapted velocity (Clifford & Langley, 1996; Clifford & Wenderoth, 1999; Bex et al., 1999; Kristjánsson, 2000, Huk et al., 2001). As expected, adaptation to scrambled flow in part of the flow-field facilitates subsequent speed comparisons between adapted and non-adapted display regions. The magnitude of this facilitation at the adapted velocity (28%) is comparable to previously reported values (20%). Consistent with past results, the facilitation effect is not as strong as the simultaneously recorded VAE.

Other aspects of our results, however, challenge and extend previous findings. First, although speed discrimination improves around the adapted velocity, the strongest enhancement is observed not at the adapted speed, but for motion slower than the adapter, with no such benefit for faster tests. This indicates that the sensory benefits of adaptation to motion are not limited to the adapted velocity, as suggested by existing research, based on changes in speed discrimination performance in reference to the adapted speed only. Second, in contrast with a previous study (Clifford & Wenderoth, 1999), and in agreement with another (Huk et al., 2001), the present facilitation effects are, once again, direction specific in that they are not observed for tests moving opposite to the adapted direction.

The present results reinforce the idea that judgments of absolute and relative speed share a common origin as adaptation alters both types of judgments in a similar way. Discrimination thresholds are reduced the most whenever perceived speed is slowed down the most, with both effects showing parallel tuning as a function of reference speed (see Figure 15). Furthermore, both adaptation effects are direction specific, supporting the notion that they are mediated by the same neural events (Bex et al., 1999a; Huk et al., 2001). The present data strengthen the argument that speed sensitivity can be adequately described with Weber fractions based on perceived, rather than physical speed (Bex et al., 1999a; Clifford & Wenderoth, 1999). Speed perception and speed discrimination performance have been convincingly linked in the exponential build-up of adaptation effects over time (Bex et al., 1999a). Here, this link is confirmed in a different context, by the parallel dependence of both effects on test speed.

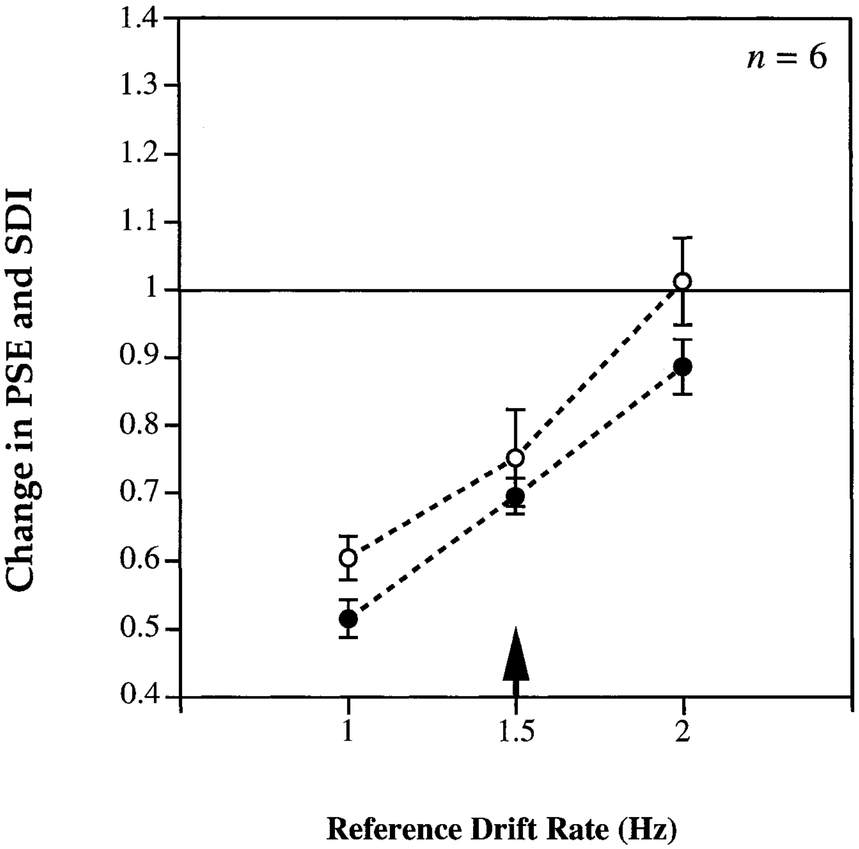


Figure 15. Changes in speed perception and speed sensitivity after adaptation to scrambled flow (Experiment 1).

The plotted values are ratios between adapted and non-adapted PSE-s (- - -●- - -) and SDI-s (- - -○- - -), respectively, averaged across all observers. Error bars show standard errors. Black arrow indicates adapting drift rate.

3.4. Summary

Taken together, the velocity aftereffects found in Experiment 1 replicate the ones described at the local level. They establish a link with previous findings and provide a meaningful baseline against which the effects of subsequent experimental manipulations can be assessed.

Following adaptation to the present scrambled flow pattern, its apparent speed is reduced, while sensitivity to speed differences is enhanced. Both effects exhibit the typical VAE tuning as a function of reference speed, and both are specific to the adapted direction of motion. The fact that the VAE in Experiment 1 retains its familiar characteristics, suggests that velocity mechanisms engaged by the scrambled flow are not fundamentally different from those mediating speed perception in local one-directional gratings. In the absence of a meaningful global configuration of motion, speed perception and speed discrimination show the same dependence on reference speed and seem to rely on the same local velocity estimates, attenuated following adaptation.

The present aftereffects, however, are also unique in that they are strictly limited to the adapting direction, suggesting prominent extra-striate involvement. This also indicates that our stimuli define a strong velocity signal, supporting unambiguous psychophysical judgments. It is also of note that the strongest benefits of adaptation to motion are seen on test velocities slower than the adapter, rather than around the adapted velocity, as postulated by existing research.

4. EXPERIMENT 2

4.1. Rationale and Hypotheses

This experiment addresses the main question of the present study - namely, whether absolute and relative velocity judgments are sensitive to the global directional structure of the radial flow. To examine this question, changes in speed perception and speed discrimination are examined concurrently, before and after prolonged viewing of expanding or contracting flow. In the test phase, probe and matching flow share the same global direction-of-motion, which is either the same or opposite to that of the adapting flow. The velocity aftereffects generated by these uniform flow patterns are then compared to those obtained with scrambled flow in Experiment 1. Another issue of interest is whether velocity estimates in contracting and expanding flow are similar and show similar adaptive dynamics.

The flow stimuli in Experiment 2 are identical to those used in Experiment 1, except that the component directions-of-motion assigned to individual sectors define uniform, rather than scrambled flow patterns. In addition to motion processing levels engaged by the scrambled flow, the uniform flow in Experiment 2 is expected to engage large-scale complex motion mechanisms, specifically sensitive to radial motion. Such mechanisms have been identified in primate extra-striate cortex beyond area MT (Tanaka, 1998; Duffy, 2004), as well as by psychophysical (e.g. Freeman & Harris, 1992, Morrone et al., 1995; Beardsley & Vaina, 2005) and imaging studies in humans (e.g.

Morrone et al., 2000). Thus any difference between the adaptation effects observed in Experiments 1 and 2 would reflect the unique contribution of these higher-order mechanisms. In the past, this approach has successfully separated complex MAEs from those produced by translational motion (Regan & Beverley, 1978; Bex et al. 1999b). Here, we employ a similar paradigm to examine the effects of global direction-of-motion cohesion on velocity estimates in radial flow.

In Experiment 2, both adaptation and test stimuli target the complex radial sensors of interest. In the case of iso-directional testing, the speed-comparison is between sets of cells (or receptive field regions) selective for the same radial direction-of-motion, after one set (or one region) has been adapted to its preferred flow direction. In the contra-directional case, the speed comparison involves the same populations of radial motion sensors, after some of them have been adapted, in part, to their non-preferred flow direction. In either case, the comparison is between receptive field regions that have been or have not been *directly* adapted and involves sensors with the same radial flow preference.

The nature of Experiment 2 is exploratory. To our knowledge, there are no published studies on velocity aftereffects in radial motion. Similarly, little is known about how complex motion sensors selective for this type of motion represent image velocity. Expectations of outcome can only rely on studies measuring changes in direction-of-motion perception following adaptation to drifting luminance-defined radial patterns (i.e. detection thresholds - Regan & Beverley, 1978; Kelly, 1989 or the MAE - Scott et al., 1966; Bex et al., 1999b). Results from these studies, however, may not be directly applicable to the VAE, in view of growing evidence that direction-of-motion and speed are not encoded and processed in the same manner (e.g. Matthews & Qian, 1999; Priebe et al., 2006; Edwards & Grainger, 2006). Similarly, some aspects of the VAE cannot be predicted from the velocity of the MAE in the same stimulus (Thompson, 1976, 1993). Thus, existing findings on adaptation effects in radial motion can only be used as tentative guidelines. Owing to methodological differences, other results, concerning sensitivity, speed perception and speed discrimination in radial motion should be considered with caution. With these reservations in mind, existing research on complex motion perception, together with results from Experiment 1, suggests several possible outcomes regarding the magnitude and the tuning of the adaptation effects in Experiment 2.

First, as pointed out earlier, the coherent flow in Experiment 2 is expected to engage additional or different extra-striate motion mechanisms, and more strongly so than the scrambled flow in Experiment 1. Since all after-effects in Experiment 1 were direction specific, adaptation to uniform radial flow is also expected to be direction specific. In other words, we predict that in Experiment 2:

1. No contra-directional VAEs will occur. Changes in speed perception and speed sensitivity will be confined to the adapted direction-of-motion, while the perception of tests moving opposite to the adapted direction will remain unaffected.

A number of studies have shown that direction-of-motion sensitivity in radial motion is better than that for translational motion (e.g. Freeman & Harris, 1992; Beardsley & Vaina, 2005). Correspondingly, adaptation to radial motion affects subsequent direction perception more profoundly than adaptation to otherwise equivalent translation (Regan & Beverley, 1978). Radial MAEs are longer lasting, harder to null and, perhaps, faster than the MAEs generated by translational motion (Bex et al.1999b). Also, adaptation to radial motion containing a natural spatial/speed gradient, conveying motion-in-depth, impairs subsequent direction detection more profoundly than adaptation to "flat" radial motion (without gradient), or containing a gradient whose sign is reversed (Kelly, 1989). Furthermore, the apparent speed of radial motion is judged to be faster than that of patterns translating or rotating at the same physical speed (Geesaman & Qian, 1996; Bex & Makous, 1997) and, in general, faster motions produce stronger aftereffects, within common parameter limits (Thompson, 1998). If the scrambled flow in Experiment 1 is conceived as a warped version of translational flow, and to the extent to which VAEs and MAEs reflect adaptive changes in the same population of sensors, we might expect that:

2. Iso-directional VAEs in Experiment 2 will be more profound than those generated by the scrambled flow in Experiment 1.

Differences between VAE magnitude in Experiment 1 and 2 may or may not be accompanied by differences in tuning. A difference in magnitude only, will indicate that complex radial motion detectors are uniquely sensitive to the global velocity in the radial pattern, while representing it in fundamentally the same way as previous motion-processing levels. In this case, the tuning function relating VAE magnitude to test speed in Experiment 2 will be parallel to that for the scrambled flow in Experiment 1. A difference in the tuning pattern, on the other hand, will suggest a qualitative difference in the representation of radial velocity signals. Such an outcome would suggest that the radial velocity channels recruited in Experiment 2 possess unique characteristics (e.g. number, shape, degree of overlap, adaptability), in comparison to those identified with motion stimuli targeting earlier levels.

Possible differences between contracting and expanding VAEs, in Experiment 2, may be interpreted along similar lines. Considering the evidence for directional asymmetries in various aspects of radial motion perception, it is likely that:

3. Expanding and contracting VAEs will differ in their magnitudes and/or their tuning.

The above hypothesis (#3) cannot be specified any further, since radial motion biases have been observed in either direction. Although some studies find that adaptation to expansion degrades subsequent motion detection more than adaptation to contraction (Kelly, 1989), contracting spirals generate expanding MAEs that are stronger and longer-lasting than the contracting MAEs, elicited by expanding spirals (Wohlgemuth, 1911; Scott et al., 1966; Reinhardt-Rutland, 1994). Yet other studies report no difference between expanding and contracting MAEs (Bex et al., 1999b). In general, research shows that speed perception in the two types of flow is comparable (Bex et al., 1998), although some results indicate that contraction may appear slightly faster in comparison to expansion (Geesaman & Qian, 1998), while others find evidence for the opposite trend (Clifford et al., 1999). Finally, while some directional asymmetries seem to be stable, others disappear with training (Scott et al., 1966). Our paradigm involves extensive practice and prolonged exposure to motion. Hence, directional asymmetries in the VAE, if observed, would most likely reflect a hard-wired property of the visual system.

What may be expected about the level of speed discrimination performance in the context of uniform flow (Experiment 2), in comparison to that in scrambled flow (Experiment 1)? Once again, weighted evidence from relevant studies suggests that a difference may be expected, but there is little certainty about its direction. Whereas perceived speed depends on the global configuration of motion (Geesaman & Qian, 1996; Bex & Makous, 1997), this has not been found for speed discrimination performance. Existing results indicate that speed discrimination thresholds are the same for radial, rotary and translational motion, although these motions are not judged as having the same speed (Sekuler, 1992; Clifford et al., 1999). This discrepancy is puzzling, in view of evidence that speed discrimination thresholds vary in proportion to perceived speed (Bex et al., 1999a; Experiment 1). Since radial flow is perceived as consistently faster than translational flow, for example, it may be expected that speed differences will be harder to detect in radial, than in translational flow. Another line of evidence, leads to a similar prediction. It has been shown that the spatial and temporal organization of velocity signals affects observers' ability to discriminate between them (e.g. Verghese & McKee, 2006). As a general rule, sensitivity to speed differences declines if the motions compared are united in the same perceptual object (e.g. Verghese & Stone, 1996) or appear to follow a common trajectory (Verghese & McKee, 2002). Since in Experiment 2, the flow patterns compared share the same global direction, they are more likely to be seen as parts of the same entity than the scrambled test patterns in Experiment 1. Hence, it is conceivable that speed discrimination will deteriorate in the context of uniform flow, in comparison to the scrambled flow where component directions cannot be grouped in any meaningful pattern. Such an outcome, however, would contradict the behavioral purpose of large-scale complex motion mechanisms, which are known to be exquisitely sensitive to the speed structure of the radial flow (Tanaka, 1998; Duffy & Wurtz, 1997a; Clifford et al., 1999; Orban et al., 2003; Srinivasan, 2004; Dyre & Andersen, 1997; Beardsley & Vaina, 2005).

Reported motion adaptation effects on speed sensitivity are more coherent, including those in Experiment 1 (e.g. Clifford & Langley, 1996; Bex et al., 1999a). In the context of the present displays, we find that prior adaptation to motion enhances speed discrimination performance. Therefore, a similar outcome is expected in Experiment 2, in that:

4. Adaptation to expansion and contraction will facilitate subsequent speed discrimination for test flow moving in the adapted direction, in proportion to the loss in apparent speed.

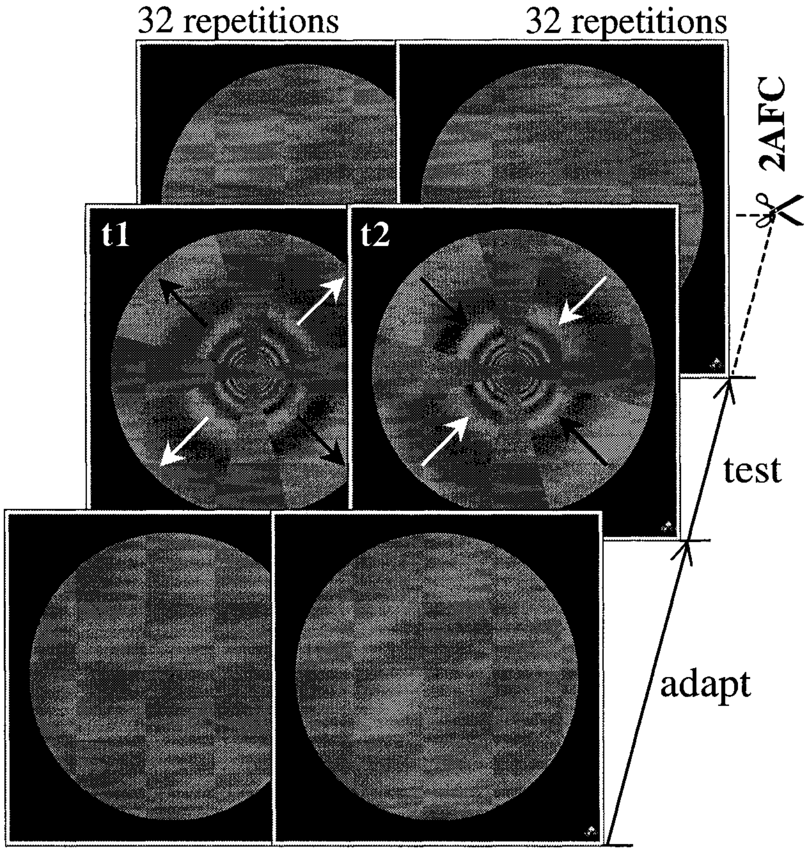
4.2. Method

4.2.1. Subjects

The same six subjects who took part in Experiment 1 completed all conditions of Experiment 2.

4.2.2. Stimuli

The spatial characteristics of all stimuli in Experiment 2 remained the same as in Experiment 1, and as described in previous sections (see General Method, Figures 6 & 7). In this experiment, however, the same flow direction was assigned to all display regions. When all sectors contained centrifugal motion, an expanding flow pattern was formed (see Figure 17 - "adapt" and t1). Similarly, centripetal motion in all sectors defined contracting flow (see Figure 18 - "adapt" and t2). All adaptation and test stimuli had a uniform global direction-of-motion, as illustrated in Figures 16, 17 and 18. For example, the adaptation stimulus in Figure 16 was expanding (black arrows) and was replaced by a test stimulus that was either expanding (same direction test, Figure 17 - t1), or contracting (opposite direction test, Figure 17 - t2). In both cases, the probe flow (black arrows) was compared to matching flow (white arrows) with the same global direction-of-motion.



BASELINE

Figure 16. Baseline speed-matching in congruent radial flow (Experiment 2). The probe flow (black arrows) and the match flow (white arrows) have the same global direction of motion.

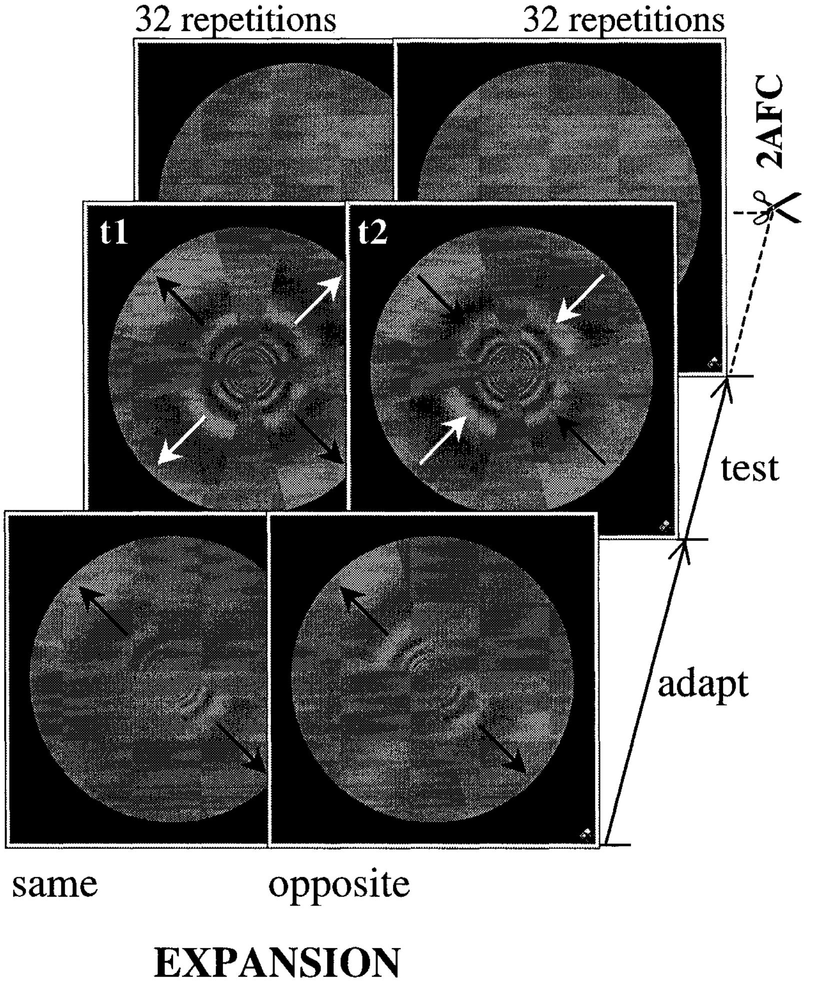


Figure 17. Speed matching after adaptation to expanding flow (Experiment 2).
The direction of the motion probe is the same as (t1) or opposite to (t2) the adapted direction. The probe flow (black arrows) and the match flow (white arrows) have the same global direction of motion.

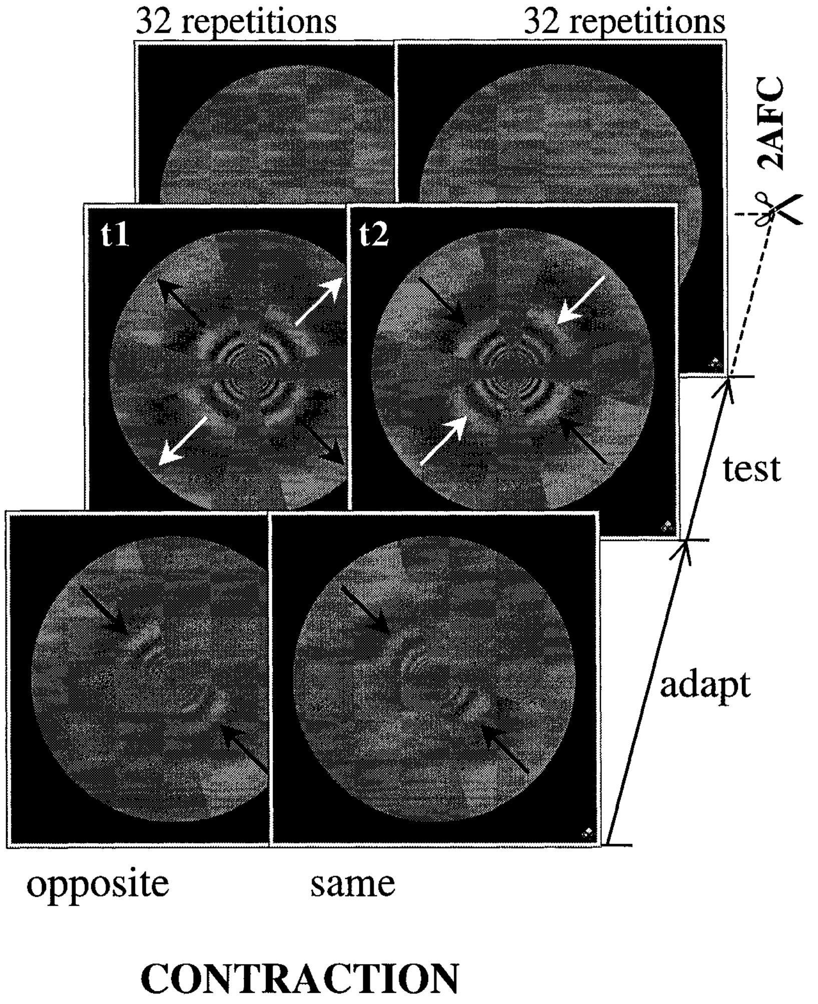


Figure 18. Speed matching after adaptation to contracting flow (Experiment 2).

The direction of the motion probe is the same as (t1) or opposite to (t2) the adapted direction. The probe flow (black arrows) and the match flow (white arrows) have the same global direction of motion.

4.2.3. Procedure

Trial Sequence

All trials in Experiment 2 had the same temporal structure as in Experiment 1 (Figures 16-18). Adaptation and test protocol remained identical as well.

Experimental Sessions

The grouping of trials in sessions is illustrated in Figures 16, 17 and 18. These three figures represent the three types of sessions in Experiment 2, where speed matching was preceded by no prior adaptation to motion (baseline, Figure 16), or by adaptation to expanding (Figure 17), or to contracting flow (Figure 18).

In all sessions, speed comparisons were made between pairs of sectors defining the same global direction of flow (i.e. white versus black arrows in t-boxes, Figures 16, 17 & 18). On half of the trials, the apparent speed of expansion in one part of the flow field was compared to that of expansion in another part of the flow field (t1-boxes in Figures 16-18). On the other half of the trials, the same comparison was carried out in the context of contracting flow (t2-boxes in Figures 16-18). Expanding (t1) and contracting (t2) tests alternated randomly within a session. Each session was run in straight and inverted projection, at each one of the three reference speeds (1Hz, 1.5Hz and 2Hz). Cumulative data from each session type generated two psychometric functions, characterizing perceived speed within the expanding and contracting test patterns, respectively, without prior exposure to motion, or following iso-directional and contra-directional adaptation, at a given reference speed. As in Experiment 1, each function was based on a total of 64 repetitions per stimulus level.

Experimental Conditions

Changes in perceived speed following adaptation to expanding and contracting flow were assessed in relation to the corresponding estimates obtained at baseline. As in Experiment 1, the VAE was measured by grouping the speed-matching data in three conditions of interest. In Experiment 2, however, this was done separately for each type of flow, as outlined below.

A: Expansion-to-Expansion Speed Matching

1) perceived non-adapted speed of expansion
   [all *t1 baseline* data in straight (Figure 16) and reversed displays].

2) perceived speed of expansion after iso-directional adaptation
   [all *t1 same motion* data in straight (Figures 17) and reversed displays].

3) perceived speed of expansion after contra-directional adaptation
   [all *t1 opposite motion* data in straight (Figures 18) and reversed displays].

B: Contraction-to-Contraction Speed Matching

1) perceived non-adapted speed of contraction

   [all *t2 baseline* data in straight (Figure 16) and reversed displays].

2) perceived speed of contraction after iso-directional adaptation

   [all *t2 same motion* data in straight (Figures 18) and reversed displays].

3) perceived speed of contraction after contra-directional adaptation

   [all *t2 opposite motion* data in straight (Figures 17) and reversed displays].

Thus in Experiment 2, three psychometric functions were obtained from each subject, for each type of flow, at each of the three reference speeds, resulting in nine functions for expansion and nine functions for contraction, respectively. All functions were based on the same cumulative number of trials as in Experiment 1. The organization of the raw data is summarized in Table B1 (Appendix B) for expansion-to-expansion speed matching, and in Table B2 (Appendix B) for contraction-to-contraction speed matching.

4.3. Results and Discussion

4.3.1. Effects of Adaptation on Perceived Speed

Individual psychometric functions obtained in Experiment 2 were analyzed in the same manner as described in Experiment 1. Again, the least squares logistic functions provided an excellent fit to the data, for all subjects and all conditions in Experiment 2. For the expansion speed-matching data, on average, the percent of variance accounted for was M=99.1% (SE=0.10) and never fell below 95.8% (see r^2 values in Table B1, Appendix B). Similarly, for the contraction speed-matching data, on average, the percent of variance accounted for was M=99.2% (SE=0.13) and never fell below 95.1% in individual cases (see r^2 values in Table B2, Appendix B).

Figures 19 and 20 present the average speed estimates for expanding and contracting probes, respectively, obtained in the three experimental conditions (baseline, iso-directional and contra-directional adaptation), as a function of reference speed (X-axis). Relative PSE values are plotted on the Y-axis, expressed as fractions of the actual drift rate of the probe. As in previous figures, a relative speed-match of 1.0 indicates veridical speed perception. The individual data on which these average estimates are based can be examined in Appendix B (Figures B1 - B6). As in Experiment 1, for both types of flow, there was good agreement between individual results.

