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Visual Evoked Potential Correlates of Cooperative
and Competitive Integration in Motion Perception

by

Mohamed Ahmad

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DEGREE OF MASTER OF SCIENCE

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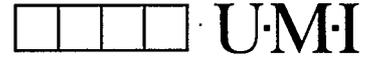
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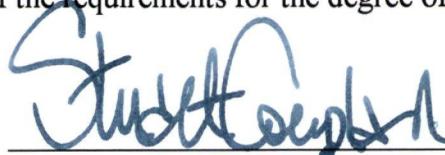
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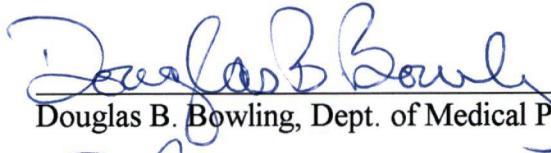


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Abstract

In their cooperative-competitive model of motion integration, Snowden and Braddick (1989a,b) propose that, when stimulated, localized motion-detecting neurons tuned to the same direction of motion mutually enhance each other's activity while suppressing the activity of neurons tuned to other directions. These interactions are presumably mediated by excitatory and inhibitory post-synaptic potentials. Visual evoked potentials (VEPs) provide an index to neuronal integration since they reflect the gross synaptic activity of thousands of cortical neurons. VEPs were recorded in eight subjects in response to random dot kinematogram (RDK) stimuli. As predicted by the cooperative-competitive model, VEP amplitude increased with the proportion of dots moving in the same direction even though the total number of RDK dots remained constant. Two subsequent experiments ruled out the combination of morphologically dissimilar VEPs evoked by dissimilar directions and the contribution of neurons sensitive to motion at stimulus edges as alternate explanations for the trend observed in the first experiment. Orthogonal directions of motion appeared to be as mutually competitive as opposite directions. Ninety seconds of motion adaptation to unidirectional rightward RDKs reduces subsequent VEP amplitudes for unidirectional rightward RDKs. These findings provide human electrophysiological support for Snowden and Braddick's (1989) cooperative-competitive visual model of motion integration.

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Table of Contents

Approval Page	ii
Abstract	iii
Acknowledgements	iv
Table of Contents	v
List of Figures	vi
Introduction	1
Cooperative-Competitive Integration in Motion Perception	2
Psychophysical Support for Cooperative-Competitive Motion Integration	6
Physiology of Motion Processing and Directionally-Selective Neurons	11
Physiological Support for Cooperative-Competitive Motion Integration	14
Motion Adaptation and Cooperative-Competitive Integration	17
Motion Visual Evoked Potentials	21
General Methods	25
Subjects	25
Stimuli and Apparatus	25
Procedure	28
General Results	29
Exp. 1: How does RDK Coherence Affect mVEP Amplitude?	31
Exp. 2: Do Different Directions of Motion Produce Equivalent mVEPs?	35
Exp. 3: Does Motion Along or Against an Edge Affect the mVEP?	38
Exp. 4: Are Orthogonal Directions of Motion Mutually Inhibitory?	41
Exp. 5: Does Motion Adaptation Produce Disinhibition of Competing Directions?	44
Discussion	47
Motion VEP Validity	47
Motion VEPs and Cooperative-Competitive Integration	50
Anatomy and Cooperative-Competitive Integration	56
Integration of Non-Translational Motion	57
Figure-Ground Segregation and Cooperative-Competitive Integration	57
Epistemology	58
Literature Cited	59

List of Figures

1	Schematic of cooperative-competitive network.	3
2	Directionally-selective channels.	4
3	Sample random dot kinematogram.	7
4	Recording of visual evoked potential.	22
5	Superimposed mVEPs from O1, O2, Oz channels.	30
6	Single subject mVEPs from RDKs of varying coherence.	33
7	Pooled amplitude and latency data for varying RDK coherence.	34
8	Addition of morphologically dissimilar mVEPs.	35
9	Single subject mVEPs for RDKs moving in each of four directions.	37
10	Pooled amplitude and latency data for RDKs moving in each of four directions.	37
11	Single subject mVEPs for square and elongated RDKs.	40
12	Pooled amplitude and latency data for square and elongated RDKs.	40
13	Single subject mVEPs for noise opposite or orthogonal to signal direction.	43
14	Pooled amplitude and latency data for opposite and orthogonal noise.	43
15	Single subject mVEPs recorded after 90 seconds of rightward adaptation.	46
16	Pooled amplitude and latency data for 90 seconds of rightward adaptation.	46
17	Superposition principle applied to mVEPs recorded from multidirectional RDKs.	52