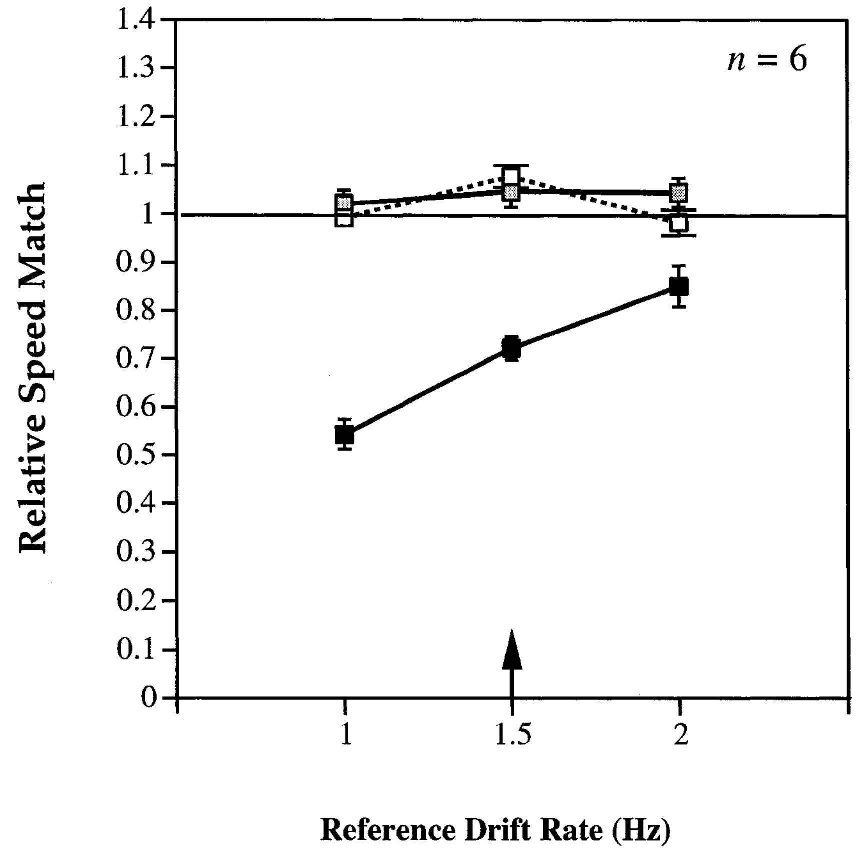


Figure 19. Effects of adaptation on the perceived speed of expanding flow (Experiment 2).

Speed matches are expressed as fractions of the reference value. Average data from all six observers at baseline (····□····), and after adaptation to iso-directional (—■—), or contra-directional (—▨—) flow. Error bars show standard errors. Black arrow indicates adapting drift rate.

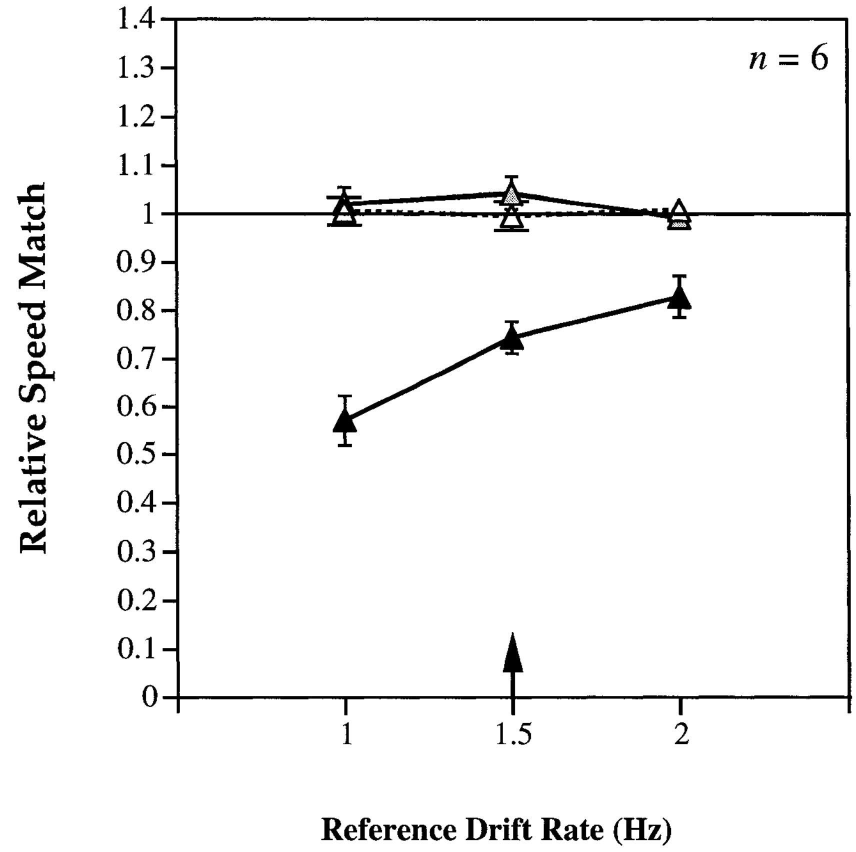


Figure 20. Effects of adaptation on the perceived speed of contracting flow (Experiment 2).

Speed matches are expressed as fractions of the reference value. Average data from all six observers at baseline (·····△····), and after adaptation to iso-directional (——▲——), or contra-directional (——△——) flow. Error bars show standard errors. Black arrow indicates the drift rate of the adapting flow.

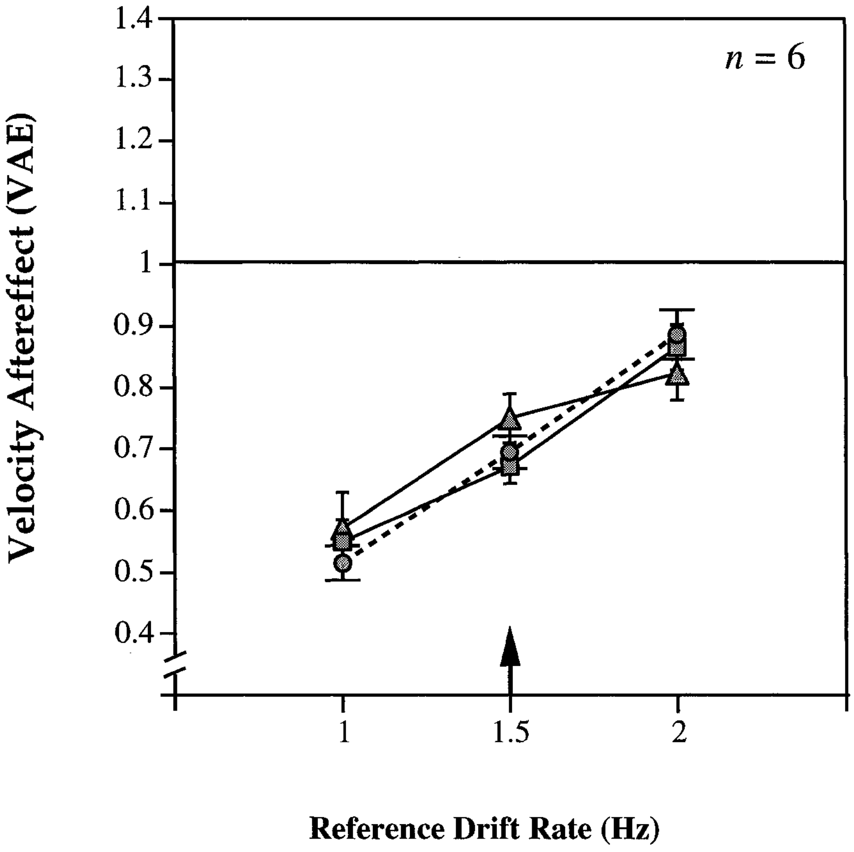


Figure 21. Comparison of iso-directional VAEs in Experiments1 and 2.

Values on the Y-axis are average ratios of post-adaptation to baseline PSE-s, for scrambled (- - -●- - -), coherently expanding (——▨——), and contracting (——▲——) flow patterns. Error bars show standard errors. Black arrow indicates the drift rate of the adapting flow.

Perceived Speed at Baseline

Without prior adaptation to motion, radial speed was matched accurately to that of the comparison flow, when both motions had the same global direction of motion. In other words, the speed of non-adapted expansion in one display region was perceived as equal to that of non-adapted expansion in a non-overlapping display region, when both stimuli were moving at the same physical speed. This was also true when probe and match stimuli were contracting. Deviations from the veridical level were small and inconsistent across reference speeds and individual subjects (Figures B1-B6, Appendix B). On average, such deviations were within 2% for expansion (Figure 19), and within 1 % for contraction (Figure 20).

Iso-directional VAE

As expected, iso-directional adaptation reduced the apparent speed of expanding and contracting probes, compared to baseline, and the magnitude of the effect was inversely related to the reference speed of the test (Figures 19 and 20, black symbols). All subjects underestimated the apparent speed of 1Hz and 1.5Hz probes (95%CI-s), but speed estimates of 2Hz probes were not always significantly lower than baseline (see Appendix B, Figures B1-B6). As in Experiment 1, no overestimation was recorded for probe speeds faster than the adapter.

Contra-directional VAE

Again, as expected, and as found for the scrambled flow in Experiment 1, the expanding and contracting VAEs in Experiment 2 were strictly direction specific, indicating prominent, direction selective involvement of extra-striate motion sensitive cortex. On average, expansion and contraction velocity estimates remained unaffected by prior adaptation to the opposite direction-of-motion. Contra-directional speed-matches were no different from those made at baseline (gray versus unfilled symbols, Figures 19 and 20). The overlap between baseline and contra-directional PSE-s is also evident in the data from individual subjects (Appendix B, Figures B1-B6).

Comparison Between Iso-directional VAEs in Experiments 1 and 2

Figure 21 displays the magnitude of the iso-directional VAEs in expanding (Experiment 2), contracting (Experiment 2) and scrambled flow patterns (Experiment 1), as a function of the drift rate of the probe. These results indicate that the three types of flow produced VAEs of the same magnitude and with the same tuning. Results from a two-way ANOVA on VAE as a function of flow type (scrambled, expanding, contracting) and reference drift rate (1Hz, 1.5Hz, 2Hz) confirmed this conclusion (see Table B3, Appendix B). Neither the main effect of flow-type, nor the interaction between flow-type and test-speed were significant. The only factor that influenced VAE magnitude was the drift rate of the probe ($\underline{F}(2,10)=89.81$, $\underline{p}<0.01$), characterizing the typical aftereffect tuning. Across flow types, on average, perceived speed was reduced by

45% for probes slower than the adapter, by 29% for probes moving at the adapted speed, and by 14% for probes moving faster than the adapter. All paired differences in mean VAE magnitude between the three speed levels were significant (Tukey HSD, $p<0.01$).

This outcome suggests a straightforward interpretation. Since neither the magnitude, nor the tuning of the VAE changed as a function of the global radial directional structure, the present data provide no evidence that the global radial motion sensors targeted by the uniform flow make a unique contribution to velocity sensing. Instead, the present results suggest, that they rely on local velocity estimates, inherited from previous levels, as perceived speed changes in the same manner and to the same extent, regardless of the pattern of motion used or its spatial extent.

The present result does not contradict findings that different flow patterns have different apparent velocities (Qian & Andersen, 1996; Bex & Makous, 1997). Complex motion sensors may rely on inherited velocity estimates but may integrate them differently into the percept of global flow speed. Although we did not test this explicitly, it is possible that the apparent speed of the uniform flow used in Experiment 2 is not the same as that of the scrambled flow in Experiment 1. Thus while within each type of flow, speed-matches may have been made between motions of different apparent velocities, our data indicate that these global velocities and the local estimates on which they are based responded in the same way to prolonged stimulation.

Before concluding, however, that radial VAEs are not different from those recorded with scrambled flow and localized sine gratings, two alternative accounts for the present findings should be examined.

The first alternative explanation concerns a potential measurement problem. Assessing the magnitude of the VAE requires a comparison between a motion probe that has been adapted and a comparison stimulus that has not been adapted. Typically, this is accomplished by presenting the match stimulus in a region of the visual field that has not been directly exposed to the adaptation stimulus. The assumption is that adaptation effects are confined to the location that is being adapted and probed, and do not "spill over" to adjacent or more remote regions. In Experiment 2, however, adaptation may not have been location specific.

Snowden & Milne (1996, 1997) have shown that prolonged exposure to radial motion in two juxtaposed display sectors produces "phantom" radial MAEs in display regions that have not been directly adapted. Presumably, partial radial flow adapts sensors with receptive fields covering a large part of the visual field, and hence, adaptation effects can be detected in display regions that are part of the adapted receptive field, but have not received direct stimulation. These "phantom" MAEs are at about half the strength of the conventional MAEs measured over the adapted location.

Although it is not known whether radial VAEs show similar spatial spreading, this remains a possibility in Experiment 2. If "phantom" VAEs have occurred following adaptation to uniform flow, they might have reduced the apparent speed of the comparison motion, leading to underestimation of the iso-directional VAEs, thus rendering them equivalent to those generated by the scrambled flow in Experiment 1. Phantom MAEs and VAEs are of less concern in the context of the scrambled flow pattern, as in this case, adaptation of the large-scale radial motion sensors is believed to be limited. The influence of this potential confound is assessed explicitly in Experiment 3.

Another account for the identical VAEs produced by the different flow patterns may be that, for some reason, the adaptation flow in Experiment 2 failed to engage the large-scale radial sensors of interest. This possibility is unlikely for at least two reasons. First, much of the existing research has isolated complex motion mechanisms successfully using impoverished or partitioned complex motion displays. Second, with the same stimuli, we find a differential effect of flow pattern on relative velocity judgments (see below). Nevertheless, Bex et al. (1998) have observed that reducing the orientation bandwidth of the radial stimulus has an impact on its perceived speed and can eliminate the speed overestimation effect documented with full-range radial motion. This suggests that although the direction selectivity of higher-order motion sensors can be revealed with piecemeal stimulation, their response to velocity may depend critically on the dimensionality of the stimulus. In the present paradigm, however, stimulus partitioning is essential to the measurement of the VAE, and therefore, cannot be avoided. Experiment 4 addresses this issue by changing the adaptation protocol in a way that optimizes the recruitment of complex motion mechanisms, specifically sensitive to radial flow.

4.3.2. Effects of Adaptation on Sensitivity to Differences in Speed

Average sensitivities to speed differences within the test flow are plotted in Figure 22, for expansion, and in Figure 23, for contraction, against the same data for scrambled flow, in Experiment 1 (horizontal line segments, re-plotted from Figure 14). Data points are average SDI-s (Y-axis), as a function of probe speed (X axis) and adaptation condition (different bar shades).

Several aspects of the results are immediately apparent in Figures 22 and 23. First, overall speed discrimination performance in the context of expanding and contracting flow patterns seems better (i.e. SDI-s are lower), in comparison to that for the scrambled flow in Experiment 1. Second, this advantage appears to be more pronounced for expansion than for contraction. Third, adaptation to expansion and contraction appears to enhance sensitivity to speed differences in the adapted direction, but only for test speeds slower than the adapter. There is no evidence for such facilitation at the adapted velocity, where, in fact, some impairment of differential speed sensitivity can be seen (i.e. adapted SDI-s increase, relative to baseline). Finally, the overall pattern of speed discrimination performance appears similar for expanding and contracting flow fields, but the variability of contraction SDI-s, averaged across conditions and subjects (average SE=1.5 %) is almost twice as high as that of expanding SDI-s (average SE=0.9 %).

Speed Discrimination as a Function of Type of Flow

The effect of flow structure on relative velocity judgments was evaluated by a three-way ANOVA on SDI (Table B4, Appendix B), with types of flow (expanding, contracting and scrambled), reference drift rate (1Hz, 1.5Hz, 2Hz) and adaptation conditions (baseline, iso-directional, counter-directional) used as main factors. While the triple interaction in this analysis was not significant, a significant main effect of flow type was found ($F(2,10)=15.836$, $p<0.01$). This effect was independent of test speed or adaptation condition. As found in Experiment 1, the main effects of test speed ($F(2,10)=13.779$, $p<0.01$) and adaptation condition ($F(2,10)=7.649$, $p<0.01$) were also significant, and so was the interaction between them ($F(4,20)=7.545$, $p<0.01$). No other interactions in this analysis were significant.

The main effect of flow structure was further examined with post-hoc and planned comparisons between means. Overall, across test speeds and adaptation conditions, speed sensitivity was superior in expansion ($M=0.09$), compared to that in contracting ($M=0.12$, Tukey HSD, $p<0.05$) or in scrambled displays ($M=0.14$, Tukey HSD, $p<0.01$). The simple effect of flow structure was most clearly expressed at baseline ($F(2,10)=25.078$, $p<0.01$); it was weaker and marginally significant after iso-directional adaptation

($F(2,10)=6.67$, $p<0.05$), and was not statistically significant after counter-directional adaptation (see Table B5, Appendix B).

Figure 24 shows the prominent effect of flow structure on baseline sensitivity to speed differences. Without prior adaptation to motion, and regardless of reference speed, SDI-s in expansion ($M=0.08$) were significantly lower than those in contraction ($M=0.12$, $F(1,5)=8.336$, $p<0.05$, planned contrast), and SDI-s in contraction were also significantly lower than those in scrambled flow ($M=0.15$, $F(1,5)=24.963$, $p<0.01$, planned contrast). The speed discrimination advantage for contraction, however, was not as consistent as the one for expansion, and therefore, did not reach significance in the overall analysis of the data.

Speed Discrimination as a Function of Adaptation Condition

For consistency with the analysis in Experiment 1, the effects of adaptation on speed discrimination performance were examined separately for expansion and contraction, respectively, as a function of reference speed.

Effect of Adaptation on SDI-s in Expansion

A two-way ANOVA was carried out on the expansion data, summarized in Figure 22. This analysis examined the influence of test speed and adaptation condition and confirmed that both factors influenced jointly speed discrimination performance as indicated by the significant interaction between them ($F(4,20)=3.193$, $p<0.05$; Table B6, Appendix B). Analyses of simple effects within this interaction revealed that test speed affected SDI-s significantly only at baseline ($F(2,10)=50.716$, $p<0.01$), in that speed sensitivity improved at faster test speeds (Table B7, Appendix B). Motion adaptation, on the other hand, affected SDI-s significantly only for probes moving slower than (1.0 Hz; $F(2,10)=6.962$, $p<0.05$), or at the same speed as the adapting motion (1.5 Hz; $F(2,10)=4.836$, $p<0.05$; see Table B8, Appendix B). Discrimination of test speeds faster than the adapter was not significantly different than baseline. Planned comparisons between means at the slowest drift rate (1Hz) indicated a significant *reduction of SDI-s* after iso-directional adaptation ($M_{iso@1Hz}=0.08$; $F(1,5)=30.449$, $p<0.01$), but not after counter-directional adaptation ($M_{contra@1Hz}=0.10$; $F(1,5)=1.775$, ns), in comparison to SDI-s at baseline ($M_{base@1Hz}=0.12$). By contrast, at the adapted drift rate (1.5 Hz) there was some *elevation of SDI-s* relative to baseline ($M_{base@1.5Hz}=0.07$). Planned comparisons at this reference level revealed that the elevation was not significant for tests moving in the adapted direction ($M_{iso@1.5Hz}=0.08$; $F(1,5)=3.125$, *ns*), but was significant for test moving opposite to the adapted direction ($M_{contra@1.5Hz}=0.11$; $F(1,5)=8.076$, $p<0.05$). Some sensitivity loss can also be noted at the fastest speeds, but it was not statistically important.

Effect of Adaptation on SDI-s in Contraction

Upon visual inspection, the pattern of speed-discrimination results for contracting tests (Figure 23) is similar to that for expansion (Figure 22). In a two-way ANOVA on contracting SDI-s, however, neither the main effect of motion adaptation nor its interaction with test speed reached significance, masked by the high variance in these data (Table B9, Appendix B). The main effect of test speed, however, was significant ($F(4,20)=12.715$, $p<0.01$). Once again, analysis of simple effects indicated that speed discrimination was significantly better for faster tests, but only prior to adaptation to motion ($F(2,10)=21.757$, $p<0.01$; Table B10, Appendix B). Also, as expected, at the slowest test speed, there was some *reduction of SDI-s* after iso-directional adaptation ($M_{iso@1Hz}=0.12$), but in the contraction data this reduction was not statistically different from baseline ($M_{base@1Hz}=0.15$). Again, as found for expansion, adaptation to contraction did not facilitate subsequent speed discrimination for tests moving at the same speed, or faster than the adapter. Instead, at these drift rates, there was a slight *increase in SDI-s* following adaptation, with no indication that this increase was direction specific. Planned comparisons between means showed that the SDI elevation reached significance only for iso-directional tests moving at the adapted speed ($M_{base@1.5Hz}=0.09$; $M_{iso@1.5Hz}=0.11$; $F(1,5)=14.439$, $p<0.05$), although the same trend was present for contra-directional tests, and for tests moving faster than the adapter.

Adaptation-Induced Changes in Speed Sensitivity in Experiments 1 and 2

Figure 25 displays changes in speed discrimination performance following iso-directional adaptation to scrambled (Experiment 1), expanding (Experiment 2) and contracting flow (Experiment 2). As in Figure 15 (Experiment 1), the change in sensitivity is represented by ratios between post-adaptation to pre-adaptation SDI-s. The general trend in the data is that adaptation effects in scrambled and uniform flow show a similar dependence on test speed (i.e. tuning) in that speeds slower than the adapter are most profoundly affected, while discrimination of faster speeds remains largely unchanged. Accordingly, the three-way ANOVA indicated a non-significant triple interaction between type of flow, test speed and adaptation condition, emphasizing that the tuning of these post-adaptation changes in discrimination ability are independent of the pattern of flow.

A closer look at the data, however, reveals that when discrimination is tested at the adapted velocity, the effects of scrambled and uniform adaptation are of the opposite sign (Figure 25, reference drift rate of 1.5Hz). While partial adaptation to scrambled flow facilitates subsequent speed discrimination between scrambled tests (Experiment 1), partial adaptation to contraction and expansion compromises subsequent sensitivity to speed differences in the same type of flow (Experiment 2). Although there is a significant loss of apparent speed for tests moving at the adapted velocity, there is no corresponding reduction in the minimum speed difference supporting reliable discrimination. The present analysis is not powerful enough to establish the statistical significance of this divergence in tuning, but it is consistently present in the average data, with both contracting and expanding tests.

Several aspects of the present speed discrimination results are intriguing, as they could not be predicted from existing research. First, we find that human sensitivity to speed differences between non-overlapping regions *within* the same flow field depends on the global directional structure of the flow. Sensitivity to relative speed is best in expansion, in comparison to contracting and scrambled displays. Speed discrimination in contraction is only slightly better than in scrambled displays, and relative speed judgments in contraction are more variable than in the context of the other two types of flow. We believe that these differences reveal the unique contribution of large-scale, radial motion mechanisms to speed discrimination performance. The advantage of expansion over contraction, in particular, is consistent with the expansion bias in neuronal preferences, where cells in primate area MST-d selective for centrifugal motion outnumber those selective for centripetal motion, as well as for other configurations of flow (e.g. Tanaka et al., 1986; Graziano et al., 1994). Accordingly, the more efficient comparison between expanding speeds across space may be attributed to the denser representation of this type of motion in extra-striate visual cortex.

The failure of previous studies to observe a differential effect of flow pattern on speed discrimination performance is most likely due to the specific context in which relative velocity judgments were made (Sekuler, 1992; Clifford et al., 1999). All existing findings are based on temporal comparisons between motion stimuli presented sequentially over the same region of the visual field. This paradigm does not necessitate the recruitment of motion mechanisms with large spatial extent as it allows the speed comparison to remain strictly local. By contrast, in the present experiments the comparison is between non-overlapping flow regions and, hence, mandates the involvement of such mechanisms.

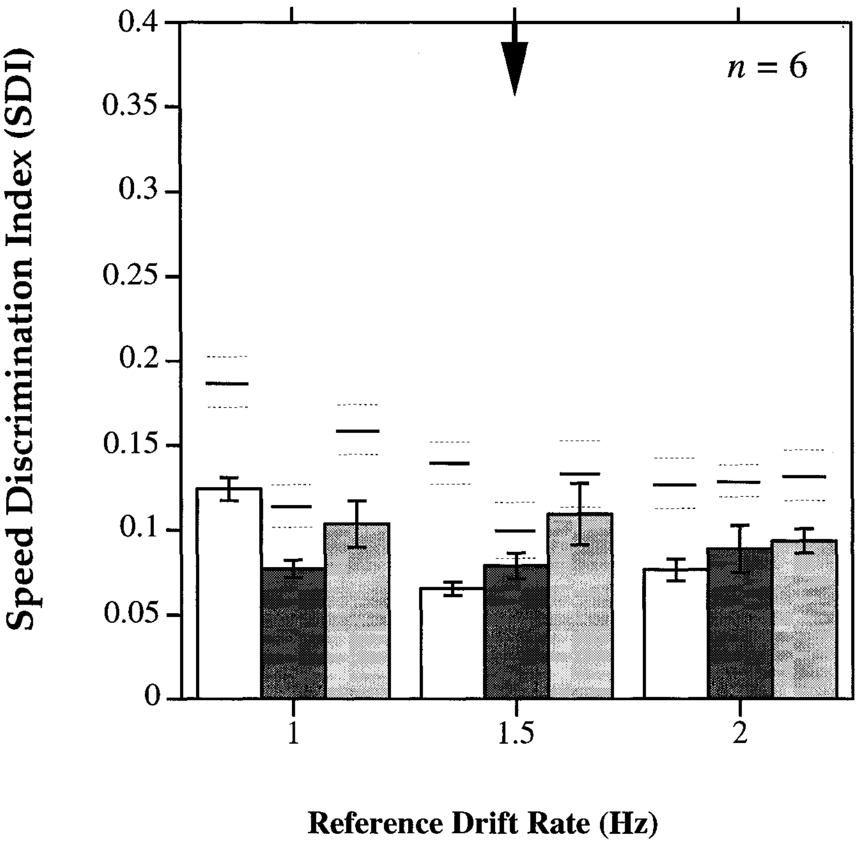


Figure 22. Effects of adaptation on differential speed sensitivity in expanding flow (Experiment 2).

SDI is a fraction of the reference value. Average data from all six observers at baseline (□) and after adaptation to iso-directional (■) or contra-directional (▒) flow. Error bars show standard errors. Horizontal lines indicate performance level for scrambled flow (see Figure 14).

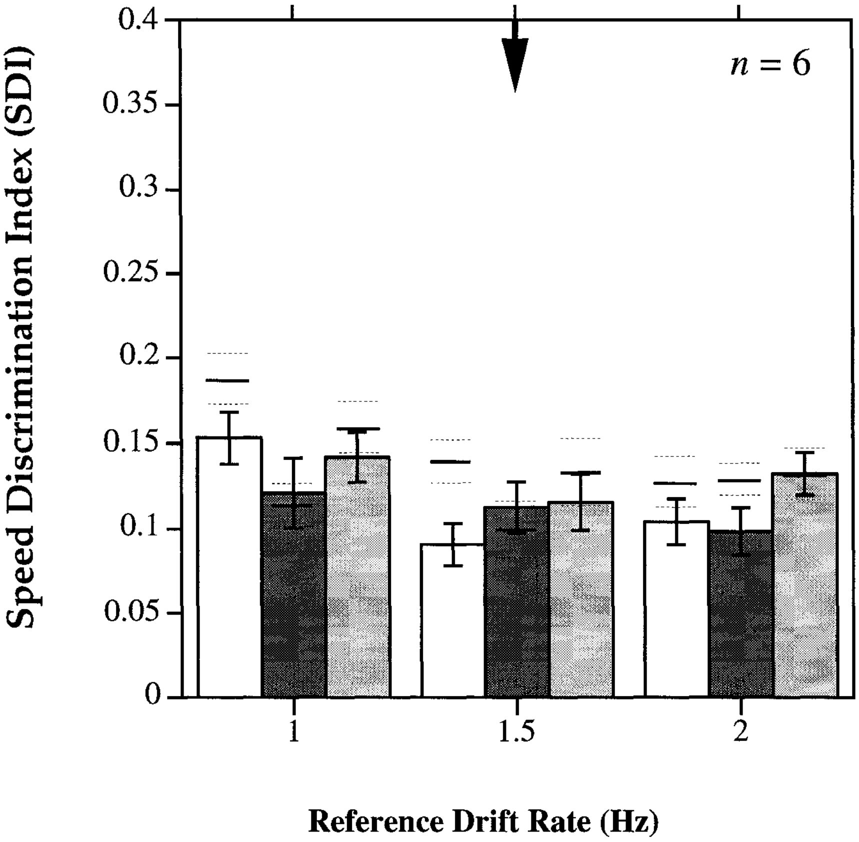


Figure 23. Effects of adaptation on differential speed sensitivity in contracting flow (Experiment 2).

SDI is a fraction of the reference value. Average data from all six observers at baseline (☐) and after adaptation to iso-directional (■) or contra-directional (▨) flow. Error bars show standard errors. Horizontal lines indicate performance level for scrambled flow (see Figure 14).

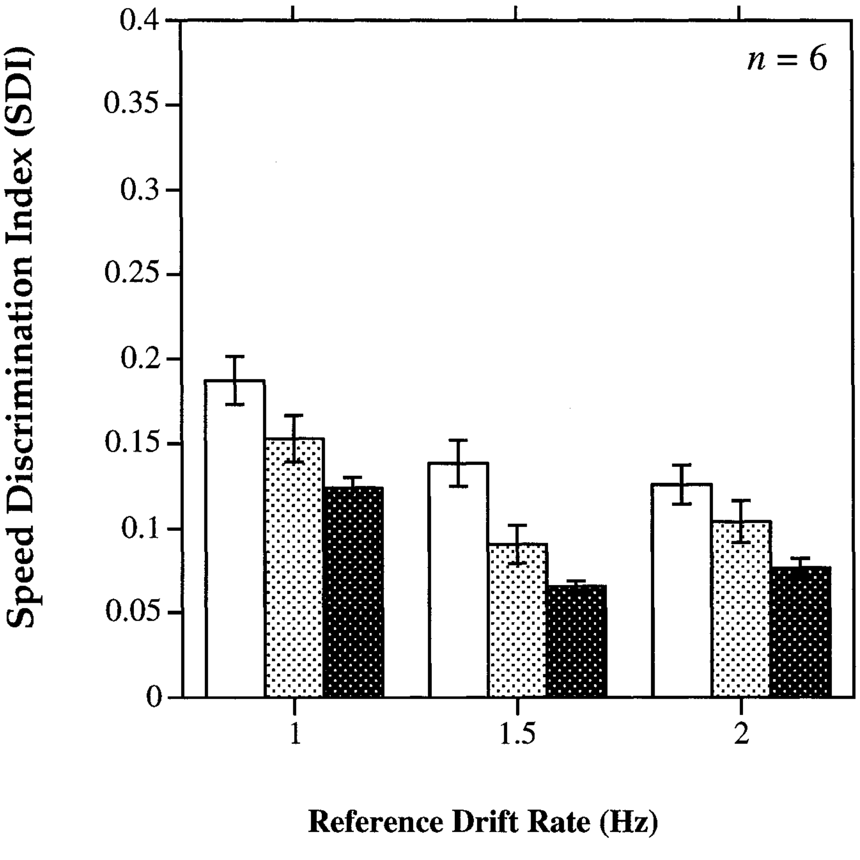


Figure 24. Effects of global flow structure on differential speed sensitivity (Experiments 1 and 2).

SDI is a fraction of the reference value. Average data from all six observer for "scrambled" (□), contracting (▨), and expanding (■) flow. Error bars show standard errors.

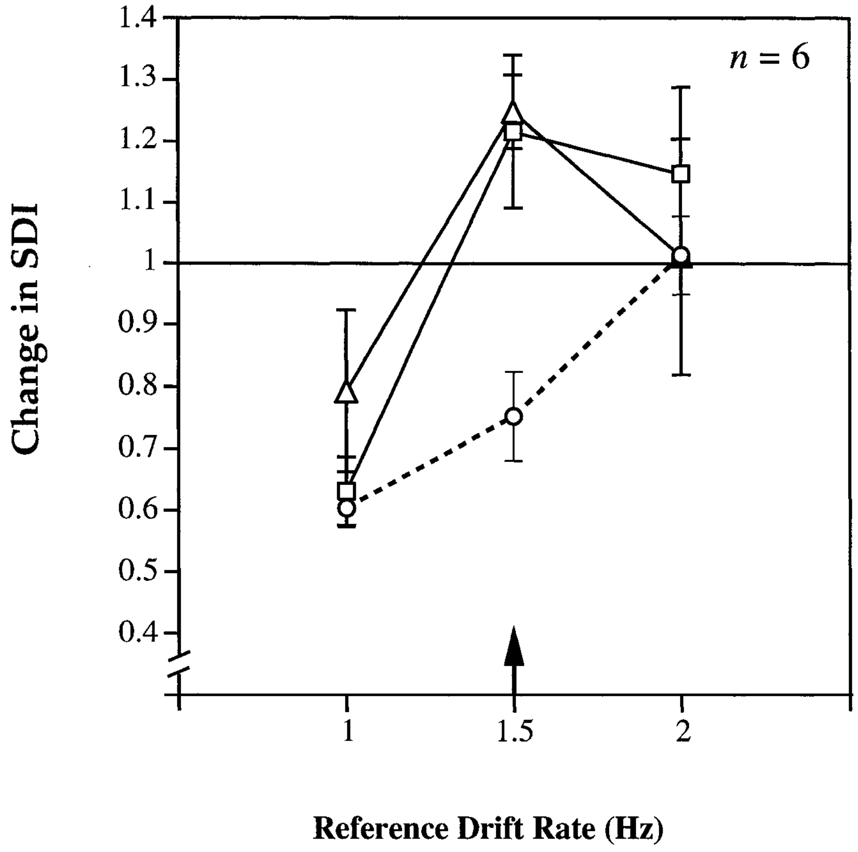


Figure 25. Comparison of changes in speed sensitivity after iso-directional adaptation (Experiments 1 and 2).

Values on the Y-axis are average ratios of post-adaptation to baseline SDI-s, for scrambled (···○···), expanding (—□—) and contracting (—△—) flow. Error bars show standard errors. Black arrow indicates the drift rate of the adapting flow.

Another finding of interest is that the differential effect of flow pattern on relative velocity judgments is most prominent at baseline, when the comparison is time-limited (500±50 ms) and is not preceded by prior exposure to motion. By contrast, adaptation to motion tends to equate speed sensitivity within the three different flow patterns, and the initial advantage of uniform over scrambled flow dissolves. One might expect that pattern-of-motion effects would be better established with prolonged viewing, as the integration of radial directional signals into a global percept takes a long time (≈ 3 minutes, Burr & Santoro, 2000), and the same applies to the extraction of a global trajectory from this motion (Verghese & McKee, 2002). Our results attest to the contrary. The definite speed discrimination advantage for expanding motion observed with brief presentation of an unexpected test pattern (contracting or expanding) implies that the detection of speed discontinuities within the flow-field *precedes* the extraction of the global direction-of-motion and its subsequent use for navigational guidance.

The decline in speed sensitivity around the adapted velocity after adaptation to uniform flow suggests that once a global velocity/trajectory percept is formed, it may interfere with subsequent relative speed judgments (Verghese & McKee, 2002). No such interference was recorded following adaptation to scrambled flow, where no meaningful global percept is formed. Further experiments are needed to clarify the nature of this interference and its direction and velocity specificity, in particular.

The difference in sensitivity to speed differences for expanding and contracting test patterns is of particular interest. It was also apparent in the data obtained throughout practice (not presented). Expansion speed-matching functions were steeper than contraction function to start with, but they also improved faster with practice. The fact that the expansion advantage persisted after at least three practice sessions suggests that it reflects a hard-wired anisotropy in the visual system. It is possible, nevertheless, that extended practice would eventually extinguish this difference in performance, as expansion and contraction SDI-s were very similar for the author. If this is the case, it may be argued that the anisotropy in MST-d itself is shaped by life-long environmental exposure and its influence on performance may be overridden with practice.

4.4. Summary

It is known that direction-of-motion perception is altered more profoundly by adaptation to radial motion than by adaptation to otherwise equivalent motions that translate in a single direction or do not form a meaningful global percept (e.g. Kelly, 1989; Bex et al., 1999b). The present results indicate that this may not apply to adaptation-induced changes in speed-of-motion perception. We find that adaptation to radial flow reduces the perceived velocity of that flow in the same manner and to the same extent, regardless of whether a meaningful global direction of motion is present (Experiment 2), or not (Experiment 1). Adaptation to scrambled, contracting and expanding radial flow patterns results in virtually identical VAEs when these effects are measured in the context of the same type of flow. This finding implies that the representation of velocity signals at motion processing levels specifically sensitive to radial flow is not fundamentally different from that at earlier levels, encoding local, one-dimensional motion. In other words, global radial motion sensors seem to estimate velocity in a way that is largely inherited from previous processing stages. Thus we find no evidence for a functional hierarchy in the extraction of speed information, similar to that extracting the direction-of-motion. The validity of this conclusion is further examined in Experiments 3 and 4.

By contrast, Experiment 2 (Figure 24) documents a robust effect of flow structure on speed-discrimination performance. Past studies find no evidence for such an influence by measuring sensitivity to speed differences between sequentially presented overlapping flow patterns. Using spatial speed matching, however, we find that detecting speed differences *within* an expanding flow field is better and more accurate than *in* contracting and scrambled displays. While this result is consistent with the expansion bias in neuronal preferences in optic-flow sensitive cortex, the influence of perceptual learning deserves further study.

The present pattern-based speed sensitivity bias seems to play a role in the initial analysis of the flow-field as it is most strongly expressed in the baseline condition, without prior exposure to motion. As expected, in Experiment 2, both perceived speed and speed sensitivity changed with adaptation to the same uniform flow as the one tested, and these changes remained related, but less perfectly so than when no coherent global direction of motion was present (Experiment 1). While speed discrimination in uniform flow improved for speeds slower that the adapter, it deteriorated around the adapted velocity. We attribute this interference to global integrative processes at that velocity, obscuring subtle speed differences between the test motions.

5. EXPERIMENT 3

5.1. Rationale and Hypotheses

Experiment 3 reassesses the aftereffects in Experiment 2, while controlling for "phantom" velocity adaptation, possibly affecting the perceived speed of the comparison stimulus (Snowden & Milne, 1997). Here, we make use of our finding that the apparent speed in the probed region remains unchanged after this region has been directly exposed to the opposite direction of motion. Since no measurable counter-directional VAEs occur at the adapted location, it is unlikely that such VAEs will occur at locations that have not received stimulation. Thus, if the match flow has a direction-of-motion opposite to the one adapted, its apparent speed should remain veridical, ensuring accurate measurement of VAEs in probe regions exposed to the adapting motion.

Experiment 3 differs from Experiment 2 only with respect to the nature of the test display, where probe flow is matched to comparison flow of the opposite sign (see t-boxes in Figures 26-28, Experiment 3), rather than to flow of the same direction (see t-boxes in Figures 16-18, Experiment 2). This change in the comparison motion allows us to investigate whether "phantom" adaptation has indeed confounded the measurement of the iso-directional VAE in Experiment 2 and to evaluate the magnitude of this influence. Consider the consequences of adaptation to expansion. In Experiment 2, the perceived speed of an expanding probe is measured against that of match flow which is also expanding (Figure 17, same direction trial, t1), while in Experiment 3, it is measured against that of a match flow which is contracting (Figure 27, same direction trial, t1). If phantom adaptation in Experiment 2 has reduced the perceived speed of the expanding match, leading to underestimation of the iso-directional VAEs, then the iso-directional VAEs in Experiment 3 will be stronger, because they would be free of this measurement error. On counter-directional trials, on the other hand, the perceived speed of a contracting probe in Experiment 2 is compared to that of match flow that is also contracting (Figure 17, opposite direction trial, t2), while in Experiment 3, it is judged against a match flow that is expanding (Figure 27, opposite direction trial, t2). In Experiment 2, no VAEs were observed in this condition, and this measurement is believed to be accurate because the comparison motion (contraction) was opposite to the adapting motion (expansion) and could not have been affected by remote adaptation. On counter-directional trials in Experiment 3, however, the apparent speed of the expanding match would be susceptible to remote adaptation, as the adapting motion is also expanding. If such influence does occur, it would reduce the perceived speed of the matching expansion, leading to a spurious increase in the perceived speed of the contracting probe. Thus the presence of "phantom" VAEs will be inferred from either one of two possible outcomes:

1. If the iso-directional VAEs in Experiment 3 are stronger than those recorded in Experiment 2.

2. If positive counter-directional VAEs are recorded in Experiment 3.

5.2. Method

5.2.1. Subjects

The same six subjects who completed Experiment 1 and 2 took part in Experiment 3.

5.2.2. Stimuli

The stimuli in Experiment 3 were identical to those in Experiment 2, except that probe and match flows in the test pattern had opposing global directions. For example, when an expanding adapter was replaced with an iso-directional probe (i.e. expansion), this probe was paired with a match flow that was contracting (Figure 27, same direction test, t1). Similarly, when an expanding adapter was followed by a counter-directional probe (i.e. contraction), this probe was paired with an expanding match (Figure 27, opposite direction test, t2). Thus expanding speed was judged against that of contraction (t1), and contracting speed was judged against that of expansion (t2). In all tests, the probe flow (black arrows) and the matching flow (white arrows) had opposite global directions-of-motion.

5.2.3. Procedure

Experimental Sessions

Experiment 3 followed the same procedure as Experiment 2. It comprised the same three experimental sessions, in which speed-matching data were collected without prior exposure to motion (baseline, Figure 26), and after adaptation to expansion (Figure 27) or contraction (Figure 28), respectively. Raw data were analyzed in the same manner as in Experiment 2, and were based on the same number of stimulus repetitions.

Experimental Conditions

As in Experiment 2, speed-matching functions were obtained for each subject, in three conditions of interest, as outlined below. Again, this was done separately for expanding and contracting probes, at each one of the three reference drift rates (1Hz, 1.5Hz, 2Hz).

A: Expansion-to-Contraction Speed-Matching

1) perceived non-adapted speed of expansion
   [all *t1 baseline data* in straight (Figure 26) and reversed displays].

2) perceived speed of expansion after iso-directional adaptation

[all *t1 same motion data* in straight (Figure 27) and reversed displays].

3) perceived speed of expansion after contra-directional adaptation

[all *t1 opposite motion data* in straight (Figures 28) and reversed displays].

B: Contraction-to-Expansion Speed-Matching

1) perceived non-adapted speed of contraction

[all *t2 baseline data* in straight (Figure 26) and reversed displays].

2) perceived speed of contraction after iso-directional adaptation

[all *t2 same motion data* in straight (Figure 28) and reversed displays].

3) perceived speed of contraction after contra-directional adaptation

[all *t2 opposite motion data* in straight (Figure 27) and reversed displays].

As in Experiment 2, in Experiment 3 three psychometric functions were obtained from each subject, for each type of flow, at each of the three reference speeds, resulting in nine functions for expanding probes and nine functions for contracting probes, respectively. The psychometric functions of interest in Experiment 3 are summarized in Table C1 (Appendix C) for expanding probes, and in Table C2 (Appendix C) for contracting probes.

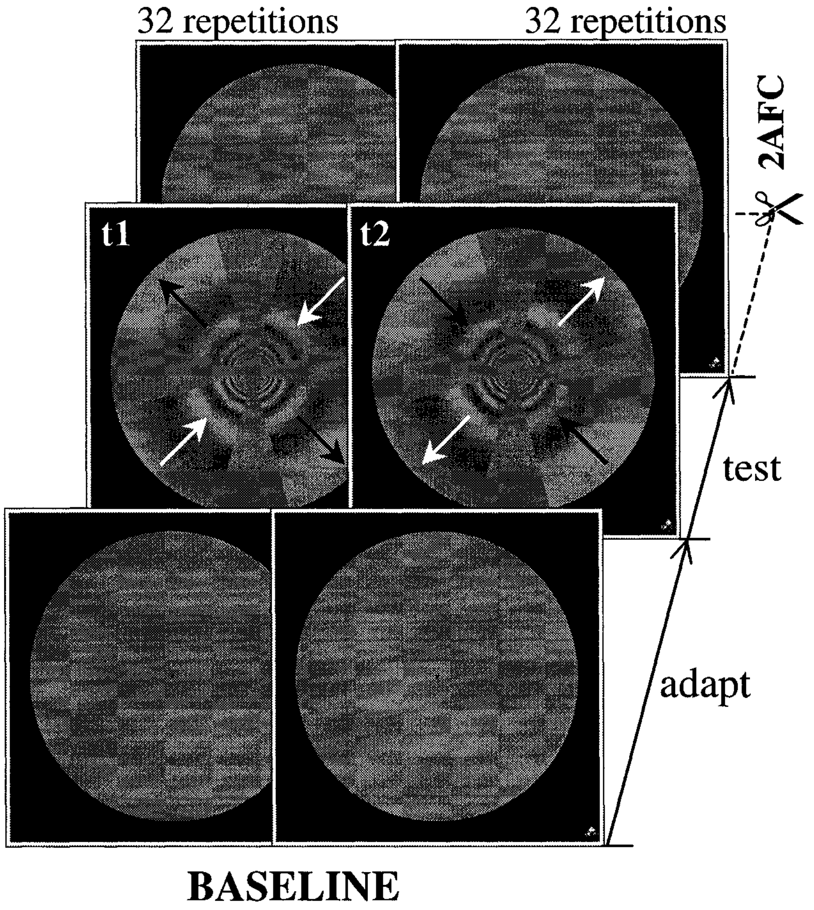


Figure 26. Baseline speed-matching in opponent radial flow (Experiment 3).

The probe flow (black arrows) and the matching flow (white arrows) have opposing global directions-of-motion.

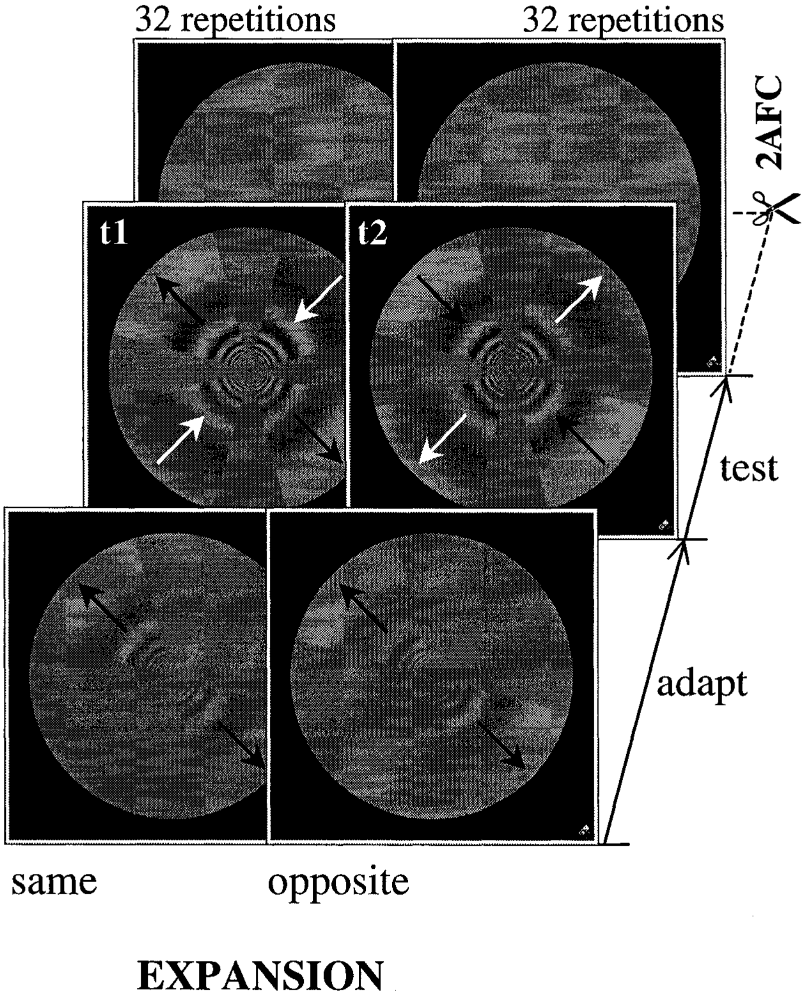


Figure 27. Speed matching after adaptation to expanding flow (Experiment 3). The probed direction-of-motion (black arrows) is the same as (t1) or opposite to (t2) the adapted direction-of-motion. The probe flow (black arrows) and the matching flow (white arrows) have opposing global directions-of-motion.

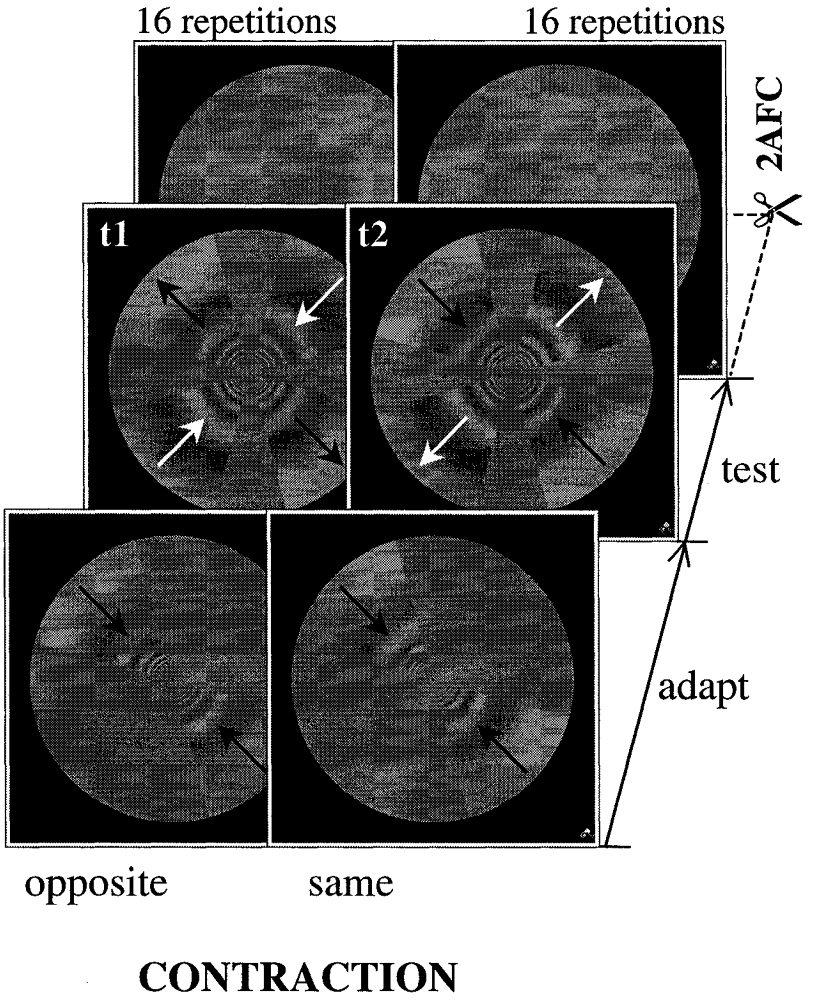


Figure 28. Speed matching after adaptation to contracting flow (Experiment 3). The probed direction-of-motion (black arrows) is the same as (t2) or opposite to (t1) the adapted direction-of-motion. The probe flow (black arrows) and the matching flow (white arrows) have opposing global directions-of-motion.

5.3. Results and Discussion

As in preceding experiments, individual psychometric performance in Experiment 3 was well described by a least squares logistic fit to the data. For expansion-to-contraction speed matching, on average, the percent of variance accounted for was M=98.8% (SE=0.18) and never fell below 94.4% (see r^2 values in Table C1, Appendix C). Similarly, for contraction-to-expansion speed matching, on average, the percent of variance accounted for was M=98.7% (SE=0.17) and never fell below 95.6% for individual subjects (see r^2 values in Table C2, Appendix C). On average, these values are only about 1% lower than those in Experiment 2 despite the more challenging nature of the opponent global speed matching. Most observers, however, needed two or three extra practice sessions until the r^2 values associated with their performance ceased to improve.

5.3.1. Effects of Adaptation on Perceived Speed

Average estimates of expanding speed, as matched to that of contraction, are presented in Figure 29. Average estimates of contracting speed, as matched to that of expansion, are shown in Figure 30. As in previous figures, average PSE-s relative to the reference level (Y-axis) are plotted as a function of probe drift rate (X-axis) and adaptation condition (baseline, iso-directional and contra-directional adaptation). Again, values of 1.0 indicate veridical speed-matches. The corresponding data from individual subjects are presented in Appendix C (Figures C1 - C6). Despite the higher level of variability in this data set, the pattern of results was consistent across observers.

Perceived Speed at Baseline

Without prior adaptation to motion, when presented at the same actual drift rate, contracting and expanding speeds were not judged as equal. On average, contracting drift rate had to be reduced by 13% to appear the same as that of expansion (Figure 29, dashed line). Similarly, on average, expanding drift rate had to be increased by 15% to be matched to that of contraction (Figure 30, dashed line). In other words, contraction was consistently seen as about 14% faster than expansion, when both motions were presented concurrently, at the same physical speed. This bias was seen across reference levels and regardless of whether the contracting flow was the match (Figure 29) or the probe (Figure 30). Although the overestimation of contracting speed was not significant for some subjects, the direction of this bias was consistent throughout (see 95%CI - open symbols / dashed lines in Figures C1-C6, Appendix C).

A similar bias was reported by Geesaman and Qian (1998), in temporal, rather than spatial speed matching. Contracting speed was overestimated by a similar amount and the effect was better established when expansion preceded contraction. The nature of this bias is not understood and it may be secondary to a decline in expanding velocity. It has been speculated that the human visual system adapts more rapidly, or is permanently adapted to expansion, due, presumably, to repeated environmental exposure to this type of flow (Lewis & McBeath, 2004). Assuming that simultaneously activated expansion and contraction detectors inhibit one another, the suppressed expansion response would provide less inhibition to contraction sensors, resulting in overestimation of contracting speed (Geesaman & Qian, 1998). It is to be noted, however, that during the first session of practice, the opposite bias was present: most observers reported difficulty comparing the speeds of the opponent test motions because the looming impression conveyed by the expanding flow dominated perception, masking the concurrent contraction. Without further instructions, speed-matching improved in subsequent runs for all subjects, suggesting that, somehow, the saliency of the looming signal subsided, or was intentionally suppressed. Since the two test flows exchanged positions randomly on each trial, deliberate selection of one flow over the other could not have been location-specific. Regardless of how the expansion dominance was resolved, this was done consistently by all subjects. This supports the idea that the expansion advantage may be transient and confined to novel situations in which flow direction is ambiguous and a quick perceptual decision is needed (Georgeson & Harris, 1978; Lewis & McBeath, 2004; Giaschi et al., 2007).

Contra-directional VAEs

As in preceding experiments, on average, velocity estimates for expansion (Figure 29) and contraction (Figure 30) remained unaffected by prior adaptation to the opposite direction-of-motion. Although contra-directional speed-matches deviated from those made at baseline for some subjects, these deviations were either insignificant or inconsistent between subjects (shaded versus open symbols, Figures C1-C6, Appendix C). In the average data for expansion (Figure 29) contra-directional PSE-s coincided with those at baseline. Similarly, average PSE-s for contracting probes were only slightly lower than baseline (Figure 30), as this difference was significant in the data from only two subjects (Figures C1-C6, Appendix C). Most important, there was no evidence that apparent speed increased, following adaptation to flow in a direction opposite to the one tested. The absence of positive counter-directional VAEs suggests that the perceived speed of the matching flow (which was in the adapted direction) was not reduced by "phantom" velocity adaptation.

Iso-directional VAEs

As expected, adaptation altered the apparent speed of flow in the adapted direction, but the magnitude of these effects depended on whether expansion or contraction was probed. Again, as previously recorded, iso-directional adaptation reduced the apparent speed of probes drifting slower than the adapter (i.e. at 1 Hz), and the magnitude of this VAE diminished as reference drift increased. This negative iso-directional VAE was observed for both types of flow, and for all subjects, (Figures 29 & 30, Figures C1-C6, Appendix C). The perceived speed of expansion, however, was less attenuated by iso-directional adaptation than the perceived speed of contraction when adapted speed was judged against that of the opposite flow. As shown in Figure 29, following iso-directional adaptation (black squares), expanding speeds equal to or above the adapted velocity were matched veridically to those of un-adapted contraction, and were overestimated, compared to baseline. By contrast, after iso-directional adaptation, contraction-to-expansion speed matches were not veridical as contracting flow at the adapted velocity was perceived as about 30% slower, compared to the same estimates made at baseline (Figure 30).

Comparison Between Iso-directional VAEs in Experiments 2 and 3

The iso-directional VAEs in Experiment 3 were further examined in comparison to the same VAEs recorded in Experiment 2. Figure 31 shows the average magnitude of the iso-directional VAE for expanding and contracting probes, as a function of reference drift rate in Experiment 2 (gray symbols), against the same measurements in Experiment 3 (black symbols). The distinction between expanding and contracting VAEs in Experiment 3 is apparent. Whereas the iso-directional VAEs for contracting probes in Experiment 3 were similar to those in Experiment 2, the effects of iso-directional adaptation on the perception of expanding speed depended strongly on the context of testing (Experiment 2 versus Experiment 3). In Experiment 2 the apparent speed of adapted expansion was judged as considerably slower than that of non-adapted expansion (Experiment 2), but less or no apparent velocity loss was recorded when the same probe was compared to non-adapted contraction (Experiment 3). In other words, a "recovery" from velocity adaptation was observed for expansion in the presence of a contracting match, but no such recovery occurred for contraction, in the presence of an expanding match.