Introduction

Although objects in the real world are perceived as wholes, the cells comprising the visual system are individually capable of detecting and representing only small parts of an object's image. At each stage of the neural hierarchy from retinal ganglion cells to visual association cortex, the outputs of many lower-order neurons are integrated by higher-order neurons into larger and more complex representations of the outside world. This hierarchical integration presumably leads to the complete representation of an object.

Neuronal integration is often nonlinear in that neurons may interact before their outputs are summed. These interactions may involve mutual facilitation among similarly-tuned neurons (cooperation) or inhibition between dissimilarly-tuned neurons (competition). As a result, the detectability of objects is enhanced by amplifying dominant stimulus features while irrelevant detail is attenuated. Recent psychophysical research suggests that the perceived coherence of moving stimuli is enhanced by cooperative-competitive networks of motion-detectors. It has been hypothesized that, within such networks, motion detectors tuned to similar directions enhance each other's activity while suppressing detectors tuned to competing directions (Snowden and Braddick, 1989a,b). The experiments described here use visual evoked

potentials as physiological measures of cooperative-competitive integration in motion perception.

Cooperative-Competitive Integration in Motion Perception

Cooperative-competitive motion integration is similar in principle to lateral inhibition. Lateral inhibition involves mutual inhibition between luminance detectors on opposite sides of an edge and tends to elevate the perceived contrast across edges. Cooperative-competitive motion integration presumably enhances the perceived coherence - or uniformity of motion - of moving stimuli.

In motion perception, cooperative-competitive integration is hypothesized to involve an interconnected network of motion detectors located within a given retinotopic area. When stimulated, local motion detectors tuned to the same direction of motion mutually enhance each others' activity while inhibiting the activity of detectors tuned to competing directions (Snowden and Braddick, 1989a,b). This model is called the cooperative-competitive integration model of motion perception and is presented in Figure 1.

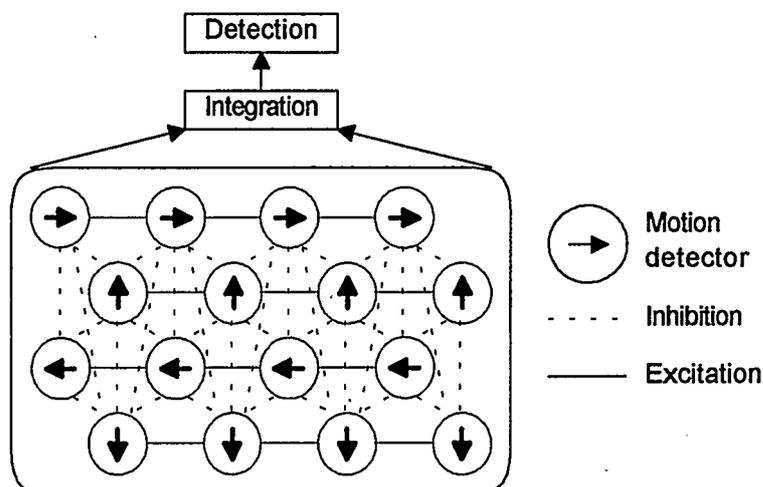


Figure 1. All motion-detecting neurons within a given segment of the visual field are assumed to interact in a cooperative-competitive network. Detectors tuned to the same direction excite each other when stimulated but inhibit all detectors tuned to competing directions. This pattern of activity tends to enhance the detectability of dominant directions relative to other directions.

Psychophysicists often describe the visual system in terms of channels or populations of similarly-tuned neurons. As Figure 2 illustrates, the motion-processing system consists of 8 to 12 directionally-selective channels; each channel is comprised of all motion-detecting neurons responsive to a 30 to 45 degree range of directions (Levinson and Sekuler, 1980; Raymond, 1993). A moving image will activate neurons primarily in the channel responsible for the object's direction of movement and if the activity exceeds some perceptual threshold level, the observer will consciously perceive motion in that direction. Thus the perceived direction of a moving stimulus depends

on the distribution of activity it evokes among the directionally-selective channels.