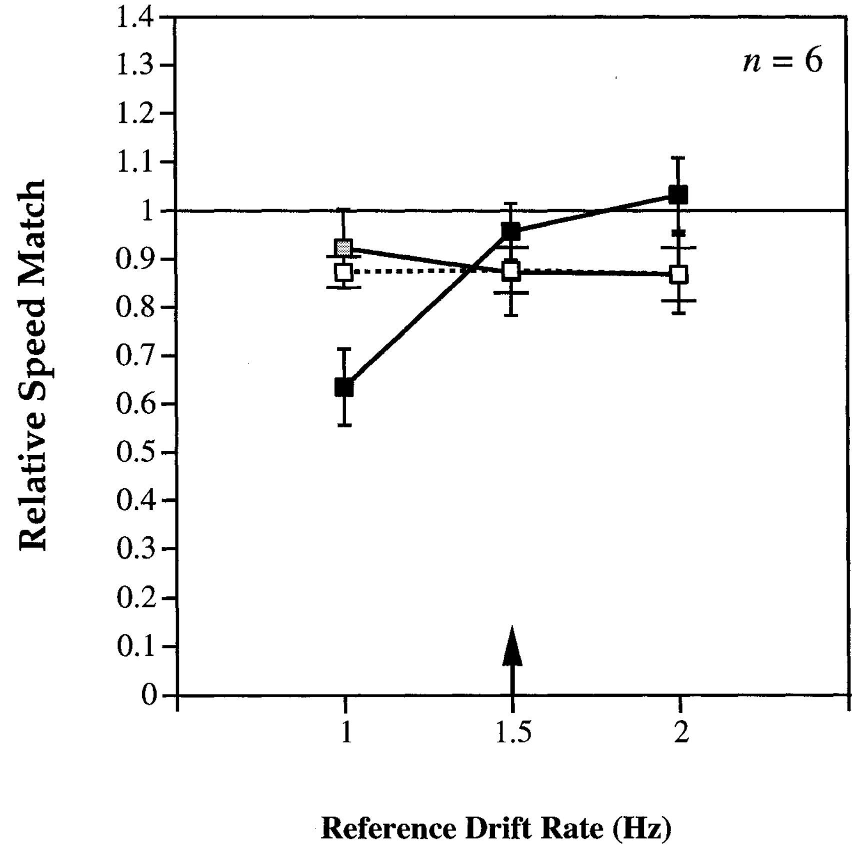


Figure 29. Effects of adaptation on the perceived speed of expanding flow (Experiment 3).

Expansion speed is compared to that of contraction. Matching values are expressed as fractions of the reference drift rate. Average data from all six observers at baseline (····□····) and after adaptation to iso-directional (—■—) or contra-directional (—▨—) flow. Error bars show standard errors. Adaptation drift rate is 1.5 Hz (black arrow).

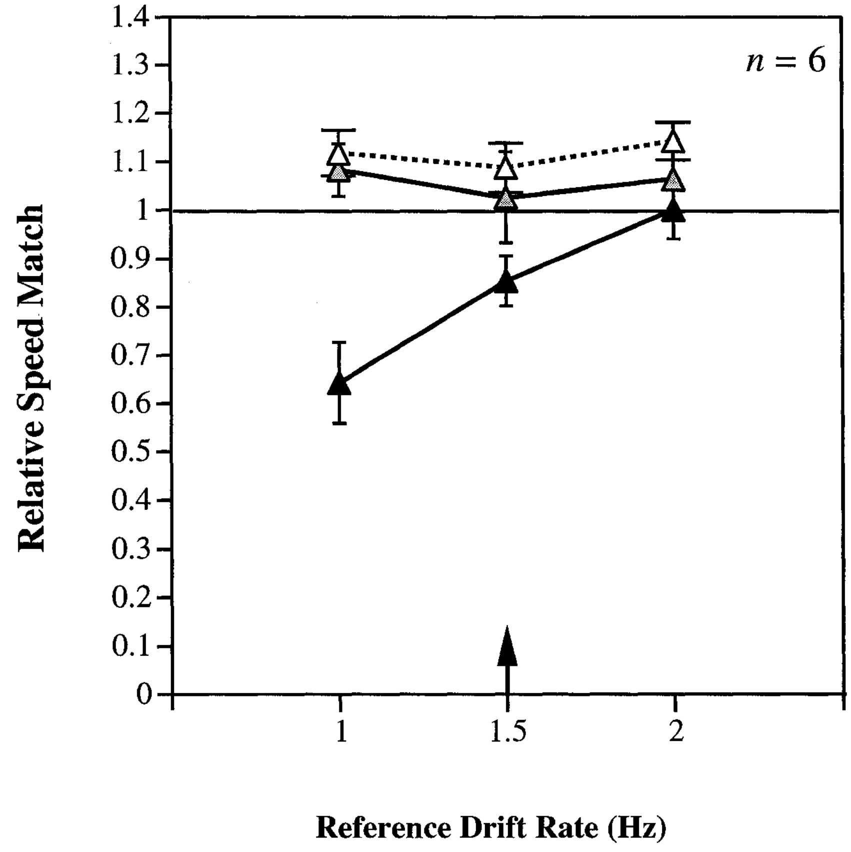


Figure 30. Effects of adaptation on the perceived speed of contracting flow (Experiment 3).

Contraction speed is compared to that of expansion. Matching values are expressed as fractions of the reference drift-rate. Average data from all six observer at baseline (····△····) and after adaptation to iso-directional (——▲——) or contra-directional (——◭——) flow. Error bars show standard errors. Adaptation drift rate is 1.5 Hz (black arrow).

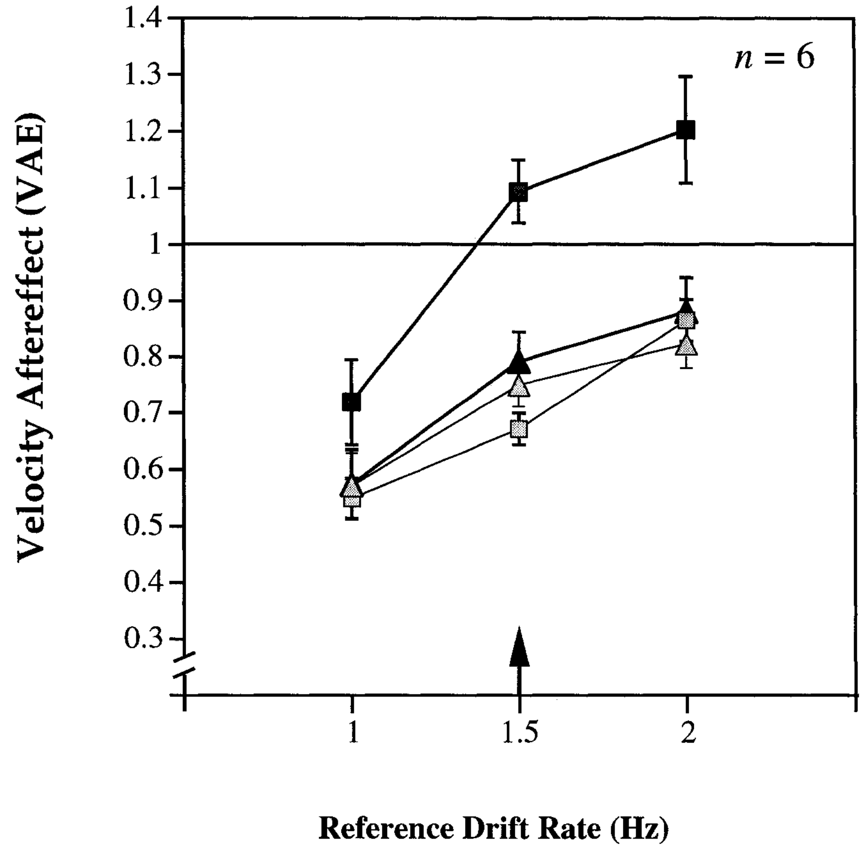


Figure 31. Iso-directional VAEs in Experiment 2 and 3.

Values on the Y-axis are average ratios of post-adaptation to baseline PSE-s for expanding (squares) and contracting probes (triangles), matched against flow in the probed direction-of-motion (—▨— , —△— , Experiment 2), or opposite to it (—■— , —▲— , Experiment 3). Error bars show standard errors. Black arrow indicates the drift rate of the adapting flow (1.5. Hz).

Results from a three-way ANOVA were consistent with these observations (Table C3, Appendix C). In this analysis, VAE magnitude was examined as a function of flow direction (expanding, contracting), reference drift rate (1Hz, 1.5Hz, 2Hz) and test context (uniform-Experiment 2, opponent-Experiment 3). The main effect of test context was significant ($F(1,5)=9.45$, $p<0.05$), but its interaction with flow direction was highly significant as well ($F(1,5)=15.77$, $p<0.01$). Simple effects analysis within this interaction confirmed that VAE magnitude depended on test context for expanding probes only ($F(1,5)=19.45$, $p<0.01$; Table C4, Appendix C), and that the difference between contracting and expanding VAEs was significant only in Experiment 3 ($F(1,5)=9.13$, $p<0.05$; Table C5, Appendix C). The main effect of test speed was also significant ($F(2,10)=102.67$, $p<0.01$; Table C3, Appendix C), in keeping with the typical VAE tuning. It also appears that the VAE tuning slope for expanding probes in Experiment 3 is steeper than that for the other VAEs (Figure 31), suggesting that velocity representation improves when this motion is presented against a contracting background. The present data, however, do not provide sufficient evidence for such a difference, as no significant interactions between test speed and flow direction, or between test speed and measurement context were found (Table C3, Appendix C). Thus, our analysis indicates a significant attenuation of the iso-directional VAE for expansion in Experiment 3, without a significant change in tuning.

The test displays used in Experiment 3 are characterized by strong motion contrast. The contrast is global in nature and concerns the entire display. It is between two opposing and coherent directions of flow with coinciding centers of motion - one expanding and the other contracting. The opposing flows coincide globally, but locally, they are not overlapping. Upon debriefing, our subjects reported that they experienced this motion contrast as a vivid relative motion in depth. According to one account, the virtual tunnel was seen as splitting, with half of it looming towards the viewer and the other half - moving backwards and further away. A common feature in all descriptions was the experience of sensory conflict and the difficulty in judging the speeds of the two flows simultaneously. It is to be noted that no rivalry was experienced in the scrambled flow in Experiment 1, where the same amounts of expansion and contraction were mixed, without forming a coherent pattern. This observation suggests that the test displays in Experiment 3 engaged independent opponent large-scale radial motion sensors drawing input from the same receptor surface. Since such sensors are rarely stimulated at the same time, their responses could not be integrated, resulting in perceptual rivalry. Although expansion and contraction often coexist in natural scenes (e.g. two-way traffic) they do not coincide spatially, as the same object translate forward and backward at the same time. Interestingly, our data indicate that observers resolved the sensory paradox consistently. Therefore, we believe that the present result reflects the nature of motion opponency at neural levels sensitive to optic flow.

Typically, perceived speed increases in the presence of motion contrast (De Bruyn & Orban, 1999) or of relative motion between different directions of motion (Edwards & Grainger, 2006). These effects have been documented only with fronto-parallel RDK motion. De Bruyn and Orban (1999) have shown that the speed enhancement could occur at different spatial scales, between superimposed, as well as between spatially segregated sheets of dots moving in opposing directions. In all cases, the enhancement effect is symmetrical in that the apparent speed of both component motions increases regardless of their motion direction (i.e. left or right, up or down). By contrast, in the present experiment, the coexistence of expansion and contraction affects their apparent speed asymmetrically. At baseline, contraction speed is perceived as faster but only after the initial dominance of expansion has been overcome. After iso-directional adaptation, the adapted speed of expansion returns to pre-adapted levels and even exceeds them, whereas no such "recovery" of apparent velocity is observed for contraction. During pilot testing, we had observed that prolonged exposure to opponent flow (expansion and contraction together) has no influence on the VAEs produced by adaptation to each motion alone. Therefore, the present selective boost in the perception of expanding velocity appears to be transient in that it is triggered by the change in flow structure between adaptation and test.

The present finding is hard to relate to existing research on complex motion perception, as expanding and contracting stimuli have been rarely presented together. The most obvious parallel is with the visual search asymmetry reported by Takeuchi (1997) who found that an expanding target popped out immediately in a field of contracting distractors, while search for a contracting target among expanding distractors was serial and time consuming. Since in this study all search items moved at the same rate, it is possible that expansion was easier to detect because its apparent speed was enhanced by the surrounding contraction, whereas no such enhancement occurred for a contracting target, surrounded by expanding distractors. Accordingly, it has been reported that search for targets defined by a speed increment is more efficient than search for a target defined by an equal decrement in speed (Irvy & Cohen, 1992). Similarly, observers are more sensitive to speed increments than to speed decrements in the same ongoing motion (Bex et al., 1999a). Although it is not entirely clear whether the selective speed enhancement causes, or is caused by attentional capture, the asymmetry seems to be mandatory and is not extinguished with practice (Takeuchi, 1997).

A sensory, rather than a cognitive interpretation of the present asymmetrical finding is also supported by spontaneous comments made by participants in our study. It was often reported that the impression of motion-in-depth declined with prolonged viewing of the expanding flow, but that looming was vividly reinstated as soon as contraction surrounded the same flow during testing. Thus the "recovery" of apparent expanding velocity may be linked to the enhanced perception of forward motion. Such a link has been previously considered by others, in attempts to explain why radial motion appears faster than otherwise equivalent translation and rotation (Bex & Makous, 1997; Bex et al., 1998). Asymmetries in the perception of motion-in-depth have also been documented. Approaching objects are easier to detect than objects receding in depth (Perrone, 1986; Shirai & Yamaguchi, 2004).

To examine explicitly whether the perception of 3D motion mediates the present VAE asymmetry, we repeated Experiment 3 after removing the spatial frequency/speed gradient from our stimuli. The spatial frequency of the sine wave was set arbitrarily at 0.5 cycles per degree. In the gradient profile this value corresponded to 9.5° eccentricity (see

Figure 4). The resulting radial flow appeared "flat", while its global direction-of-motion was preserved. The sole purpose of this additional testing was to establish whether the expansion/contraction asymmetry in the iso-directional VAE persists in the absence of motion contrast in depth, while 2D radial motion opponency is still present. Other aspects of the data were considered irrelevant, given that the speed content as well as the overall appearance of the motion flow was changed. Therefore, the outcome from this experiment will be presented in part only, in relation to the relevant question.

Three observers, including the author, ran the modified version of Experiment 3. Their average iso-directional VAEs are presented in Figure 32, for the "flat" (dashed lines) and for the "3D" flow-fields (solid lines), respectively. The corresponding individual data are presented in Figure C7, Appendix C. These results indicate that adaptation to the "flat" flow resulted in a strong reduction of its apparent speed, regardless of whether the centrifugal or the centripetal direction was tested. Thus the expansion-specific recovery from velocity adaptation recorded with the original flow seems to depend on the contrast between forward and backward motion-in-depth, rather than on the global motion contrast per se.

What may be the neural basis for this selective enhancement of the perception of approaching velocity, which is otherwise attenuated following adaptation, as indicated by results in Experiment 2? More research is needed before attempting to answer this question. Evidence should be sought within structures sensitive to both radial motion and motion in depth as no such asymmetry has been reported between opponent translational motions. The present asymmetry in the VAE implies an asymmetrical interaction between opponent radial motion sensors, or between preferred and anti-preferred responses within the large receptive field of the same cell. It is known that in MT, connections between motion detectors with opposite motion preferences are mostly inhibitory (Snowden et al., 1991). Although, typically, stimulation in the non-preferred direction causes no change or reduction in firing rate, it may also lead to increase in the response of a cell to its preferred motion (Petersen et al., 1985, Heeger et al., 1999). The latter physiological phenomenon is known as dis-inhibition and may play a role in the present experiments (Krekelberg et al., 2006c). Our findings suggest that both motion opponency and dis-inhibition may operate differently at levels of motion analysis concerned with the extraction of behaviorally meaningful 3D-motion signals. Based on partial evidence, this possibility has been suggested by several authors (Geesaman & Qian, 1998; Morrone et al., 2000; Krekelberg et al., 2006c; Heeger et al., 1999). We speculate that the functional connectivity between opponent radial motion sensors may be asymmetrical and unique, since a contracting background can enhance the perception of approaching motion, and reestablish its true velocity. We suspect that the level of activity in a contraction sensitive network may be critical for maintaining sensitivity to approaching objects, regardless of stimulus history. This, of course, is just an intriguing hypothesis, awaiting empirical tests.

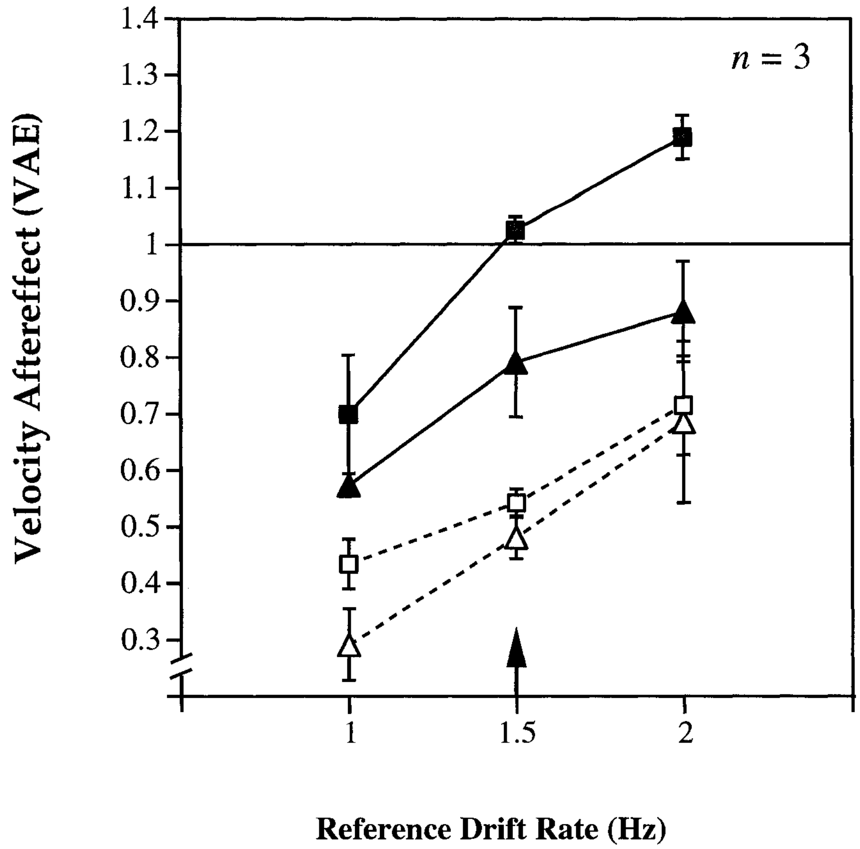


Figure 32. Iso-directional VAEs as a function of the 3D quality of the radial flow (Experiment 3).

Values on the Y-axis are average ratios of post-adaptation to baseline PSE-s for expanding probes with (—■—, 3D) or without a velocity gradient (---□---, FLAT), and for contracting probes with (—▲—, 3D) or without a velocity gradient (---△---, FLAT). Error bars show standard errors. Data from three observers (see Figure C7, Appendix C).

5.3.2. Sensitivity to Speed Differences in Opponent Flow

Average SDI-s (Y-axis) are presented for expansion-to-contraction speed-matching (Figure 33), and for contraction-to-expansion speed-matching (Figure 34), against the same data for scrambled flow (horizontal line segments, re-plotted from Figure 14, Experiment 1). Speed sensitivity data are plotted as a function of probe speed (X axis) and adaptation condition (different bar shades). Despite the subjective difficulty in comparing the speeds of two opponent flow patterns, performance level was not worse than that for the scrambled flow, although individual variability was much higher. Given the asymmetrical VAE findings, these two data sets were analyzed in comparison to one another. A three-way ANOVA was carried out on SDI-s in Experiment 3, as a function of probe direction (expanding, contracting), test speed and adaptation condition (Table C6, Appendix C). None of these factors exerted a significant influence on SDI-s.

These results indicate that sensitivity to speed differences was similar regardless of whether contraction or expansion was probed, and adaptation to motion did not alter speed sensitivity consistently either. In the same task, on the other hand, the perceived speed of the component motions was judged differently both before and following adaptation, and systematic VAEs were recorded. This is in sharp contrast to the correlated changes in speed perception and speed discrimination performance following adaptation to scrambled flow in Experiment 1. Taken together, these findings support the view that relative and absolute velocity judgements may respond differently to changes in the global stimulus context and may be constrained differently under certain condition, especially when higher levels of complex motion analysis are involved (Clifford et al., 2000).

Also, by contrast with our previous findings, no significant effect of test speed was found: speed discrimination did not improve as test motion became faster. In fact, we note the opposite trend (see Figures 33 and 34, white bars). This suggests that as the consolidation of the two global opponent velocity signals improved at faster speeds (Khuu & Badcock, 2002), the global rivalry between them intensified as well, interfering with the relative velocity judgments. An interference effect related to the global pattern of motion was also detected in Experiment 2.

Finally, it should be noted that speed discrimination in Experiment 3 was not effortless despite the clear perceptual segregation between the probe and the comparison flow. This is at odds with much of the evidence that speed discrimination improves if the component motions are seen as distinct perceptual entities, with distinct trajectories (Verghese & McKee, 2006). It may be argued, however, that expansion and contraction were not simultaneously (or equally) available to perception. Thus the test display supported the formation of only one perceptual object at a given moment in time, while the rivaling flow was seen as a background.

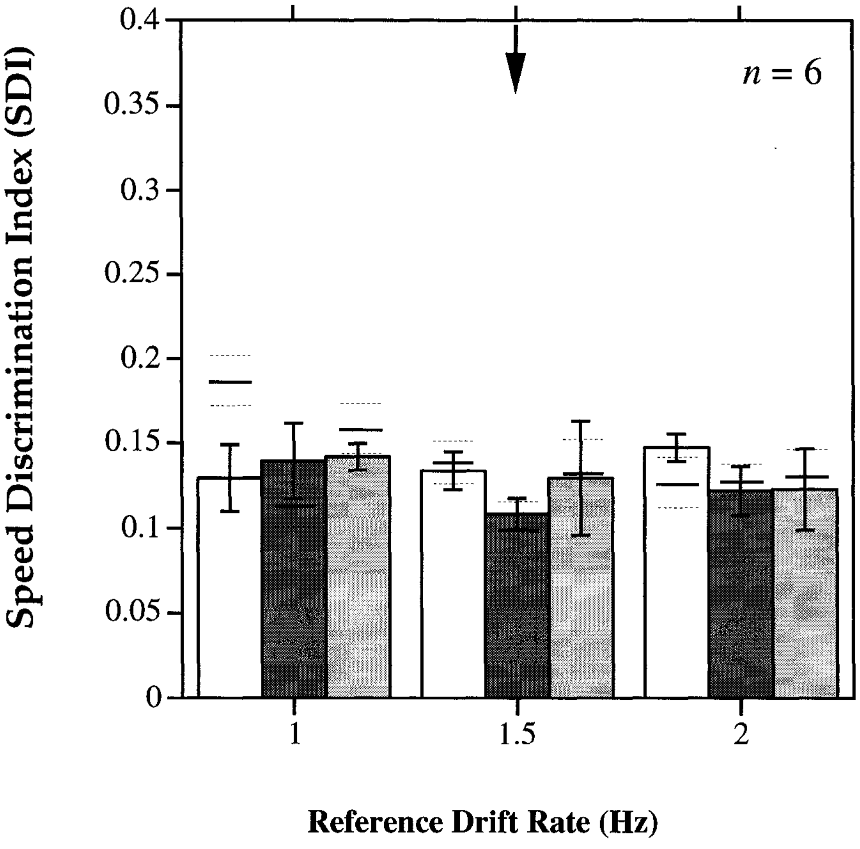


Figure 33. Effects of adaptation on differential speed sensitivity in expansion-to-contraction speed matching (Experiment 3).

SDI is a fraction of the reference value. Average data from all six observers at baseline (☐), and after adaptation to iso-directional (■) or contra-directional (▨) flow. Error bars show standard errors. Horizontal lines indicate performance level for scrambled flow (see Figure 14).

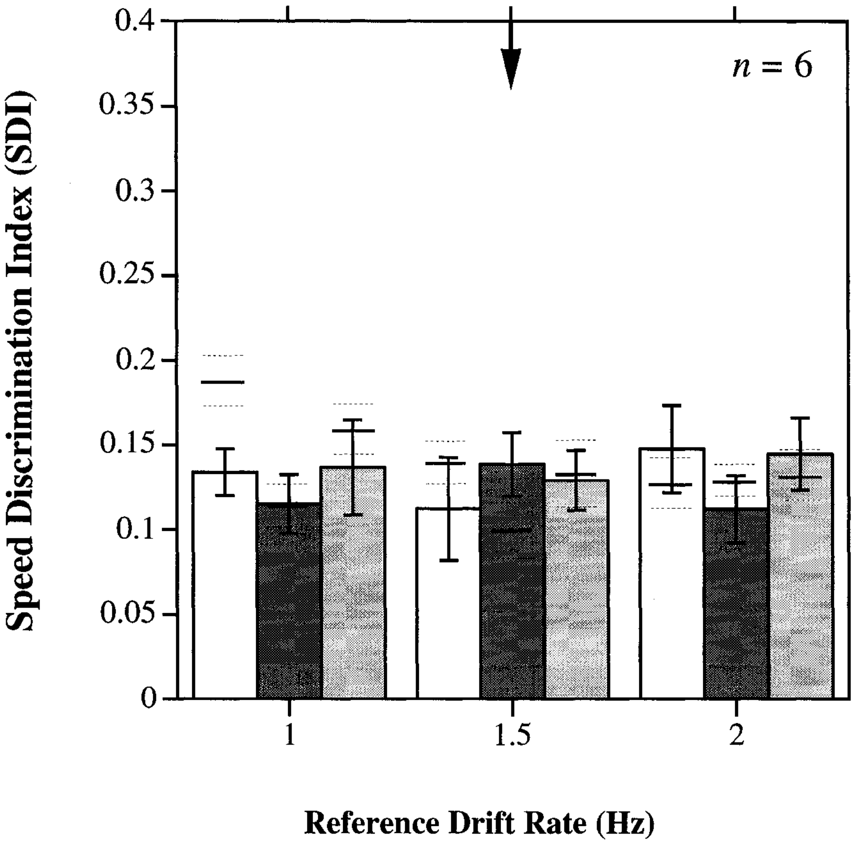


Figure 34. Effects of adaptation on differential speed sensitivity in contraction-to-expansion speed matching (Experiment 3).

SDI is a fraction of the reference value. Average data from all six observers at baseline (□), and after adaptation to iso-directional (■) or contra-directional (▨) flow. Error bars show standard errors. Horizontal lines indicate performance level for scrambled flow (see Figure 14).

5.4. Summary

Two aspects of these results are important. First, negative iso-directional VAEs in Experiment 3 were not stronger than those in Experiment 2, and they were, in fact, weaker, for expanding probes, in particular. No positive counter-directional VAEs were documented in Experiment 3 either. This is the opposite of what one might expect if the VAEs in Experiment 2 were underestimated due to adaptation spreading to non-adapted locations. Results are therefore inconsistent with the presence of "phantom" VAEs, reducing the apparent speed of the comparison stimulus. Thus radial VAEs are unlike the radial MAEs in that they seem to be confined to the adapted location. This validates the findings in Experiment 2 and supports the conclusion that global velocity estimates in radial flow are largely inherited, as they seem to build upon signals extracted at earlier motion processing levels.

At the same time, we find that the perception of radial flow velocity in one part of the visual field is not independent of the direction of flow in neighboring regions. In other words, although global radial velocity estimates seem to have local origins, and seem to arise independently for contraction and expansion, respectively, the final velocity percept is sensitive to the global motion context of which it is a part. The perception of expanding velocity, in particular, is strongly susceptible to transient contextual modulation. When expanding and contracting flow are concurrently present, the 3D impression of looming is enhanced and so is the speed of the approaching stimulus. When adapted expansion is judged in this context, its perceived speed recovers instantly to veridical levels. The modulation is asymmetrical in that no such recovery occurs for contraction. Motion in depth, task novelty and change in the flow pattern support the effect, while stimulus familiarity or longer exposures tend to reverse it, leading to some overestimation of contracting speed. We propose that these contextual influences reflect unique aspects of motion opponency in optic flow sensitive networks extracting motion-in-depth.

6. EXPERIMENT 4

6.1. Rationale and Hypotheses

Experiment 4 addresses the potential concern that the adaptation flow in preceding experiments did not engage sufficiently or selectively the large-scale radial motion sensors of interest. Such a possibility challenges the validity of our conclusions as it offers an alternative explanation of why uniform flow (Experiment 2) produced VAEs identical to those elicited by the scrambled flow (Experiment 1). Therefore, Experiment 4 reexamines the iso-directional VAEs obtained in Experiment 1 and 2 using an adaptation protocol known to recruit selectively optic flow-sensitive cortical regions in the human brain.

There is growing evidence that complex motion sensors beyond area MT are uniquely sensitive to changes in the flow pattern and some of their essential properties may not be revealed with continuous exposure to the same motion (Geesaman & Qian, 1998; Paolini et al., 2000, Beardsley & Vaina, 2005; Smith et al., 2006). This was convincingly demonstrated in a human fMRI study, where continuous exposure to unchanging translation, or to radiation/rotation/spiral motion activated the same area within MT+ complex, but when the same motions periodically reversed direction, anatomically separate loci emerged (Morrone et al., 2000). Gradual and abrupt reversals were equally effective, suggesting that the optic-flow response was not an artifact of the transition itself, but depended specifically on the change in the flow direction. Selective activation was determined relative to that elicited by locally matched random motion, which was also continuous or inverting, depending on the type of active stimulus used. Morrone et al. (2000) related the capacity of the inverting flow to activate preferentially an optic-flow sensitive region in the human MT+ cortex to the unique transient properties of neurons in homologue regions in primates (i.e. MST-d; Duffy & Wurtz, 1997b; Paolini et al., 2000).

Furthermore, Morrone et al. (2000) found evidence that the translation-sensitive and the optic-flow-sensitive regions are not only anatomically, but also functionally distinct from one another. First, they observed that the optic-flow region responded more strongly to inverting than to continuous flow, whereas the opposite was true for the translation-sensitive region. Second, although both regions responded to continuous motion, the optic flow region also responded to the corresponding control stimulus, whereas the translation region did not. The fact that motion in random directions activated the optic flow region but failed to activate the translation-sensitive region suggested a functional distinction between these two areas in MT+. The authors suspected that optic flow neurons did not exhibit the same type and the same degree of mutual inhibition as neurons selective to one-directional flow and, therefore, remained responsive when confronted with multiple motion directions (Morrone et al., 2000).

In Experiment 4 we apply the flow inversion used by Morrone et al. (2000) to maximize flow-specific neuronal engagement during uniform and scrambled flow adaptation. Although the present scrambled flow is not strictly translating, globally, it is not radiating either. In that sense, it shares features with both the one-directional and the concentric random stimuli used by Morrone et al. (2000). The present uniform radial flow, on the other hand, is well suited to activate the optic-flow region identified with the radial RDK-s used by Morrone et al. (2000). Therefore, we expect that periodic inversion of the present scrambled and uniform radial flow-fields will emphasize the distinction between the neuronal populations involved. A better separation between the neural responses to our stimuli may reveal a distinction between the psychophysical adaptation effects they elicit.

In Experiment 4, after prolonged viewing of direction reversals in scrambled or congruent radial flow, observers judged the perceived speed of the same type flow, in either one of the adapted directions. To facilitate comparison with our previous findings, cumulative exposure to each adapting direction was kept identical to that for the continuous flow (Experiments 1,2 & 3). Simultaneous measurement of visual evoked potentials and the MAE has shown that intermittent and continuous stimulation produce identical adaptation effects, as long as net stimulus duration remains the same (Heinrich et al., 2005). In the present study, on each trial, only a single flow direction is probed. Our preceding results indicate that the perceived speed of the motion probe will be affected only by the same direction component of the adaptation stimulus. Thus in Experiment 4, adaptation intervals containing the opposite motion may be considered as "blank", or neutral, as they are not expected to alter the perceived speed of the probe. In that sense, with respect to the probed direction of motion, adaptation to inverting flow may be regarded as intermittent.

It is known that adaptation to alternating opposing motions results in a minimal or no MAE since neuronal responses to each opponent direction are attenuated but remain balanced. It has been reported, however, that prolonged exposure to inverting motion reduces but does not extinguish the VAE (Thompson, 1976). This strengthens the argument that the VAE does not arise in the same way as the MAE and cannot be explained in the same manner. Based on this single but trustworthy report (Thompson, 1976), we expect that:

1. Adaptation to inverting flow in Experiment 4 will produce measurable VAEs, weaker than the ones recorded with continuous adaptation to unchanging flow (Experiments 1 and 2).

In the fMRI study by Morrone et al. (2000), the inverting random flow did not activate strongly either the translation-sensitive or the optic-flow-sensitive areas in the human MT+ complex. By contrast, the inverting radial flow activated selectively only the optic-flow region and this response was stronger than that to inverting translation in the translation-sensitive region. If our scrambled and uniform adaptation stimuli engage similar MT+ cortex selectively, we expect that in Experiment 4:

2. Inverting radial uniform flow adaptation will produce stronger VAEs than inverting scrambled flow adaptation.

If, on the other hand, our uniform flow does not engage optic flow processing mechanisms selectively, then no difference between the VAEs elicited by uniform and scrambled inverting flow should be found.

In addition to its primary purpose, Experiment 4 also explores directional asymmetries in the VAEs that might be accentuated by flow inversion. In Experiment 3 we found that expanding and contracting velocities interact asymmetrically when presented simultaneously over non-overlapping display regions. In Experiment 4 a temporal interaction between these motions is possible, as they alternate over the same retinal region. Moreover, observations with the opponent test fields used in Experiment 3 suggest that the change in flow direction is likely to repeatedly reinstate and enhance the impression of motion-in-depth. Both temporal order and motion-in-depth can modulate the apparent speed of radial motion, as suggested by some existing results (Geesaman & Qian, 1998; Clifford et al., 1999). As the apparent expanding and contracting velocities may not be equal when presented successively, this may introduce an asymmetry in the corresponding VAEs.

Results from Experiment 4 are only preliminary, as they are based on limited data. Nevertheless, they are considered informative, as they are consistent and comparable to preceding results.

6.2. Method

6.2.1. Subjects

Two of the six subjects who completed all preceding experiments took part in Experiment 4. One of them was the author and the other one was experimentally naive.

6.2.2. Stimuli

All stimuli were identical to those used in Experiments 1 and 2, except that they were presented differently during the adaptation phase on each trial.

6.2.3. Procedure

Trial Sequence

The temporal structure of all trials in Experiment 4 was as described in Experiment 1 (Figures 9 & 10) and Experiment 2 (Figures 17 & 18), except for changes made to the adaptation protocol.

(1) Adaptation Phase

In Experiment 4, the adaptation flow reversed its direction every 1.25 seconds. Adaptation lasted for 4 minutes on the first trial of each session, and was “topped-up” by 10 seconds on subsequent trials. Thus, cumulative exposure to each adapting direction was 2 minutes on the first trial, and ≈ 5 seconds on subsequent trials - i.e. the same as in Experiments 1 and 2. The starting direction of motion in the adapting sequence was counterbalanced across sessions, which also counterbalanced the flow direction, immediately preceding the test.

(2) Test Phase

All aspects of testing were identical to those in Experiments 1 and 2. In the test display, observers compared the perceived speed of the probe flow presented in the adapted pair of sectors, to that of the same type of flow in a non-adapted pair of sectors. Depending on the type of flow tested, the apparent speed of a scrambled probe was matched to that of a scrambled match (Figures 9 & 10, t-boxes), expanding speed was matched to that of non-adapted expansion (Figure 17, t1 box), or contracting speed was matched to that of non-adapted contraction (Figure 17, t2 box).

Experimental Sessions

Experiment 4 consisted of two types of sessions - one for scrambled, and one for uniform radial flow. Scrambled-flow sessions were identical to those in Experiment 1 (Figures 9 & 10), except that the adapting flow periodically reversed its direction. Uniform-flow sessions were the same as in Experiment 2 (e.g. Figure 17), except that expansion and contraction alternated throughout adaptation. Since no changes were made to the test protocol, adaptation effects for the two subjects were evaluated against their baseline data in Experiments 1 and 2. All aftereffects were regarded as iso-directional, as counter-directional adaptation was previously found to be ineffective.

Experimental Conditions

Table D1 (Appendix D) summarizes the conditions of interest and the corresponding psychometric functions derived from the raw data. The number of sessions and the number of trials in each session were as stated in Experiment 1 (Figures 9 and 10) and in Experiment 2 (Figure 17), yielding the same total number of observations per stimulus level (i.e. 64). Data from all inverting scrambled flow sessions were collapsed into a single speed-matching function. Data from all inverting uniform flow sessions defined two speed-matching functions - one for expanding, and one for contracting probes. As in preceding experiments, separate measurements were taken at each one of the three reference speeds. Results were then compared to the corresponding baseline data in Experiments 1 and 2. All other aspects of data collection and analysis were as previously described.

6.3. Results and Discussion

The r^2 values reported in Table D1 (Appendix D) indicate that the logistic fit to the raw data accounted almost completely for the variation in individual psychometric performance.

6.3.1. Effects of Adaptation to Inverting Flow on Perceived Speed

Scrambled Flow

Figure 35 presents the individual estimates of scrambled flow speed, without prior adaptation to motion (Experiment 1, baseline sessions), after adaptation to continuous scrambled flow of the same direction (Experiment 1, iso-directional sessions), and after adaptation to inverting scrambled flow (Experiment 4). Results from both observers indicate a significant reduction in perceived speed after adaptation to inverting flow, as indicated by the non-overlapping 95% confidence limits around adapted and baseline PSE-s. In keeping with previous findings, the reduction was significant only for probes moving at the same speed or slower than the adapter, with little or no effect at faster speeds. Remarkably, results also reveal that the VAE from adaptation to inverting scrambled flow is significantly weaker than the iso-directional VAE from adaptation to continuous scrambled flow (Experiment 1). For both observers, direction inversion reduced the magnitude of the VAE by about 50% in comparison to the same effect recorded with continuous flow.

Expanding Flow

Estimates of expanding flow speed without prior adaptation to motion (Experiment 2, baseline expansion-to-expansion speed matching), after adaptation to expansion (Experiment 2, iso-directional sessions), and after adaptation to alternating expansion/contraction (Experiment 4) are plotted for both observers in Figure 36. Again, alternate adaptation to expansion/contraction resulted in a significant apparent loss of expanding speed, inversely proportional to the reference drift rate. This VAE, however, was not different from that elicited by continuous adaptation to expansion alone (Experiment 2). The equivalence in the effects of inverting and continuous radial flow adaptation is evident in the speed-matching data from both observers, especially at the adapted velocity.

Contracting Flow

The corresponding speed estimates for contracting probes are presented in Figure 37. Data from baseline contraction speed matching (Experiment 2) are plotted against those obtained after adaptation to contraction only (Experiment 2, iso-directional sessions), and after adaptation to alternating expansion/contraction (Experiment 4).

Contraction VAEs following adaptation to inverting flow were identical to those obtained with continuous adaptation for the author, and were only slightly attenuated for the other observer. These preliminary observations suggest that inverting and continuous radial flow adaptation have very similar effects on perceived speed, regardless of whether expansion or contraction was probed.

6.3.2. Effects of Inverting Flow Adaptation on Speed Sensitivity

The individual SDI-s characterizing the speed-matching performance in Experiment 4 are presented in Figures D1, D2 and D3 (Appendix D), for scrambled, expanding and contracting flow, respectively. For comparison, these figures also show the corresponding baseline and iso-directional SDI-s, re-plotted from Experiments 1 and 2. Given the limited nature of these observations, they are included for reference only. Nonetheless, visual inspection suggests that inverting and continuous flow adaptation have comparable effects on speed discrimination performance in that a consistent improvement is seen for test motions slower than and in the same direction as the adapter.

The concordant results from both observers in Experiment 4 allow some preliminary inference. What may account for the finding that the VAEs produced by inverting scrambled flow are weaker than those produced by inverting coherent radial motion? From a hierarchical point of view, it may be argued that the coherent radial flow engages motion-processing levels beyond those responding to the scrambled flow. This would mean that the coherent flow activates a larger pool of neurons and defines a stronger velocity signal, which, in turn, produces a stronger VAE, consistent with the stronger complex MAEs documented. If this is so, however, such a difference should occur, regardless of whether adaptation is continuous or inverting. Our findings are inconsistent with this explanation. They indicate that, as far as the VAE is concerned, motion-pattern effects are only observed when opponent directions alternate during stimulation but not when the direction of the adapting stimulus is maintained. Furthermore, in the fMRI study by Morrone et al. (2000), the translation-specific response was localized to a smaller area than the optic-flow-specific response, but the amplitude of the former was larger. Such evidence argues against a cumulative, hierarchical scheme. The overall strength of the neural response associated with complex and translational flow seems comparable, and adaptation to continuous flow results in VAEs that are insensitive to the global pattern of motion. Instead, our findings suggest that responses specific to the global pattern of motion arise in populations of neurons that diverge in extra-striate motion sensitive cortex, both in anatomical and functional terms. Therefore, differential adaptation effects would occur only if the task and stimuli tap the unique functional properties of these populations. For example, a difference between the MAEs from complex and translational motion does not necessarily imply an initial difference in overall response levels. Instead, it might reflect a higher degree of direction-selectivity in optic flow sensitive regions, in comparison to regions sensitive to one-directional flow. Accordingly, adaptation to complex motion would result in a stronger direction-specific imbalance (i.e. the MAE), than adaptation to translational flow.

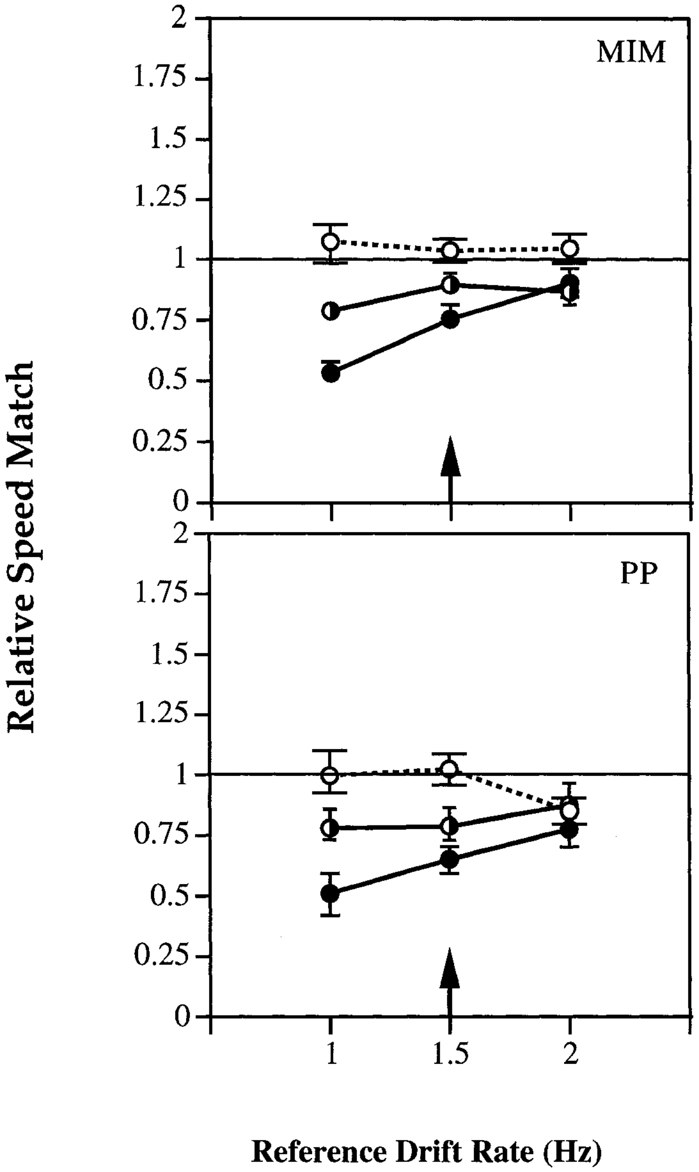


Figure 35. Effects of inverting scrambled-flow adaptation on perceived speed in scrambled flow (Experiment 4).

Probe speed is matched to that of non-adapted flow of the same type. PSE-s relative to the reference level are shown for the author (MIM) and a naive observer (PP), at baseline (····○···· Experiment 1), and after adaptation to scrambled flow that does not change (—●— Experiment 1) or periodically reverses direction (—◐— Experiment 4). Error bars indicate the 95% CI-s associated with each estimate.

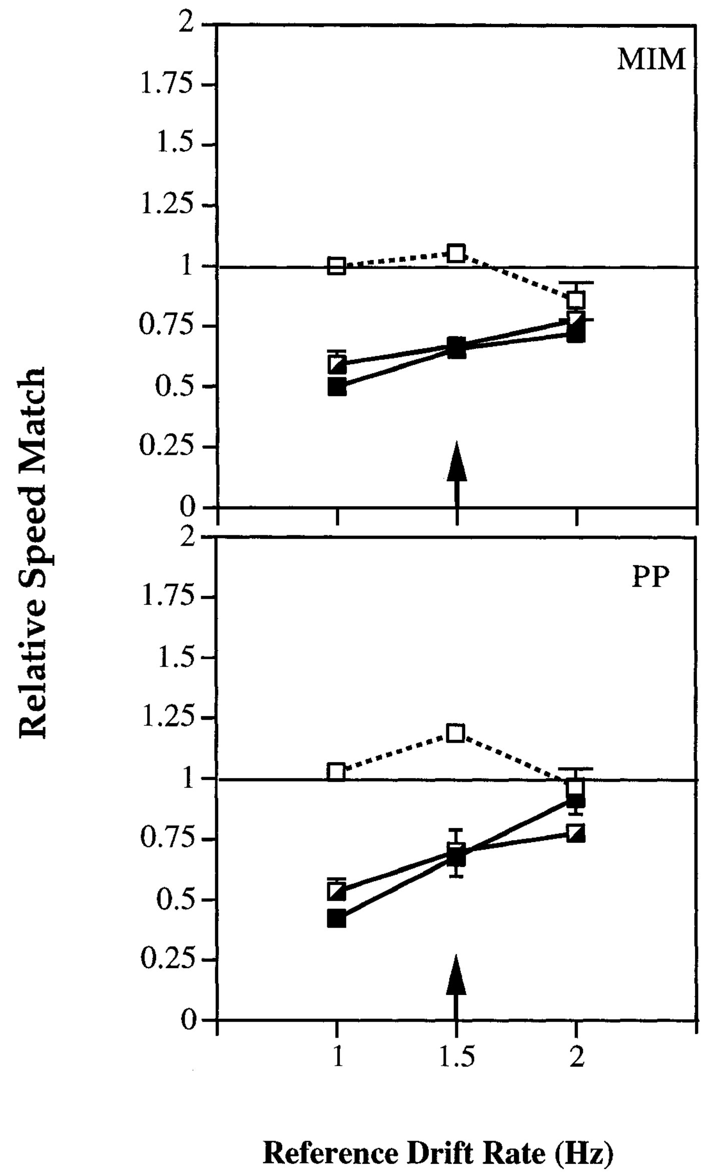


Figure 36. Effects of inverting uniform-flow adaptation on perceived speed of expansion (Experiment 4).

Probe speed is matched to that of non-adapted flow of the same type. PSE-s relative to the reference level are shown for the author (MIM) and a naive observer (PP), at baseline (····□···· Experiment 2), and after adaptation to expansion only (——■—— Experiment 2) or to alternating expansion / contraction (——◪—— Experiment 4). Error bars indicate the 95% CI-s associated with each estimate.

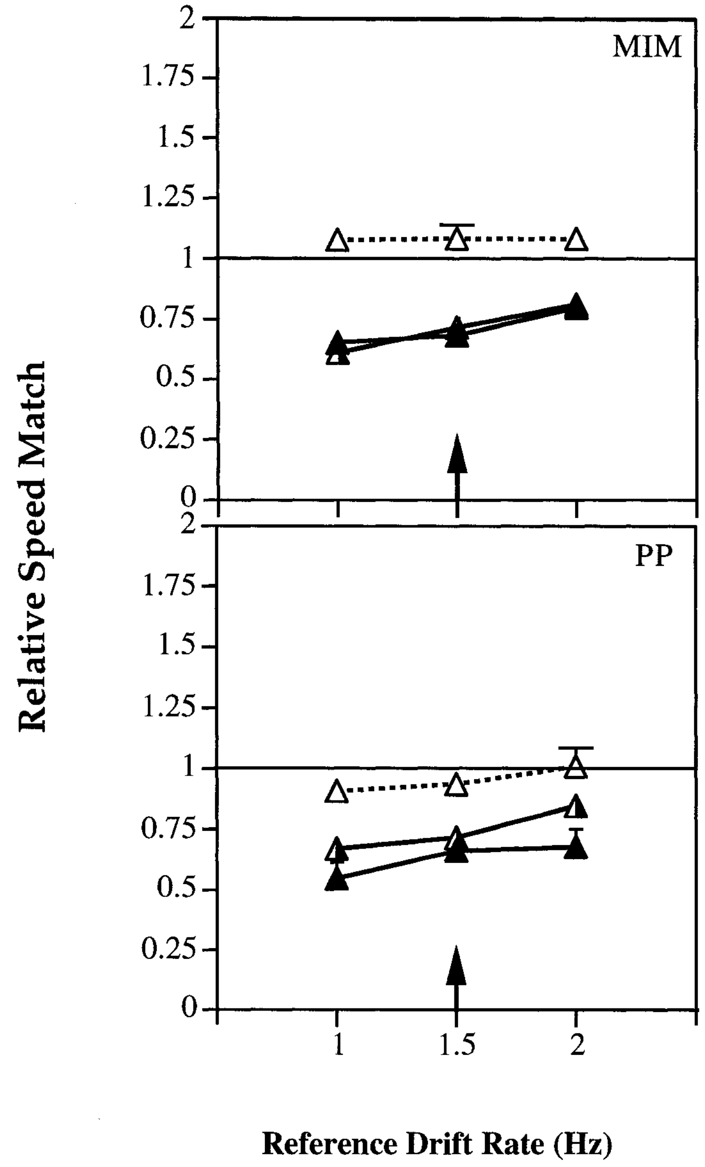


Figure 37. Effects of inverting uniform-flow adaptation on perceived speed of contraction (Experiment 4).

Probe speed is matched to that of non-adapted flow of the same type. PSE-s relative to the reference level are shown for the author (MIM) and a naive observer (PP), at baseline (····△···· Experiment 2), and after adaptation to contraction only (—▲— Experiment 2) or to alternating expansion / contraction (—△— Experiment 4). Error bars indicate the 95% CI-s associated with each estimate.

Why does flow-inversion produce distinct VAEs depending on whether the global pattern of motion is coherent or scrambled, whereas continuous stimulation does not? What unique aspect of optic flow processing underlies this distinction? Several possibilities will be considered.

First, the different VAEs elicited by the inverting scrambled and coherent radial flow might reflect different temporal integration limits for these two types of motion. If the scrambled radial signal requires more time to reach full strength than the coherent radial signal, the 1.25 seconds' exposure episodes might have placed the scrambled flow at a disadvantage, thus reducing the VAE it produces. There is no research evidence, however, to support this proposal. To the contrary, it has been shown that detection of one-directional signals which do not form a complex global pattern of motion becomes optimal within a 1 second exposure, whereas detection of global radial motion continues to improve for up to 3 seconds (Burr & Santoro, 2001). In addition, results in Experiment 1 and 2 indicate that baseline speed discrimination for both scrambled and uniform flow improves similarly as test speed increases, implying comparable temporal integration dynamics (see Figures 14, 22 & 23, white bars across reference speed).

Second, it may also be argued that large-scale radial motion sensors adapt faster and/or sustain their adapted state longer than smaller-scale neurons selective for one-directional flow. In this case, intermittent exposure to uniform radial flow in a given direction would result in a higher level of cumulative adaptation than the same intermittent exposure to scrambled flow. Although the time-course of adaptation to optic flow stimuli deserves further study, existing evidence is inconsistent with such an explanation. It is known that the VAE in localized moving sine-gratings recovers quite slowly (i.e. 22 seconds), and recovery is negligible within the first two seconds after removal of the adapter (Clifford & Langley, 1996; Bex et al., 1999a). On the other hand, both psychophysical and physiological studies describe the optic flow response as persistent and "sluggish" (Burr & Santoro, 2001; Duffy & Wurtz, 1997c), making it unlikely that the VAE from coherent radial motion will establish itself faster than the 3-5 seconds needed for a full-strength VAE in translational motion.

As a third possibility, a closer look at the components of the neural response to radial motion may offer a better solution. Morrone et al. (2000) reasoned that flow inversion taps the transient response properties of global optic-flow sensors, and existing evidence indicates that these properties are unique. About half of the optic flow sensitive neurons in area MST-d show a distinct response to motion offset, onset or to the transition between different flow patterns (Duffy & Wurtz, 1997c; Paolini et al., 2000). This transient response is non-linear in that it cannot be predicted by how the cell responds to the stimuli preceding and following the transition. It is suspected that these "transition-tuned" signals carry important information, but it is still unclear what this information may be. The outcome from Experiment 4 suggests they may be essential for online velocity perception, in the presence of recurrent changes in flow structure or direction of motion. Results in Experiment 2 and 3 support this idea, as pattern-specific effects were observed only when the brief test period was not preceded by prolonged exposure to motion, or with changes in the overall pattern of flow between adaptation and testing. The sustained component of the optic flow response, on the other hand, may carry primarily direction-of-motion and trajectory information. As these two response components may adapt differently, speed-based and direction-based motion aftereffects may show different characteristics.

Finally, motion opponency may also account for the attenuation of the VAE for the scrambled flow only, and not for the uniform flow. Typically, the interaction between motions with opponent directions is studied when these motions are concurrently present (Snowden et al., 1991; Heeger et al., 1999). By contrast, in Experiment 4, opponent motions alternate in succession. It is important to note that in this context motion opponency is still possible. Here, however, it is not between two actual signals, but between a residual signal, from the preceding adaptation episode, and the opponent signal from the ongoing motion. If inhibition between these signals builds up throughout the adaptation sequence, it will reduce the overall potency of the adapting flow. From this perspective, the present outcome is consistent with mutual suppression between sequentially presented opponent scrambled flow patterns, but not between expanding and contracting flow. As physiological observations indicate, the nature and degree of motion opponency varies substantially between different extra-striate cortical regions (e.g. Heeger et al., 1999, Morrone et al., 2000).

6.4. Summary

Preliminary results in Experiment 4 indicate that adaptation to inverting radial flow with a scrambled global direction of motion produces weaker VAEs than adaptation to inverting radial flow with a coherent global direction. This difference attests that the adaptation stimuli used in this study address optic-flow mechanisms selectively, but the distinction is not detectable psychophysically with adaptation to continuous, unchanging flow. The present findings parallel the imaging results by Morrone et al. (2000), and implicate the transient properties of radial motion sensors in velocity processing and perception. They also demonstrate that flow inversion attenuates the VAEs from scrambled, but not from uniform flow, in comparison to the effects of continuous stimulation. This supports the hypothesis that mutual suppression between opponent velocity signals may not be a prominent characteristic of mechanisms extracting global 3D optic flow information.

7. GENERAL DISCUSSION

In the experiments described in this thesis, human observers judged the speed of large-scale radial motion, simulating approach or withdrawal, relative to the eye. To explore the nature of these global velocity judgements, estimates of flow speed were obtained before and after prolonged exposure to the same type of flow, in the same direction, or opposite to it. This investigation was motivated by the behavioral importance of this global velocity signal, as well as by the scarce attention devoted to it in the otherwise vast literature on motion adaptation and complex motion perception in humans. The specific experimental findings were discussed at some length in previous sections. This closing chapter highlights the main aspects of the present results, while considering some of their conceptual, empirical and functional implications.

7.1. Velocity Adaptation in Radial Flow is Inherited from Earlier Levels

The main outcome from this study is that velocity adaptation in radial flow elicits perceptual changes that are independent of the global direction of flow, and are not fundamentally different from those observed with local one-dimensional motion. Apparent flow speed was reduced after exposure to the same flow in the same direction, and the size of this VAE depended inversely on the speed of the test. Expanding, contracting and scrambled flow patterns produced VAEs with the same typical tuning, familiar from measurement of local VAEs. These findings suggest that higher-order sensors, selective for behaviorally meaningful patterns of motion, are not uniquely involved in velocity estimation per se. Instead, they seem to represent global flow velocity on the basis of local estimates extracted at earlier levels. Our data provide no evidence that the mechanisms encoding global radial flow velocity are fundamentally different from those identified with stimuli targeting earlier motion processing stages. Accordingly, the present radial VAEs seem confined to the adapted location, which strengthens the argument that they are not generated by specialized complex motion detectors with large spatial extent (Experiment 3).

This general outcome argues against a hierarchical view of velocity coding, presuming an evolution of velocity sensitive mechanisms from one processing stage to the next (Heeger, 1987; Perrone, 2005). Instead, the present results are consistent with evidence that image velocity is extracted by distributed and similarly designed mechanisms, found at lower as well as at higher motion processing stages (Priebe et al., 2006). As proposed by Grzywacz and Yille (1990), both V1 and MT seem to be involved primarily in local velocity estimation, whereas higher-order areas sensitive to optic flow patterns of motion are best suited to integrate these local inputs across space, while assigning global velocities to discrete perceptual objects. In accord with the present results, the involvement of these large-scale sensors may not be revealed unless velocity re-assignment is needed due to changes in stimulus context and the formation of new perceptual objects.

It is an open question, however, whether the present global VAEs will retain their invariant tuning if the radial flow is defined differently. Physiological recordings indicate that extra-striate motion sensitive neurons do not respond optimally to sine-gratings, as their velocity preference seems better established if moving bars or dot textures are used (Schrater & Simoncelli, 1998; Priebe et al., 2006). The stimulus specificity of velocity coding, in general, and of the VAE, in particular, is an important topic for future research. Addressing these issues requires attention to the more complex Fourier content of motion stimuli other than sine-gratings. Spatial and temporal image filtering methods are becoming increasingly popular and seem promising in addressing this methodological challenge (Alais et al., 2005).

As mentioned earlier, the typical VAE tuning, evident in the present results, is best accounted for by the ratio model of perceived speed (Thompson, 1982; Smith & Edgar, 1994; Hammett et al., 2005). This model, however, is strictly based on temporal frequency responses to local motion in a given direction, defined by a single spatial frequency and presented in the central visual field. By contrast, the present data are based on a single, large-scale estimate of perceived speed. This global estimate arises from a wide distribution of local speeds, extending into the far periphery. Yet we find that adaptation to this global signal and to simplified versions of its local components has very similar consequences on perceived speed. This similarity in perceptual outcome implies that although the ratio model is concerned with early motion analysis in the primary visual cortex, its principles are applicable to the perception of more complex motion stimuli, engaging lower, as well as higher-order motion processing stages.

In the present flow-fields, both spatial and temporal frequencies are locally specified. In principle, the ratio model could be applied to various points in the flow-field, yielding a local estimate of perceived speed. Most points in the present stimulus lay beyond 20° from fixation, and will thus engage preferentially the fast M-temporal mechanism which is known to be dominant in the visual periphery (e.g. Hess & Snowden, 1992). Accordingly, the ratio model predicts that exclusive adaptation of the fast-M temporal mechanism will generate exclusively negative local iso-directional VAE, regardless of the particular speed of the test. Indeed, this is what the present results indicate.

A quantitative application of the ratio model to the present stimulus context, however, calls for its further development. The description of the underlying temporal filters needs to be specified across a range of spatial frequencies and orientations, for M-scaled stimuli at different locations throughout the visual field. Such scaled adjustments are expected to equate perceived speed and VAEs across eccentricity, by equating "cortical velocity" as demonstrated with different measures of perceived speed (e.g. lower threshold of motion and MAE cancellation speed, Johnston & Wright, 1983). An extended application of the ratio model may be helpful in addressing the question of how a unitary velocity percept arises from local measurements in the context of different global patterns of flow.

7.2. Radial Velocity Aftereffects Are Direction Specific

Another important aspect of the present results is that there was no transfer of adaptation effects between opposite flow directions. The perceived speed of the radial flow was unaffected by prior adaptation to the opposite flow direction. This result was obtained consistently, regardless of the congruence of the flow pattern (Experiments 1 & 2), or the context of adaptation and testing (Experiments 3 & 4). In addition, an adaptation-induced improvement in speed discrimination performance was also recorded and it was also found to be direction-specific (Experiment 1 & 2). By contrast, the apparent speed of local sine gratings is usually reduced following contra-directional adaptation, indicating that velocity adaptation with these stimuli is only partially direction specific (Thompson, 1981; Smith, 1985; Smith & Edgar, 1994; Müller et al, 2004). Therefore, the complete direction specificity of the adaptation effects recorded here appears to be related to unique aspects of the present motion displays.

Few adaptation studies have used test stimuli moving either in the adapted direction or contrary to it, to assess the extent to which the resulting perceptual changes are direction specific. By employing scaled concentric sine-gratings very similar to ours Kelly (1989) found that the elevation in contrast thresholds for radial motion detection was a lot stronger following iso-directional adaptation. This direction specificity, however, was abolished when the spatial gradient in the stimulus was removed or reversed. Similarly, we observed some counter-directional VAEs with the "flat" radial flow employed for control purposes in Experiment 3 (data not presented). So far, only one other study, using rotary motion, has reported VAEs that are completely direction specific (Rapoport, 1964). It is noteworthy that the present VAEs were found to be completely direction specific even in the scrambled version of the displays, suggesting that a robust directional signal was derived from small display regions, *prior to* the involvement of large-scale pattern-of-motion detectors in areas MST and beyond. The fact that these disjoint directional signals were strongly defined suggests that small-scale motion mechanisms have received optimal input from spatially limited display regions. Such optimization appears to be related to the scaling of the stimulus waveform with eccentricity and to the three-dimensional quality of the flow (Kelly, 1989; Virsu & Hari, 1996). It may be reinforced by the radial arrangement of local motion vectors, matching the organization of directional preferences in area MT (e.g. Movshon et al., 1986; Britten, 2004).

The present result is consistent with physiological evidence that motion responses in extra-striate cortex and in human area V3A are strongly direction selective, whereas motion stimulation of areas V1, V2 and V3 produces considerable amounts of general activation, that is not specific to the direction-of-motion (Huk et al., 2001). It has also been found that prolonged stimulation in the preferred direction-of-motion sharpens the directional tuning of extra-striate neurons, thus enhancing their selectivity for the adapted direction (Xu et al., 2001; Kohn & Movshon, 2004). No such enhancement of direction selective responses has been observed in V1. Thus it appears that speed perception in the present flow fields is mediated by neurons with narrow directional preference, found in areas heavily implicated in pattern of motion analysis (MT+) and the extraction of depth information from motion (V3A; e.g. Orban et al., 2003). By contrast, localized drifting sine-gratings do not target these areas as effectively, and accordingly, the VAEs they generate are less direction specific.

Overall, this aspect of our results suggests that although speed encoding does not seem to evolve in a hierarchical manner, speed signals become more tightly attached to directional signals as one moves from one processing stage to the next. Accordingly, recent reports indicate that the speed-related tuning of neurons in areas MST and 7a is not independent of their directional tuning (Phinney & Siegal, 2000). The direction-specificity and direction tuning of the VAE are important topics for future research, aiming to understand the joint encoding of motion direction and speed. So far, researchers of the VAE have been little concerned with this issue. A common data-driven assumption of the ratio model has been that the temporal mechanisms underlying perceived speed are only partially direction selective. The outcome from the present investigation challenges the generality of this premise.

Typically, the absence of cross-adaptation effects between stimuli with different characteristics is taken as evidence that the neural events elicited by these stimuli are functionally, and, perhaps, anatomically, independent (Thompson, 1981). In the present study adaptation to flow in a given direction had no effect on the perceived speed of oppositely directed motion flow, indicating that expanding and contracting velocities, although similar in origin, are derived along separate lines. This implies that the responses of neurons with preference for centrifugal and centripetal directions are channeled along distinct networks, defining global motion sensors selective for expansion and contraction, respectively.

While such functional separation may emerge relatively early in the visual system, the present findings suggest that it is fully established at higher motion processing stages. Supporting evidence comes from results in Experiments 3 and 4. In Experiment 4 we find that alternating opposing coherent flow patterns (expansion / contraction) produce their adaptation effects independently, in that the resulting VAEs are equivalent to those produced by continuous adaptation to each flow alone. By contrast, adaptation to the same inverting motions embedded in an incongruent global pattern produces VAEs that are considerably weaker than the corresponding effects of continuous adaptation. Furthermore, in Experiment 3 we find that expanding and contracting velocities rival when presented together in non-overlapping display regions, and that simultaneous perceptual access to these signals is difficult. There is no experience of sensory conflict, however, when these same motions are rendered "flat", or form an incongruent pattern, nor between translating motions of opposing directions. The perception of motion contrast in depth deserves further attention, as it does not seem to involve the same type of suppressive opponency, typical for opposite fronto-parallel motions (Snowden et al., 1999). It may be concluded that both the global structure and the three-dimensional quality of the flow support the direction specificity of the present adaptation effects.

7.3. Radial Velocity Aftereffects Are Sensitive to Measurement Context

While the tuning and the direction specificity of the present VAEs remained invariant across all experimental conditions, VAE magnitude did not show the same resilience to measurement context. In particular, the perceived speed of adapted expansion, which was found to be strongly attenuated in comparison to that of non-adapted expansion (Experiment 2), bounced back to pre-adapted levels when judged against non-adapted contraction (Experiment 3). Intriguingly, no such recovery from velocity adaptation was observed when the apparent speed of adapted contraction was measured against that of non-adapted expansion.

Several authors have pointed out that the very act of measuring a perceptual aftereffect may affect its expression, leading to controversial interpretations of the same adaptation process (e.g. Pantle, 1998; Wade, 1994). This measurement reactivity has been widely recognized and explored by a number of MAE studies (e.g. Murakami & Shimojo, 1995; Wade et al., 1996, Wade & Salvano-Pardieu, 1998). Owing to the use of invariant stimuli, VAE research has been less concerned with this issue. Nevertheless, some contextual influences have been noted. For example, the presence of a stationary stimulus during adaptation or testing is not equivalent to a neutral background as it influences the measurement of perceived speed (Thompson, 1993).

Results from Experiments 2 and 3 indicate that the introduction of relative motion to the test display, following uniform adaptation, modulates the size of the VAE. This influence is not entirely unexpected: motion contrast alters the magnitude of the MAE when the probed region is surrounded or flanked by stimuli moving in different directions (Murakami & Shimojo, 1995; Wade et al., 1996). In such contexts, the resulting MAE can be suppressed or enhanced, depending on whether the surround motion is in the same direction as the MAE, or opposite to it, respectively. In addition, motion contrast between adjacent display regions increases the un-adapted perceived speed of translating RDK-s (De Bruyn & Orban, 1999).

The present contextual modulation, however, is unlike the above effects documented with translating motion as it depends on the sign of the motion contrast between the test and comparison regions. Whereas the perceived speed of expanding motion, following adaptation, is restored by the presence of a contracting stimulus during testing, contracting VAEs remain invariant, regardless of the global direction of the comparison flow. Furthermore, the modulation itself and its asymmetrical nature, depend critically on the perception of motion-in-depth elicited by the radial flow (Experiment 3). Although we came across this result accidentally, it reveals a unique, spatially based interaction between mechanisms selective to opposing optic-flow motion. It may be worthwhile to explore the time scale of this interaction, in relation to other direction asymmetries, favoring the perception of approaching motion.

7.4. Sensitivity to Speed Differences in the Context of Radial Flow

Another significant aspect of the present results concerns the link between speed discrimination performance and the perception of absolute speed. Experiments 1 and 2 provide additional, independent evidence that sensitivity to speed differences is inversely related to the apparent speed of the test motion and can be adequately described by a Weber fraction, based on perceived, rather than physical speed (Bex et al., 1999a). In the present study, speed discrimination improved in proportion to the loss in perceived speed, with largest benefits for tests slower than the adapter which were slowed down the most, following adaptation. In addition to being related in magnitude, both the VAE and the speed discrimination enhancement were direction specific, suggesting that relative and absolute velocity judgments have a common neural origin (Huk et al., 2001).

The above conclusion leads to a general simple prediction: if speed perception and speed sensitivity are so closely related, one might expect that any factor that alters perceived speed will also alter speed sensitivity in a predictable manner. Relatively speaking, motions that appear to be moving slower will have a speed discrimination advantage over motions that appear to be moving faster. In the context of complex motion, however, this prediction has not been borne out (Sekuler, 1992; Bex et al., 1998; Clifford et al., 1999; Clifford et al., 2000). Existing research indicates that whereas the absolute speed of radial motion is judged to be consistently faster than otherwise equivalent rotation and translation, speed discrimination thresholds in radial flow are equivalent to these for rotation and translation. This discrepancy has remained unresolved. It has lead to speculations, however, that relative speed judgments are constrained by earlier motion mechanisms, whereas higher level processes mediate the perception of speed (Clifford et al., 2000).

Results from the present work, however, suggest a different conclusion. In Experiment 2 we report a robust effect of flow pattern on baseline sensitivity to speed differences: observers were consistently better at detecting speed discrepancies within an expanding flow field, than in contracting displays. Accordingly, in Experiment 3, contraction was judged as consistently faster than expansion, when the two motions were repeatedly pitted against one another (see also Geesaman & Qian, 1998). Contrary to existing findings, this suggests that relative and absolute velocity judgments remain related in the context of radial flow but the manner in which motion speed is compared is critical in demonstrating this link. This issue needs to by reexamined by more sensitive paradigms, specifically designed to measure speed discrimination thresholds.

It is possible that the global pattern of motion affects speed discrimination performance only in split-flow spatial speed-matching, while this influence had remained undetected by previous studies, using sequentially presented overlapping flow patterns. The radial bias in speed perception, on the other hand, has been confirmed with both spatial and temporal tasks (Geesaman & Qian, 1998). It appears that large-scale radial motion mechanisms mediate relative speed judgments only if local comparisons are precluded, whereas judgments of absolute speed are always based on the integrated, global percept of flow. This implies that relative speed judgments have flexible access to early, as well as late processing stages, depending on the demands of the task. Trends in our pilot data also suggest that sensitivity to speed differences improves with practice but the rate of improvement is steeper is the context of expanding flow. This experience dependent plasticity is not typical for processes limited early in the visual system and deserves further attention.

The issue of task specificity in speed discrimination performance has been remarked upon by many researchers (e.g. Thompson, 1993; Johnston et al., 1999). It should not be regarded as a methodological nuisance as it appears to be theoretically important. What may explain the lack of pattern-of-motion effects on speed discrimination *between* sequential flow patterns and the presence of such effects in speed comparisons made between regions *within* the flow pattern? One possibility is that optic flow mechanisms are uniquely sensitive to the spatial distribution of local velocities within the flow field, whereas detecting flow acceleration and deceleration could be delegated to sensors of limited spatial extent.

In a natural context, distortions in the flow velocity structure signify changes in the surrounding three dimensional layout in relation to the observer's position. While this type of information is critical for navigational control in flying species, its use in human goal directed behavior has not received much attention. Nonetheless, it has been shown, for example, that asymmetries in the velocity distribution within an otherwise symmetrical radial flow field can bias subsequent judgments of heading, in that ego-motion trajectory is perceived to be curved (Dyre & Andersen, 1997). A specialized mechanism detecting this information efficiently would be certainly beneficial.

7.5. Functional Implications

Taken together, the present findings indicate that the perception of radial flow velocity can be profoundly distorted by prolonged or repetitive viewing. The potentially detrimental consequences from such adaptation, however, can be quickly offset by the response of large-scale optic flow mechanisms, which remain sensitive to changes in the flow pattern and support velocity constancy for behaviorally relevant motion. Such mechanisms respond uniquely to the occurrence of disparate velocity signals, and prioritize the accurate and efficient perception of expanding/approaching velocity. Results from this study draw attention to the transient response properties of these sensors, as they seem to modulate the velocity percept during flow transitions, rather than being concerned with the extraction of the velocity signal per se.

The outcome from the present experiments confirms that velocity adaptation can be in itself beneficial by improving sensitivity to speed differences in unchanging or repetitive flow. We report for the first time, however, that the greatest enhancement of speed discrimination occurs for test speeds *slower* than the adapter, with smaller and less consistent facilitation at the adapted speed and no improvement for speeds faster than the adapter. This represents an important extension of existing research in showing that the post-adaptive facilitation of speed sensitivity is not confined to the adapted velocity. Such a finding challenges the common assumption that the main functional benefit from sensory adaptation is to increase sensitivity to the most recently encountered, prevailing speed. Obviously, explanations of the facilitation effect based on response tuning changes in neurons selective for the adapted velocity are insufficient, as it is unclear how and why responses to slower velocities should be more strongly affected (e.g. Clifford & Ibbotson, 2003; Krekelberg, 2006a).

The finding that adaptation affects most profoundly speeds below the adapted level, offers a new perspective on its functional role. Sensory adaptation would be "maladaptive" if optimizing information transmission interferes with the organism's ability to meet its behavioral needs. In any case, the benefit of increased relative speed sensitivity must be weighted against the cost of misperceiving absolute speed. Underestimation of object speed would be detrimental to navigation and defensive behavior. On the other hand, absolute speed is irrelevant to more cognitive tasks such as scene analysis and motion-based segmentation.

The present results indicate that the visual system applies its adaptive capacity in a flexible and intelligent manner. It appears that the prevailing background speed is used as a criterion in evaluating the potential behavioral importance of subsequent speed signals. The occurrence of faster speeds is more likely to require immediate action as, normally, these are associated with rapidly approaching objects that may enter in physical contact with the observer. Accordingly, laboratory results indicate that absolute speed is preserved, or even enhanced for faster tests, following adaptation. Speed discrimination ability is of little relevance in this context, and could be allowed to remain at pre-adapted levels or to drop. On the other hand, encountering slower speeds following adaptation is more likely to indicate a transition towards a more stable environment, which needs to be monitored and inspected. In this context there is no harm in reducing the background speed signal, while enhancing sensitivity to future changes in speed. Thus, according to the most recent speed range encountered, adaptation prioritizes either optimal signal transmission (Wainwright, 1999) and representation efficiency (Barlow, 1990), or the preparation of an adequate behavioral response (Gray, 2005; Shaplee et al., 2006).

Taken together, the results presented in this thesis reinforce the idea that motion adaptation has a dual effect on human velocity sensing. It appears that two separate processes are at work, one aiming to improve sensitivity to speed differences and the other - to preserve the veridical perception of speed. Until a better understanding of the neural code for perceived speed emerges, linking adaptation effects at the physiological and psychophysical level will remain a challenge.

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Appendix A

Individual Data and Statistical Analyses in Experiment 1

Table A1

R- squared values for the logistic fit through individual speed-matching data (scrambled flow) in Experiment 1

	Adaptation conditions								
Adapt →	Baseline			Scrambled Flow			Scrambled Flow		
	▶ *no motion* ◀			▶ *iso-directional* ◀			▶ *contra-directional* ◀		
Test →	Scrambled Probe Scrambled Match			Scrambled Probe Scrambled Match			Scrambled Probe Scrambled Match		
	Reference TF (Hz)			Reference TF (Hz)			Reference TF (Hz)		
Observer	1	1.5	2	1	1.5	2	1	1.5	2
BGM	0.989	0.998	0.997	0.992	0.998	0.992	0.984	0.996	0.997
JY	0.989	0.997	0.997	0.989	0.994	0.995	0.995	0.994	0.987
MIM	0.984	0.996	0.997	0.999	0.998	0.999	0.999	0.999	0.999
AP	0.995	0.990	0.995	0.966	0.994	0.998	0.985	0.993	0.996
KP	0.992	0.994	0.994	0.996	0.992	0.993	0.996	0.997	0.994
PP	0.998	0.998	0.996	0.973	0.995	0.999	0.987	0.999	0.999

Table A2

ANOVA summary table for SDI as a function of probe speed and adaptation condition (scrambled flow, Experiment 1)

Source	df	SS	MS	F
Within Subjects				
Probe Speed	2	0.009	0.005	4.549*
Error	10	0.010	0.001	
Adaptation Condition	2	0.014	0.007	6.243*
Error	10	0.011	0.001	
Speed × Condition	4	0.008	0.002	4.232**
Error	20	0.010	0.000	

*$p \leq .05$
**$p \leq .01$

Table A3

Simple effects of probe speed on SDI by adaptation condition (Experiment 1)

Source	df	SS	MS	F
Within Subjects				
@Baseline	2	0.012	0.006	11.71**
Error	10	0.010	0.001	
@Same direction	2	0.002	0.001	1.33
Error	10	0.010	0.001	
@Opposite direction	2	0.002	0.001	2.22
Error	10	0.010	0.001	

Table A4

Simple effects of adaptation condition on SDI by probe speed/TF (Experiment 1)

Source	df	SS	MS	F
Within Subjects				
@Probe TF=1Hz	2	0.002	0.001	11.81**
Error	10	0.016	0.008	
@Probe TF=1.5Hz	2	0.002	0.001	2.92
Error	10	0.006	0.003	
@Probe TF=2.0Hz	2	0.0001	0.00005	0.15
Error	10	0.0003	0.00003	

*$p \leq .05$
**$p \leq .01$

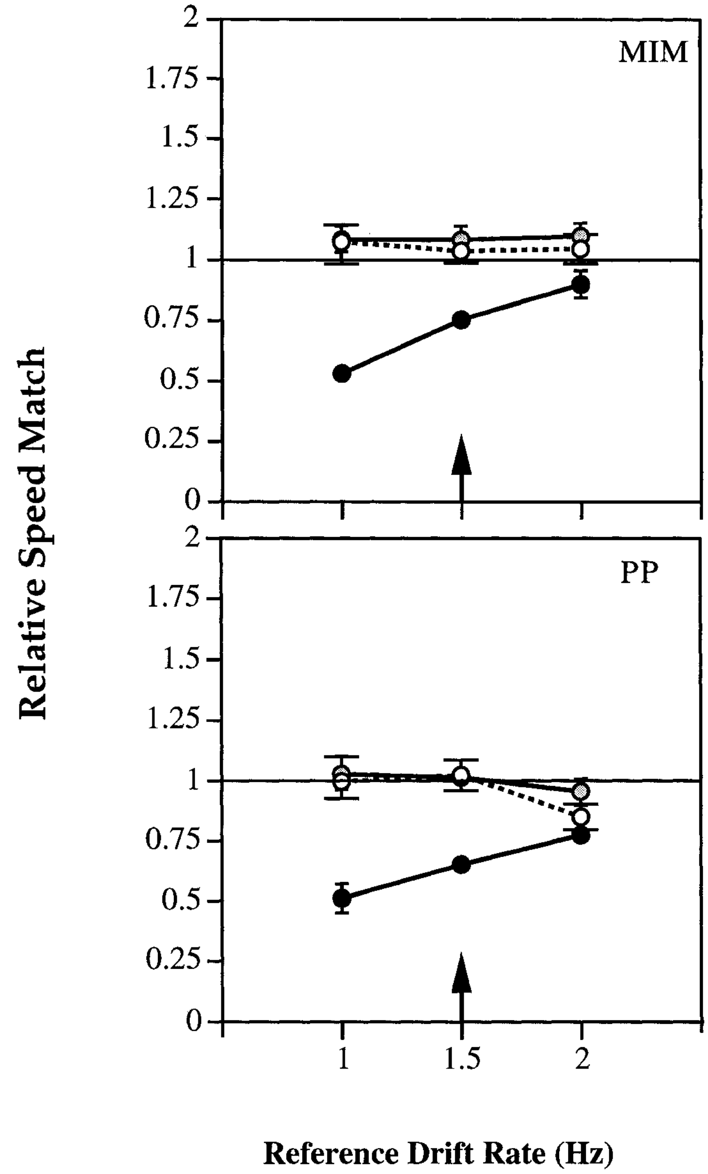

Figure A1. Effects of adaptation on the perceived speed of "scrambled flow" (Experiment 1). Speed matches are fractions of the reference value. Data from subjects MIM (the author) and PP (inexperienced, naïve observer) at baseline (····○····) and after adaptation to iso-directional (——●——) or contra-directional (——◍——) flow. Error bars indicate 95% confidence limits.

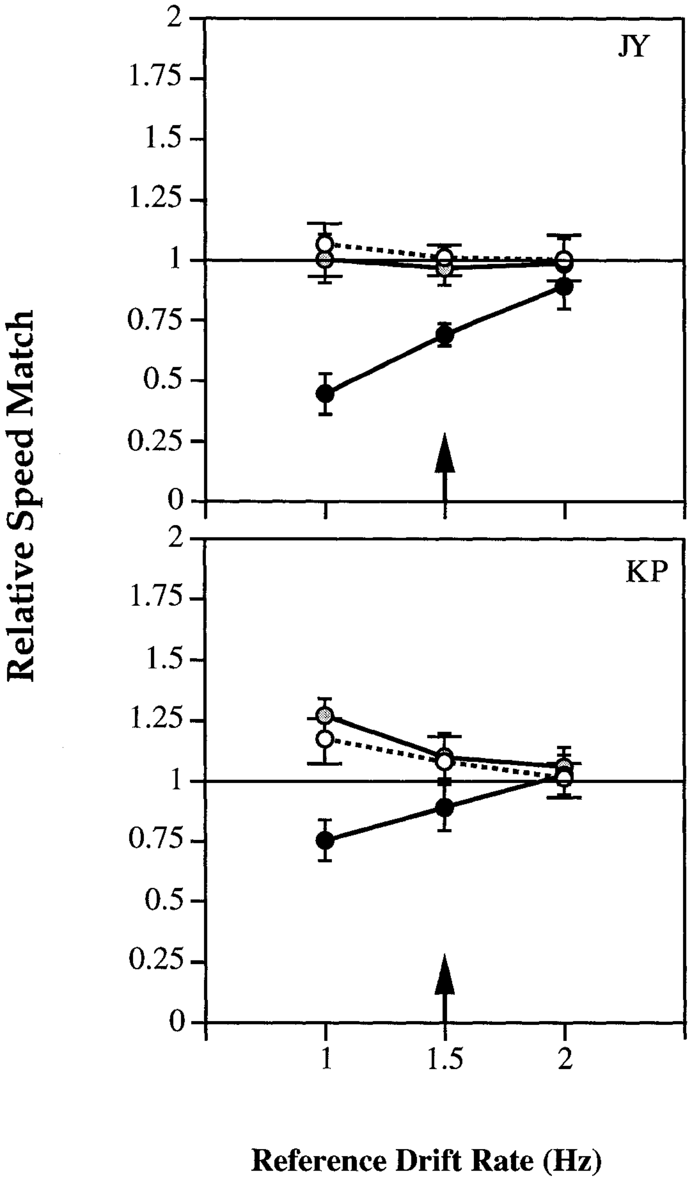

Figure A2. Effects of adaptation on the perceived speed of "scrambled flow" (Experiment 1). Speed matches are fractions of the reference value. Data from subjects JY and KP (experienced, naïve observers) at baseline (····○····) and after adaptation to iso-directional (—●—) or contra-directional (—◍—) flow. Error bars indicate 95% confidence limits.

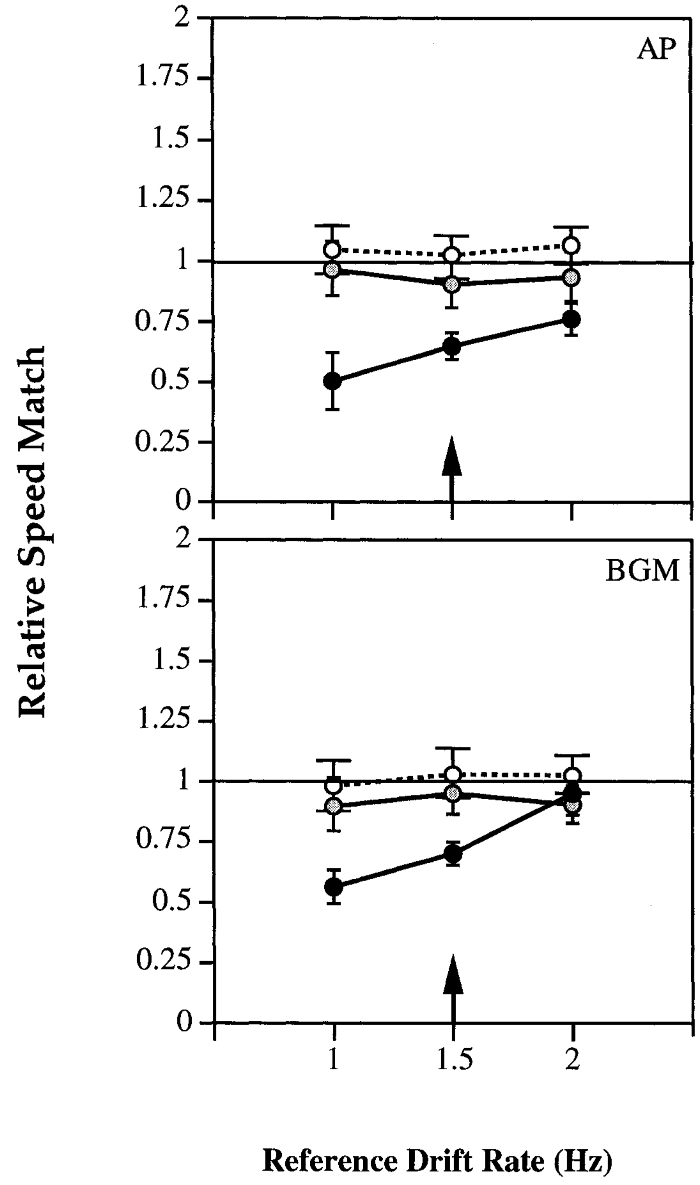

Figure A3. Effects of adaptation on the perceived speed of "scrambled flow" (Experiment 1). Speed matches are fractions of the reference value. Data from subjects AP and BGM (inexperienced, naïve observers) at baseline (····○···) and after adaptation to iso-directional (—●—) or contra-directional (—◍—) flow. Error bars indicate 95% confidence limits.

Appendix B

Individual Data and Statistical Analyses in Experiment 2

Table B1

R- squared values for the logistic fit through individual data for expansion-to-expansion speed matching in Experiment 2

	Adaptation conditions								
Adapt →	Baseline			Expansion			Contraction		
	▸ *no motion* ◂			▸ *iso-directional* ◂			▸ *contra-directional* ◂		
Test →	Expanding Probe Expanding Match			Expanding Probe Expanding Match			Expanding Probe Expanding Match		
	Reference TF (Hz)			Reference TF (Hz)			Reference TF (Hz)		
Observer	1	1.5	2	1	1.5	2	1	1.5	2
BGM	0.994	0.995	0.993	0.999	0.999	0.999	0.995	0.997	0.989
JY	0.998	0.998	0.999	0.989	0.983	0.999	0.999	0.998	0.999
MIM	0.999	0.958	0.985	0.999	0.999	0.999	0.999	0.999	0.994
AP	0.998	0.999	0.999	0.999	0.997	0.996	0.988	0.973	0.999
KP	0.996	0.995	0.997	0.992	0.999	0.986	0.996	0.994	0.991
PP	0.999	0.999	0.984	0.988	0.951	0.986	0.987	0.999	0.974

Table B2

R- squared values for the logistic fit through individual data for contraction-to-contraction speed matching in Experiment 2

	Adaptation conditions								
Adapt →	Baseline			Contraction			Expansion		
	▸ *no motion* ◂			▸ *iso-directional* ◂			▸ *contra-directional* ◂		
Test →	Contracting Probe Contracting Match			Contracting Probe Contracting Match			Contracting Probe Contracting Match		
	Reference TF (Hz)			Reference TF (Hz)			Reference TF (Hz)		
Observer	1	1.5	2	1	1.5	2	1	1.5	2
BGM	0.987	0.995	0.994	0.996	0.996	0.996	0.997	0.997	0.994
JY	0.974	0.992	0.999	0.978	0.985	0.998	0.997	0.990	0.996
MIM	0.985	0.979	0.985	0.999	0.999	0.999	0.994	0.999	0.999
AP	0.996	0.991	0.998	0.974	0.988	0.996	0.989	0.992	0.981
KP	0.983	0.979	0.998	0.994	0.987	0.997	0.996	0.996	0.996
PP	0.999	0.999	0.989	0.989	0.976	0.985	0.973	0.994	0.987

Table B3

ANOVA summary table for VAE as a function of probe drift rate (1Hz, 1.5Hz, 2Hz) and type of flow (scrambled, expanding, contracting) in Experiments 1 and 2

Source	df	SS	MS	F
Within Subjects				
Probe Speed (TF)	2	0.886	0.443	89.811**
Error	10	0.049	0.005	
Type of Flow	2	0.004	0.002	0.217
Error	10	0.089	0.009	
Speed × Flow Type	4	0.038	0.009	1.661
Error	20	0.113	0.006	

*$p \leq .05$
**$p \leq .01$

Table B4

ANOVA summary table for SDI as a function of type of flow (scrambled, expanding, contracting), probe speed (1Hz, 1.5Hz, 2Hz) and adaptation condition (baseline, iso-directional, counter-directional) in Experiments 1 and 2

Source	df	SS	MS	F
Within Subjects				
Flow Type	2	0.054	0.027	15.836**
Error	10	.017	.002	
Probe Speed/TF	2	0.022	0.011	13.779**
Error	10	0.008	0.001	
Flow × Speed	4	0.001	0.0001	0.786
Error	20	0.008	0.0001	
Adaptation Condition	2	0.015	0.007	7.649**
Error	10	0.010	0.001	
Flow × Adaptation	4	0.006	0.002	1.947
Error	20	0.016	0.001	
Speed × Adaptation	4	0.018	0.004	7.545**
Error	20	0.012	0.001	
Flow× Speed× Adapt	8	0.006	0.001	1.275
Error	40	0.025	0.001	

$*p \leq .05$
$**p \leq .01$

Table B5

Simple effects of flow type on SDI by adaptation condition, across reference speed (Experiment 1, Experiment 2)

Source	df	SS	MS	F
Within Subjects				
@Baseline	2	0.034	0.017	25.08**
Error	10	0.010	0.001	
@Same direction	2	0.012	0.006	6.67*
Error	10	0.010	0.001	
@Opposite direction	2	0.014	0.007	3.98
Error	10	0.020	0.002	

*$p \leq .05$
**$p \leq .01$

Table B6

ANOVA summary table for SDI as a function of probe speed (1Hz, 1.5Hz, 2Hz) and adaptation condition (baseline, iso-directional, counter-directional) for expanding flow in Experiment 2

Source	df	SS	MS	F
Within Subjects				
Probe Speed/TF	2	0.003	0.002	8.293**
Error	10	0.002	0.0001	
Condition	2	0.004	0.002	10.010**
Error	10	0.002	0.0001	
Speed X Condition	4	0.010	0.002	3.193*
Error	20	0.015	0.001	

*$p \leq .05$
**$p \leq .01$

Table B7

Simple effects of test speed on SDI by adaptation condition in expansion (Experiment 2)

Source	df	SS	MS	F
Within Subjects				
@Baseline	2	0.012	0.006	50.716**
Error	10	0.001	0.0001	
@Same direction	2	0.0002	0.0001	0.612
Error	10	0.010	0.0001	
@Opposite direction	2	0.0002	0.0001	0.318
Error	10	0.010	0.001	

Table B8

Simple effects of adaptation condition on SDI by test speed in expansion (Experiment 2)

Source	df	SS	MS	F
Within Subjects				
@ 1 Hz	2	0.006	0.003	6.962*
Error	10	0.001	0.0001	
@ 1.5 Hz	2	0.006	0.003	4.836*
Error	10	0.010	0.001	
@ 2 Hz	2	0.0002	0.0001	0.759
Error	10	0.010	0.001	

*$p \leq .05$
**$p \leq .01$

Table B9

ANOVA summary table for SDI as a function of probe speed (1Hz, 1.5Hz, 2Hz) and adaptation condition (baseline, iso-directional, counter-directional) for contracting flow in Experiment 2

Source	df	SS	MS	F
Within Subjects				
Probe Speed/TF	2	0.011	0.005	12.715**
Error	10	0.004	0.0001	
Condition	2	0.004	0.002	1.359
Error	10	0.013	0.001	
Speed X Condition	4	0.006	0.001	2.566
Error	20	0.011	0.001	

$^{*}p \leq .05$
$^{**}p \leq .01$

Table B10

Simple effects of test speed on SDI by adaptation condition in contraction (Experiment 2)

Source	df	SS	MS	F
Within Subjects				
@Baseline	2	0.012	0.006	21.757**
Error	10	0.001	0.0001	
@Same direction	2	0.002	0.001	0.764
Error	10	0.010	0.001	
@Opposite direction	2	0.002	0.001	4.247
Error	10	0.001	0.0001	

*$p \leq .05$
**$p \leq .01$

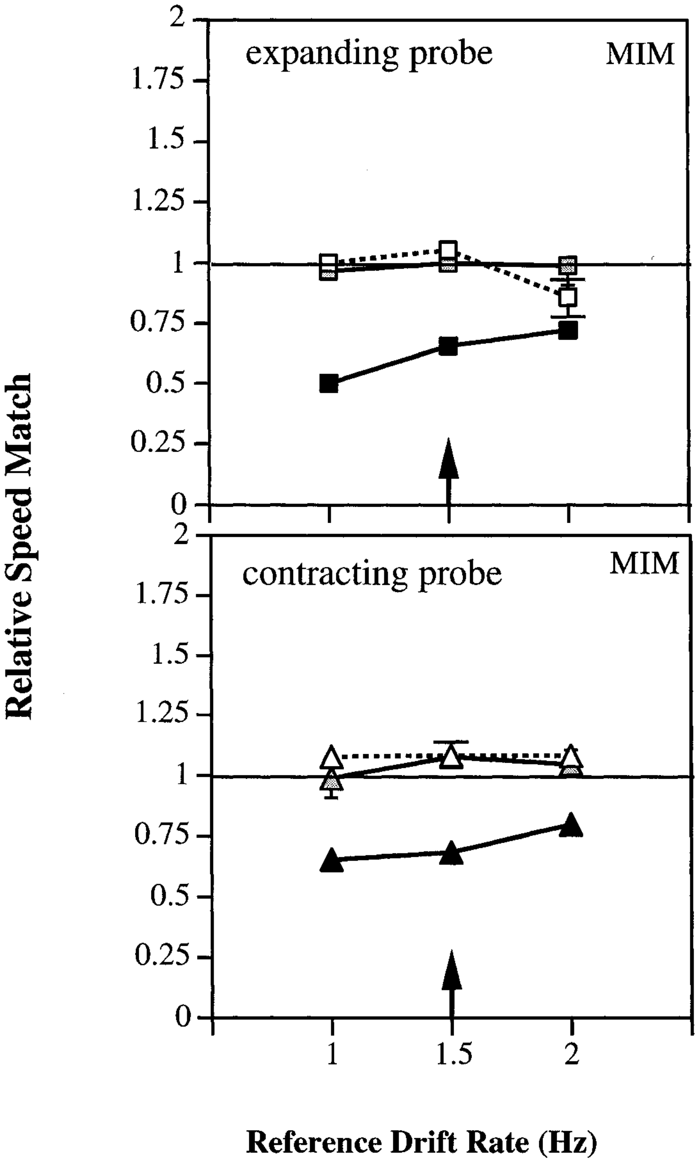

Figure B1. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Speed matches are PSE-s expressed as fractions of the reference value. Data for subject MIM (the author) at baseline (open symbols) and after adaptation to iso-directional (black symbols) or contra-directional flow (gray symbols). Error bars indicate 95% confidence limits.

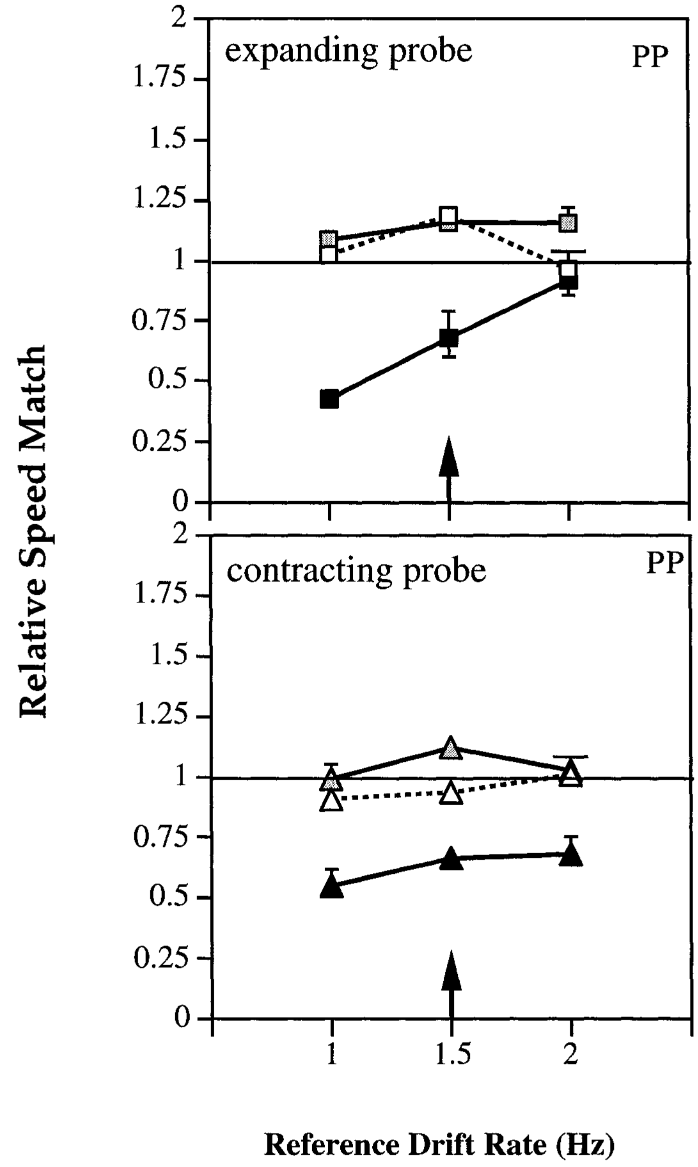

Figure B2. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Speed matches are PSE-s expressed as fractions of the reference value. Data for subject PP (inexperienced, naive observer) at baseline (open symbols), and after adaptation to iso-directional (black symbols) or contra-directional flow (gray symbols). Error bars indicate 95% confidence limits.

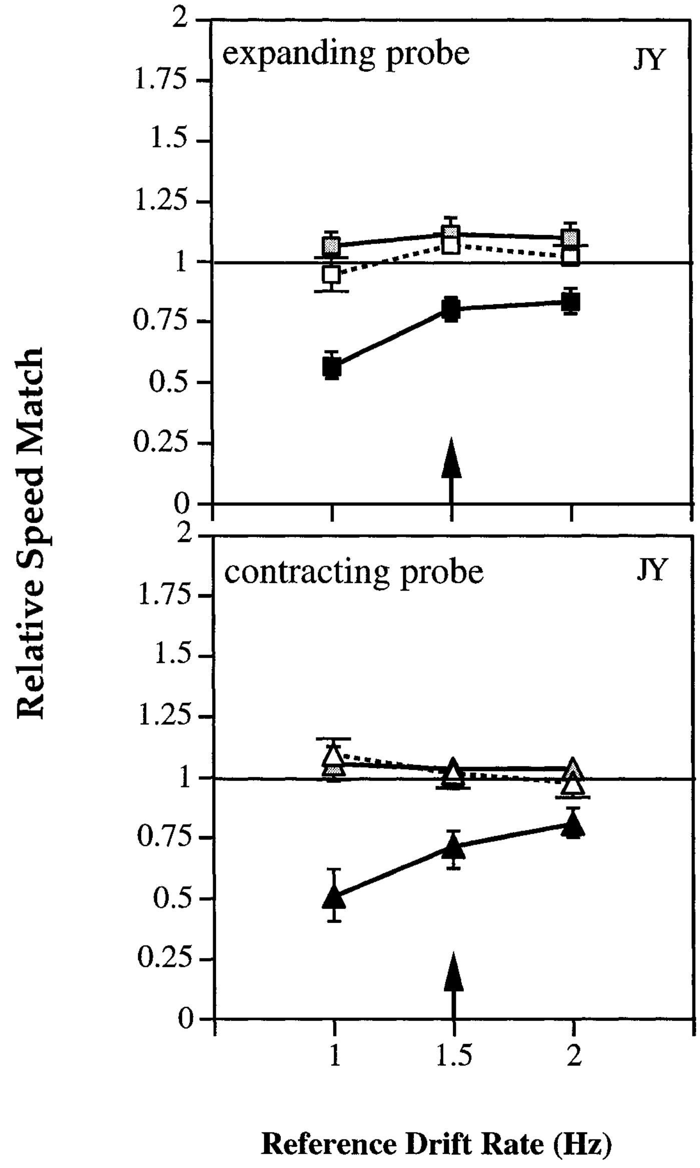

Figure B3. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Speed matches are PSE-s expressed as fractions of the reference value. Data for subject JY (experienced, naive observer) at baseline (open symbols), and after adaptation to iso-directional (black symbols) or contra-directional flow (gray symbols). Error bars indicate 95% confidence limits.

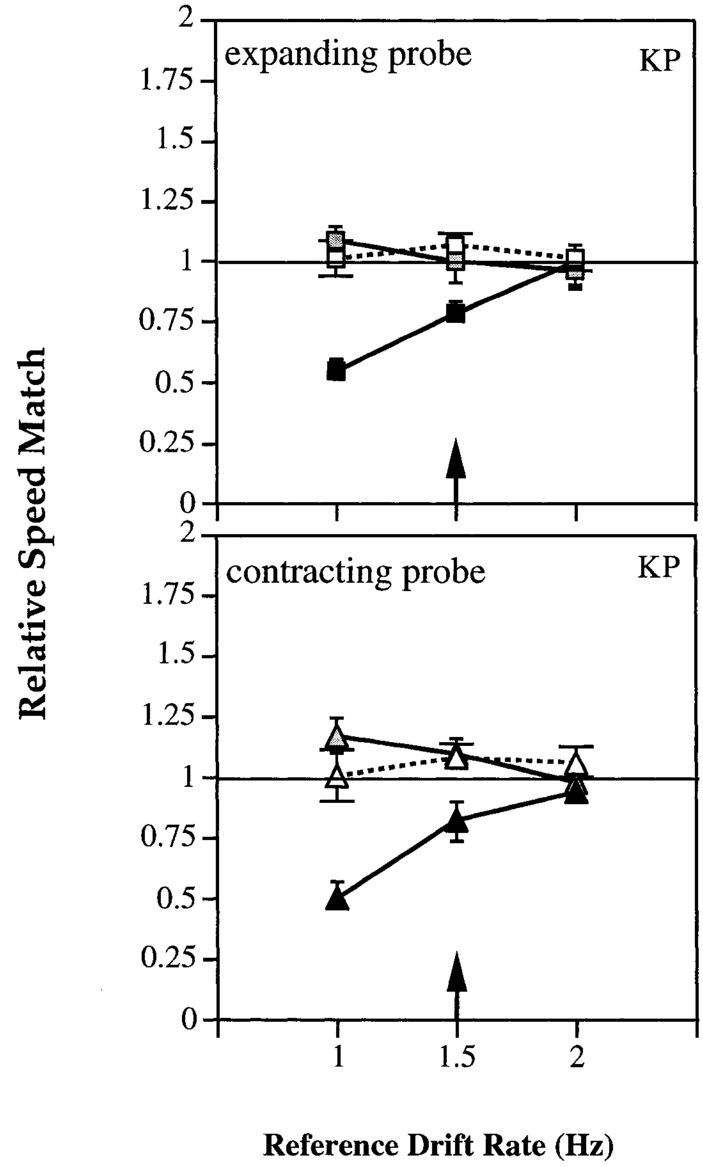

Figure B4. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Speed matches are PSE-s expressed as fractions of the reference value. Data for subject KP (experienced, naive observer) at baseline (open symbols), and after adaptation to iso-directional (black symbols) or contra-directional flow (gray symbols). Error bars indicate 95% confidence limits.

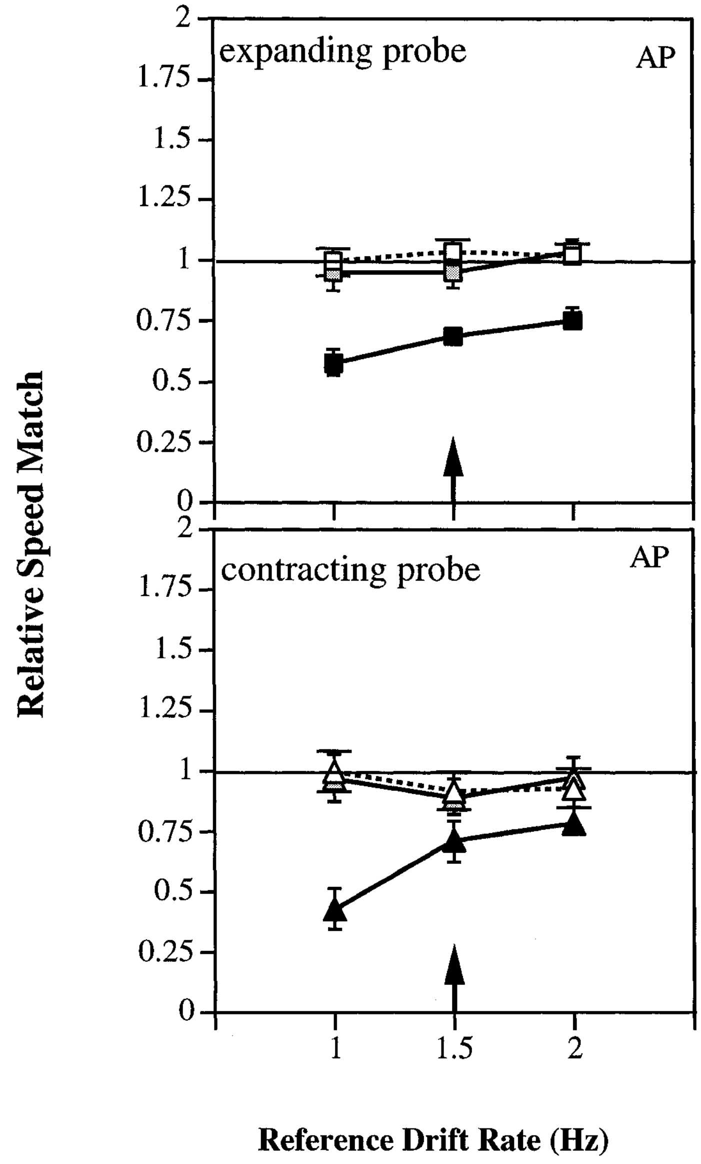

Figure B5. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Speed matches are PSE-s expressed as fractions of the reference value. Data for subject AP (inexperienced, naive observer) at baseline (open symbols), and after adaptation to iso-directional (black symbols) or contra-directional flow (gray symbols). Error bars indicate 95% confidence limits.

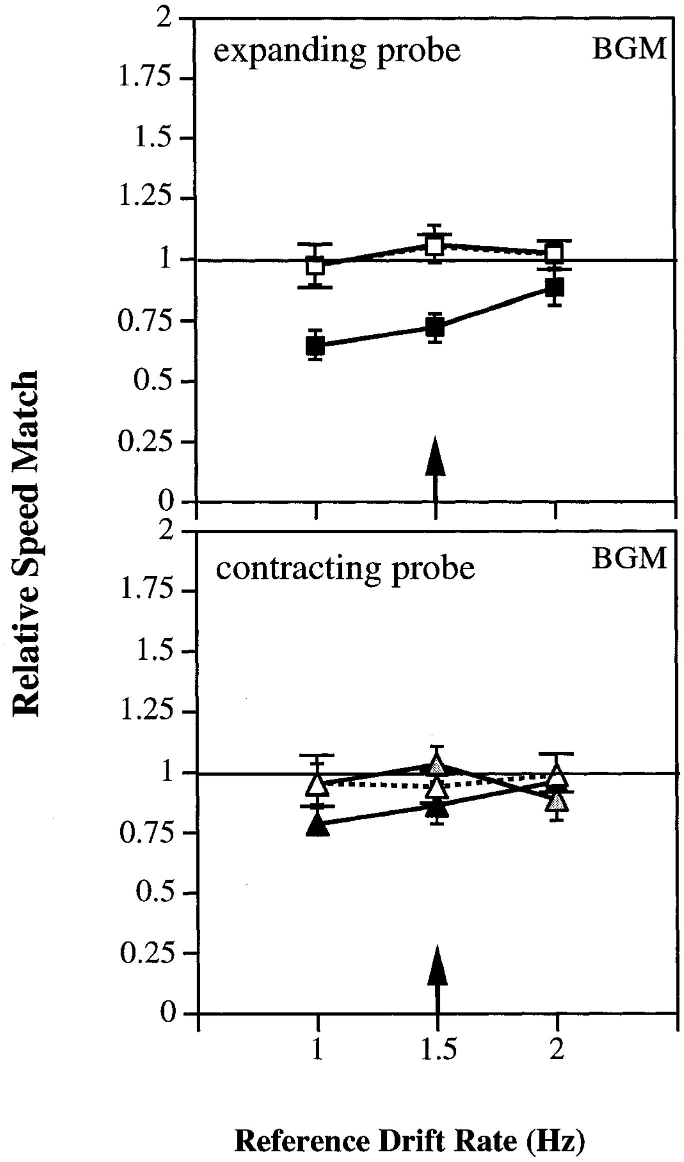

Figure B6. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Speed matches are PSE-s expressed as fractions of the reference value. Data for subject BGM (inexperienced, naive observer) at baseline (open symbols), and after adaptation to iso-directional (black symbols) or contra-directional flow (gray symbols). Error bars indicate 95% confidence limits.

Appendix C

Individual Data and Statistical Analyses in Experiment 3

Table C1

R- squared values for the logistic fit through individual speed-matching data (expansion) in Experiment 3

	Adaptation conditions								
Adapt →	Baseline			Expansion			Contraction		
	▸ *no motion* ◂			▸ *iso-directional* ◂			▸ *contra-directional* ◂		
Test →	Expanding Probe Contracting Match			Expanding Probe Contracting Match			Expanding Probe Contracting Match		
	Reference TF (Hz)			Reference TF (Hz)			Reference TF (Hz)		
Observer	1	1.5	2	1	1.5	2	1	1.5	2
BGM	0.944	0.985	0.995	0.978	0.997	0.985	0.947	0.999	0.954
JY	0.995	0.998	0.997	0.954	0.999	0.990	0.997	0.990	0.995
MIM	0.996	0.998	0.998	0.970	0.996	0.996	0.995	0.996	0.999
AP	0.999	0.997	0.990	0.983	0.987	0.998	0.998	0.955	0.997
KP	0.987	0.995	0.994	0.975	0.996	0.988	0.983	0.963	0.972
PP	0.984	0.995	0.973	0.995	0.990	0.999	0.992	0.999	0.996

Table C2

R- squared values for the logistic fit through individual speed-matching data (contraction) in Experiment 3

	Adaptation conditions								
Adapt →	Baseline			Contraction			Expansion		
	▶ *no motion* ◀			▶ *iso-directional* ◀			▶ *contra-directional* ◀		
Test →	Contracting Probe Expanding Match			Contracting Probe Expanding Match			Contracting Probe Expanding Match		
	Reference TF (Hz)			Reference TF (Hz)			Reference TF (Hz)		
Observer	1	1.5	2	1	1.5	2	1	1.5	2
BGM	0.974	0.999	0.963	0.995	0.967	0.999	0.987	0.988	0.959
JY	0.994	0.999	0.981	0.976	0.990	0.979	0.956	0.997	0.992
MIM	0.983	0.995	0.978	0.994	0.998	0.999	0.962	0.985	0.999
AP	0.995	0.972	0.994	0.990	0.995	0.997	0.997	0.987	0.995
KP	0.989	0.988	0.992	0.991	0.968	0.974	0.999	0.960	0.983
PP	0.992	0.993	0.971	0.999	0.999	0.999	0.997	0.983	0.997

Table C3

ANOVA summary table for iso-directional VAE-s as a function of test context (same flow- Experiment 2; opponent flow - Experiment 3), reference drift rate (1Hz, 1.5Hz, 2Hz) and flow direction (expanding, contracting)

Source	df	SS	MS	F
Within Subjects				
Test Context	1	0.503	0.503	9.450*
Error	5	0.266	0.053	
Probe Speed	2	1.452	0.726	102.671**
Error	10	0.071	0.007	
Test × Speed	2	0.055	0.027	3.030
Error	10	0.091	0.009	
Flow Direction	1	0.274	0.274	5.188
Error	5	0.264	0.053	
Test × Flow	1	0.319	0.319	15.768**
Error	5	0.101	0.020	
Speed × Flow	2	0.041	0.020	2.470
Error	10	0.082	0.008	
Test × Speed × Flow	2	0.020	0.010	0.959
Error	10	0.103	0.010	

$*p \leq .05$
$**p \leq .01$

Table C4

Simple effects of test context on iso-directional VAE by flow direction, across reference speed (Experiments 2 & 3)

Source	df	SS	MS	F
Within Subjects				
@Expanding Probe	1	0.812	0.812	19.45**
Error	5	0.210	0.042	
@Contracting Probe	1	0.011	0.011	0.33
Error	5	0.160	0.032	

Table C5

Simple effects of flow direction on iso-directional VAE by test context, across reference speed (Experiments 2 & 3)

Source	df	SS	MS	F
Within Subjects				
@ Uniform test (Experiment 2)	1	0.001	0.001	0.10
Error	5	0.040	0.008	
@ Opponent test (Experiment 3)	1	0.592	0.592	9.13*
Error	5	0.325	0.065	

*$p \leq .05$
**$p \leq .01$

Table C6

ANOVA summary table for SDI as a function of flow direction (expanding, contracting), probe drift rate (1Hz, 1.5Hz, 2Hz) and adaptation condition (baseline, iso-directional, counter-directional) in Experiment 3

Source	df	SS	MS	F
Within Subjects				
Flow Direction	1	0.0001	0.0001	0.001
Error	5	0.018	0.004	
Probe Speed	2	0.001	0.001	0.323
Error	10	0.021	0.002	
Flow X Speed	2	0.001	0.0001	0.275
Error	10	0.015	0.002	
Adaptation	2	0.003	0.002	0.419
Error	10	0.038	0.004	
Flow X Adaptation	2	0.001	0.0001	0.118
Error	10	0.024	0.002	
Speed X Adaptation	4	0.004	0.001	0.382
Error	20	0.047	0.002	
Flow X Speed X Adaptation	4	0.006	0.002	1.185
Error	20	0.027	0.001	

$^{*}p \leq .05$
$^{**}p \leq .01$

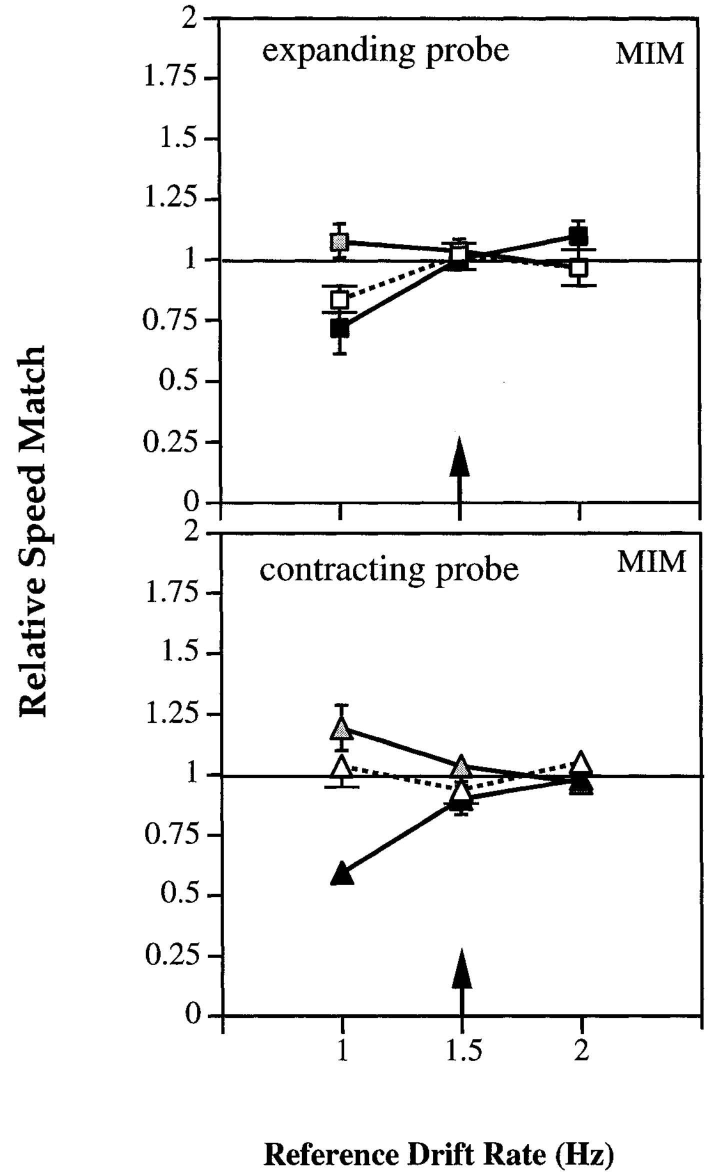

Figure C1. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 3). Speed matches are PSE-s expressed as fractions of the reference value. Probe speed is matched to that of the opponent flow. Data for subject MIM (the author) at baseline (open symbols), and after adaptation to iso-directional (black symbols) or contra-directional flow (shaded symbols). Error bars indicate 95% confidence limits. Same caption applies to figures C2-C6.

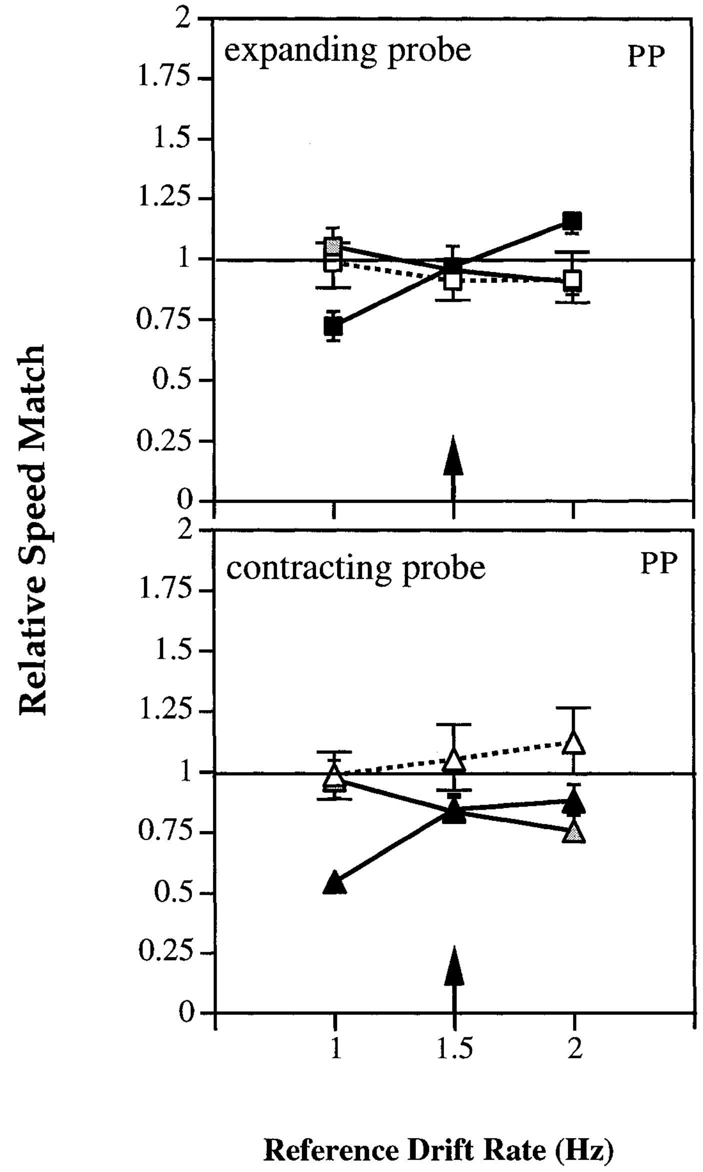

Figure C2. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 3). Probe speed is matched to that of the opponent flow. Data for subject PP (inexperienced, naïve observer).

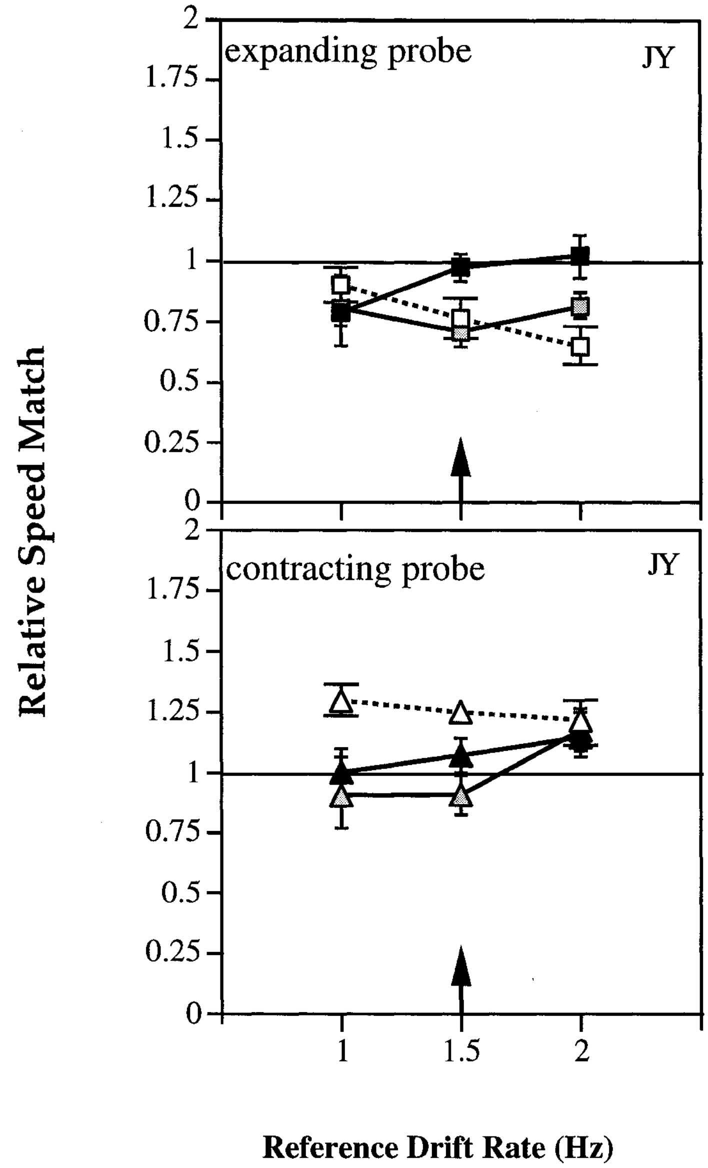

Figure C3. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 3). Probe speed is matched to that of the opponent flow. Data for subject JY (experienced, naïve observer).

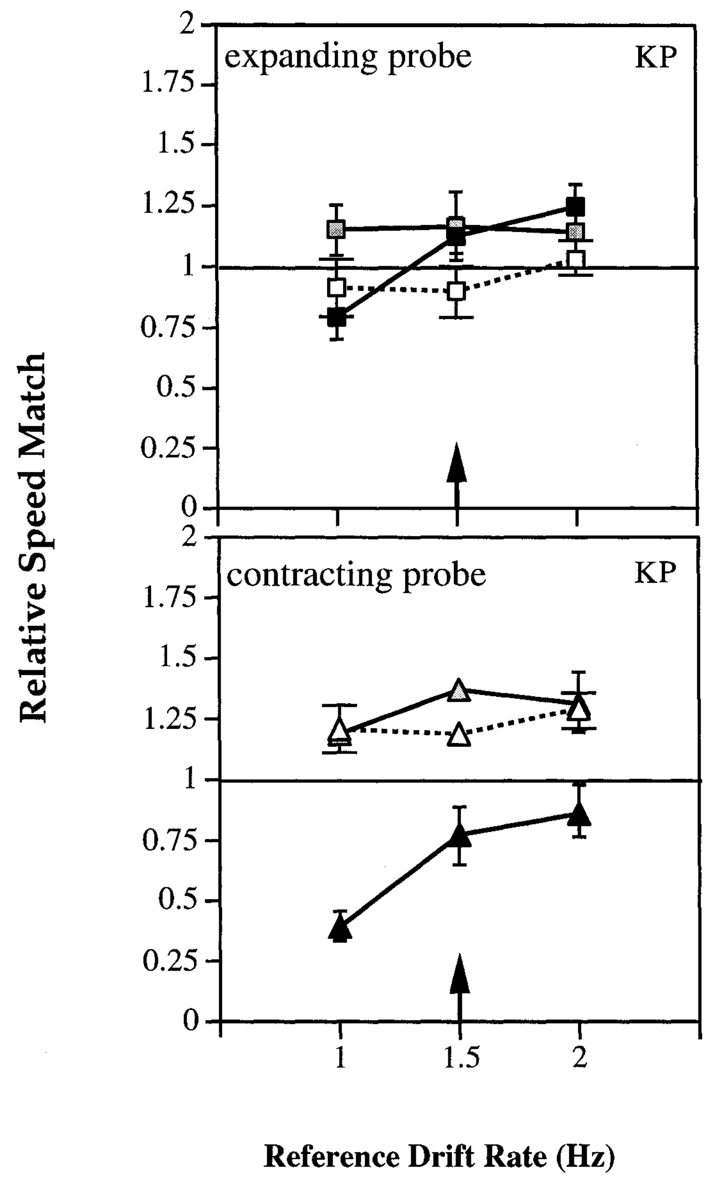

Figure C4. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 3). Probe speed is matched to that of the opponent flow. Data for subject KP (experienced, naïve observer).

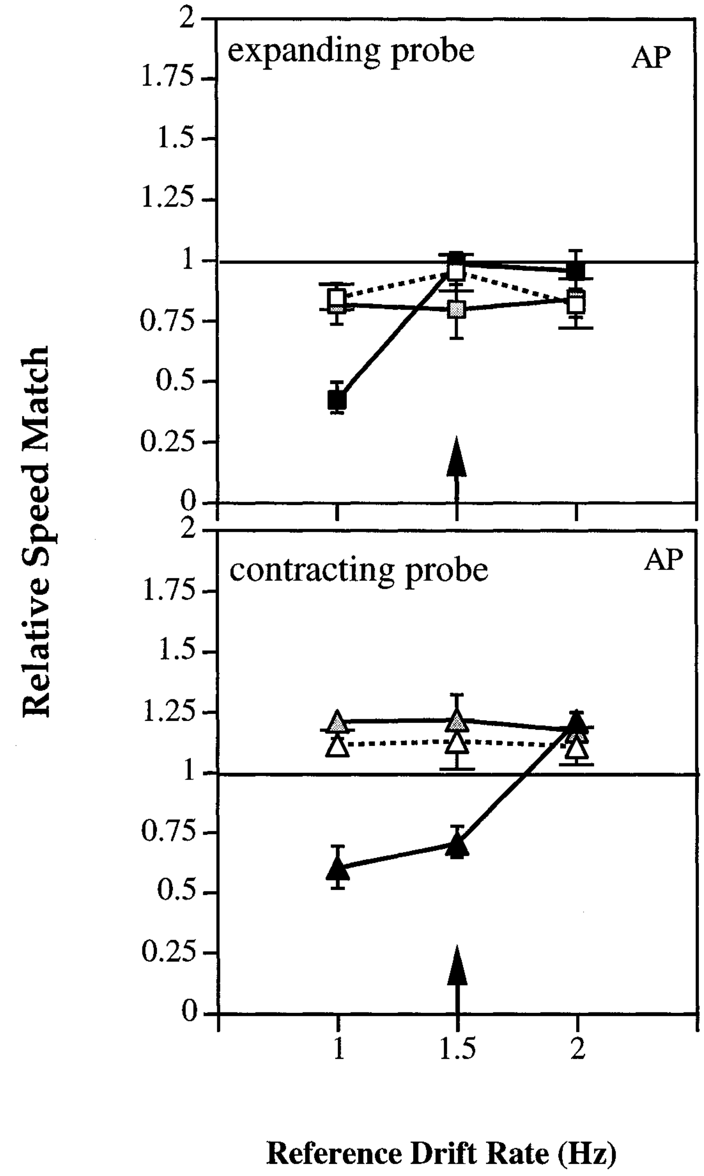

Figure C5. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 3). Probe speed is matched to that of the opponent flow. Data for subject AP (inexperienced, naïve observer).

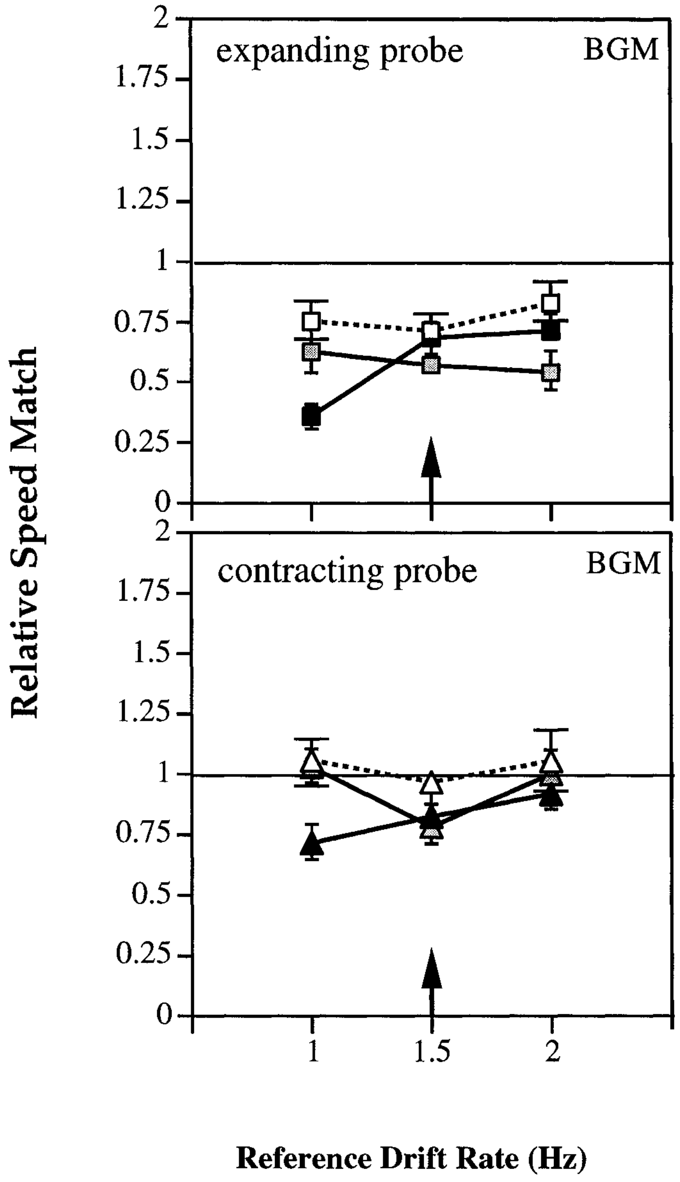

Figure C6. Effects of adaptation on the perceived speed of expanding and contracting flow (Experiment 2). Probe speed is matched to that of the opponent flow. Data for subject BGM (inexperienced, naïve observer).

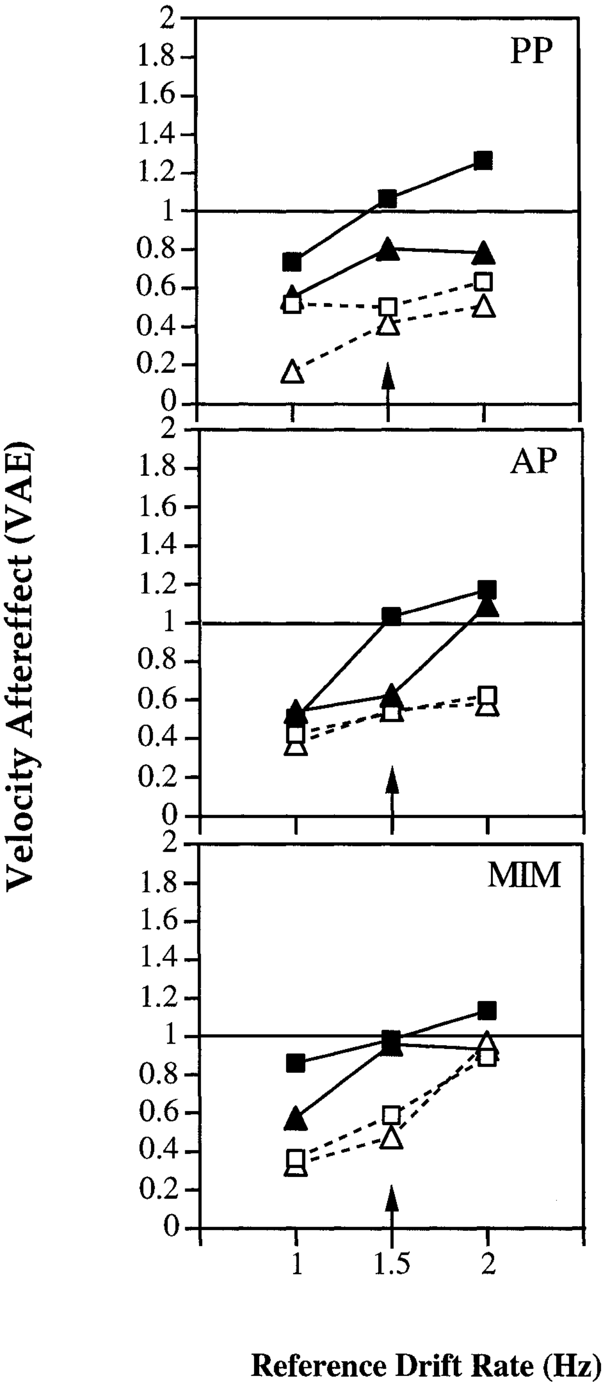

Figure C7. Iso-directional VAE-s following adaptation to 3D flow (filled symbols) and to "flat" flow (open symbols) in Experiment 3. Individual data for expanding (—■— , - - -□- - -) and contracting probes (—▲— , - - -△- - -).

Appendix D

Individual Data in Experiment 4

Table D1

R- squared values for the logistic fit through individual speed-matching data in Experiment 4

	Adaptation conditions								
Adapt →	Scrambled Flow ▶ *reverses direction* ◀			Uniform Flow ▶ *reverses direction* ◀			Uniform Flow ▶ *reverses direction* ◀		
Test →	Scrambled Probe Scrambled Match			Expanding Probe Expanding Match			Contracting Probe Contracting Match		
	Reference TF (Hz)			Reference TF (Hz)			Reference TF (Hz)		
Observer	1	1.5	2	1	1.5	2	1	1.5	2
PP	0.987	0.998	0.987	0.995	0.999	0.999	0.987	0.999	0.999
MIM	0.996	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999

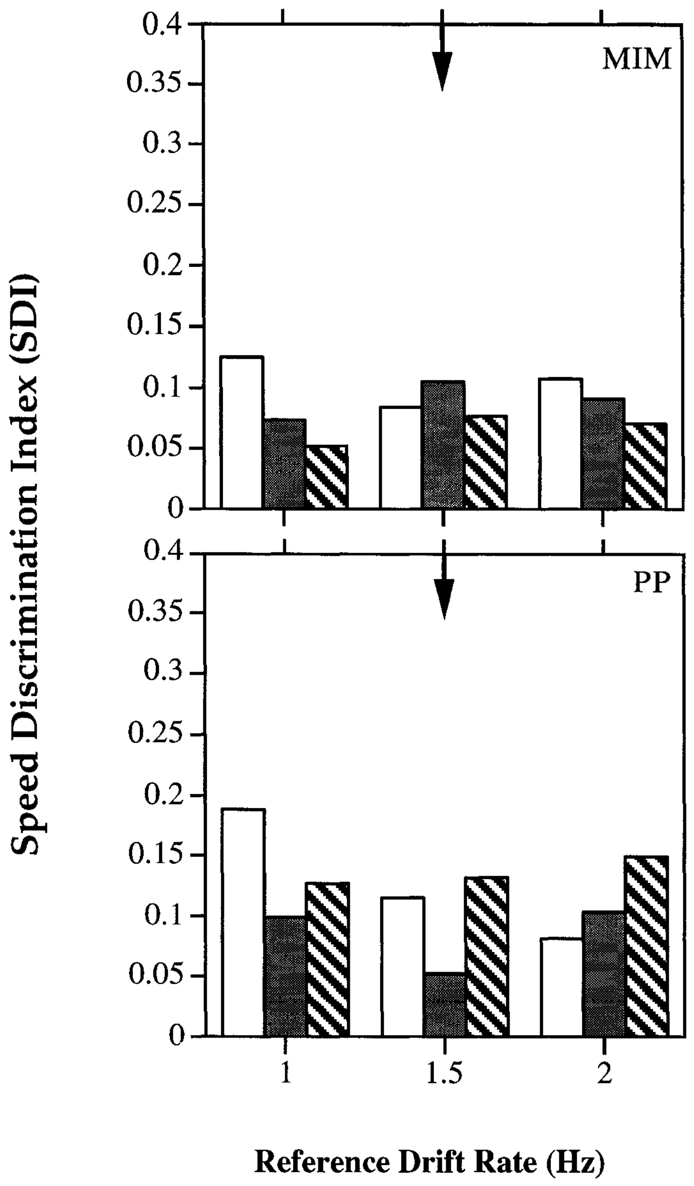

Figure D1. Effects of alternate opponent-flow adaptation on speed sensitivity in scrambled flow. Probe speed is matched to that of non-adapted flow of the same type. Data is for the author (MIM) and an inexperienced naive observer (PP), at baseline (☐ Experiment 1), and after adaptation to scrambled flow that does not change (■ Experiment 1) or periodically reverses direction (▨ Experiment 4).

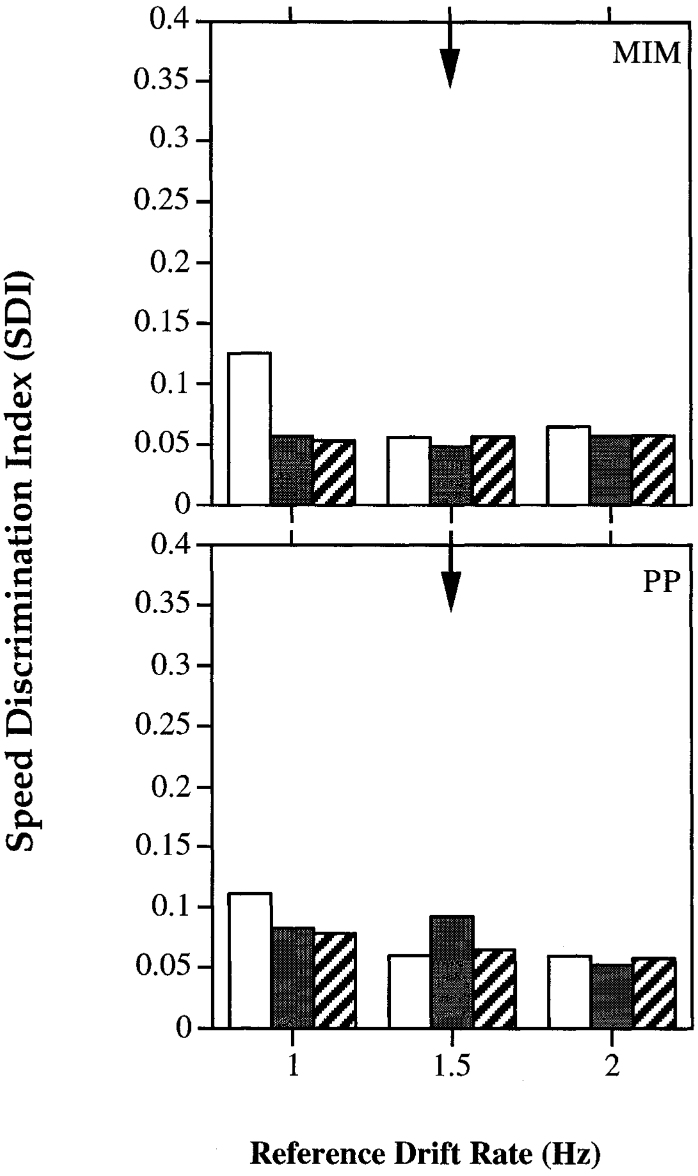

Figure D2. Effects of alternate opponent-flow adaptation on speed sensitivity in expanding flow. Probe speed is matched to that of non-adapted flow of the same type. Data is for the author (MIM) and an inexperienced naïve observer (PP), at baseline (☐ Experiment 2), and after adaptation to expanding flow that does not change direction (■ Experiment 2) or alternates with contraction (▨ Experiment 4).

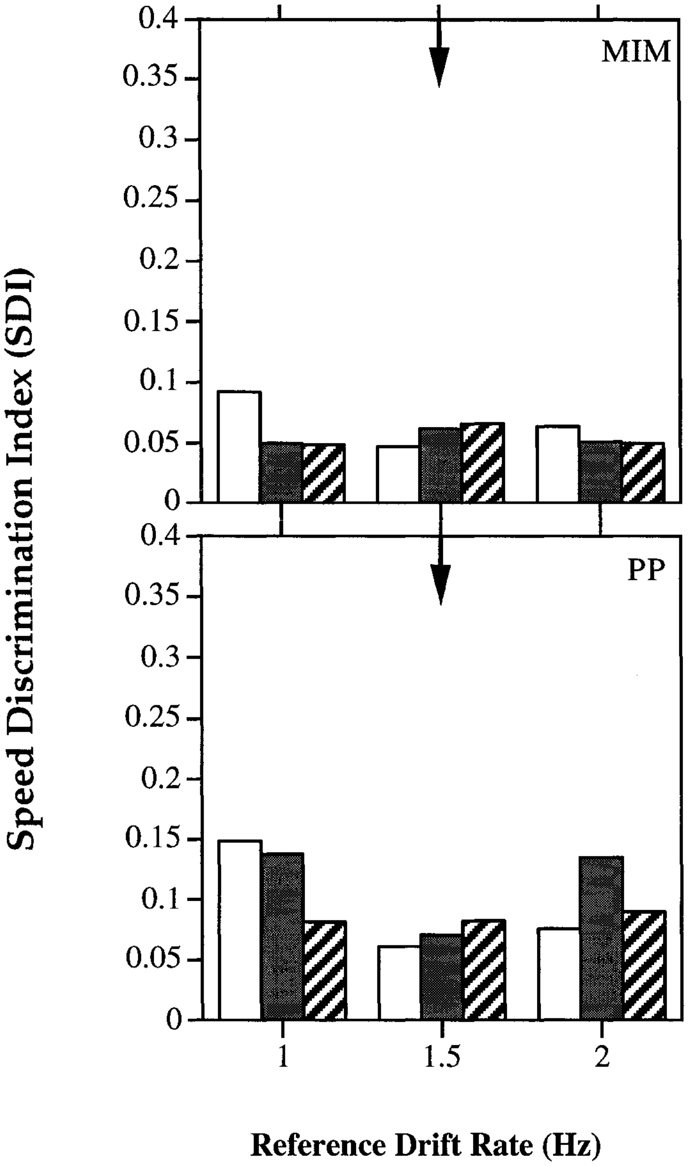

Figure D3. Effects of alternate opponent-flow adaptation on speed sensitivity in contracting flow. Probe speed is matched to that of non-adapted flow of the same type. Data is for the author (MIM) and an inexperienced naïve observer (PP), at baseline (☐ Experiment 2), and after adaptation to contracting flow that does not change direction (■ Experiment 2) or alternates with expansion (▨ Experiment 4).