Although the channels may share some overlap, linear models of integration assume they operate independently (ie. without interacting). Described in terms of channels, cooperative-competitive motion integration involves intrachannel facilitation and mutual interchannel inhibition.

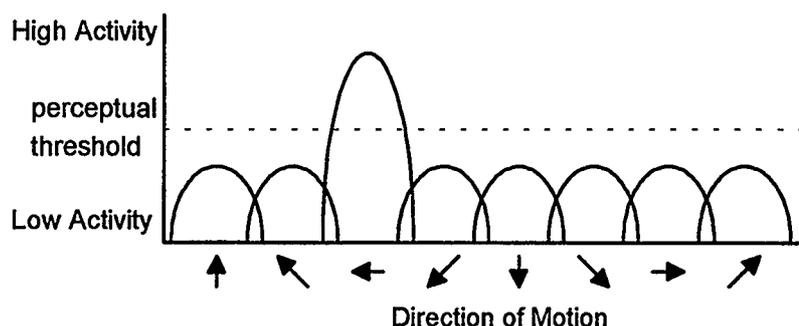


Figure 2. All motion detectors tuned to similar directions are organized into channels. Each channel is responsive to a 30 to 45 deg range of directions. When a channel's activity exceed some perceptual threshold, motion in that direction is perceived.

The cooperative-competitive integration of neural activity presumably enhances global direction detectability by improving the perceptual coherence of moving stimuli. This is especially important when stimuli are not moving in a uniform direction such as a tree in the wind. Such stimuli activate a broad range of motion-detectors possibly precluding detection of the overall direction of motion. When one direction of motion is dominant, motion-detector activity will be most concentrated in the dominant direction's

channel. Intrachannel facilitation will be greatest in the dominant direction and will be lesser in other channels. Furthermore, the dominant channel will undergo less interchannel inhibition from the weaker competing channels. As a result, activity in the dominant direction will increase at the expense of activity in other directions and the dominant direction will appear more coherent than it actually is. For example, a slight breeze may cause individual leaves on a tree to move in different directions at different velocities. The local motions of individual leaves are still visible but the overall direction of motion is generally obvious.

Because of cooperative-competitive integration, dominant motion signals are amplified and less-dominant motion signals are attenuated. In an ideal motion-detection system, a rigidly moving object should activate only one directional channel: the channel responsive to the object's direction of movement. However in reality, the visual system is not immune to noise. Sources of noise include the visual system's background activity, the aperture problem/ and multiple contours or regions of the same object not moving in synchrony such as in the tree example above.

The physical laws governing object motion permitted the evolution of signal-enhancing mechanisms within the visual system. Since objects generally move uniformly, the predominant direction must be the correct direction and other directions must be incorrect. Since proximal retinal images tend to

belong to the same object, the visual system can safely assume they should move in the same direction (Yuille and Grzywacz, 1988). Moving objects also tend to move along a constant trajectory over time (Anstis and Ramachandran, 1983). As a result, the dominant direction should be amplified and other directions attenuated. The cooperative-competitive network described above accommodates all these requirements and its neural implementation is not difficult to envisage (see below). The model is rationally sound. Lappin and Kottas (1976) offer an example of committee members who must cooperate on popular consensus and suppress dissent in order to speak with one voice - or at least appear to. In motion perception, the prime role of cooperative-competitive integration is to extract the global direction of stimulus motion from disparate local motion signals.

Psychophysical Support for Cooperative-Competitive Motion Integration

Nonlinear integration in motion perception was first described using a class of stimuli called random dot kinematograms (RDKs). RDKs, which were first described by Braddick (1974), are square patches of hundreds of randomly positioned tiny dots as illustrated in Figure 3. At regular temporal intervals, all the dots simultaneously undergo apparent motion which is a discrete spatial displacement rather than a continuous drift. If all the dots in an RDK are displaced in the same direction, and displacement size and time interval between displacements are small enough - 100 ms and 10 min-arc, the

RDK appears to move smoothly and uniformly; the perception is of global motion. As a result, apparent motion is an adequate simulation of real motion (Barbur, 1981; Anstis et al., 1985). Perceived motion in television and film is actually apparent motion since the actions are presented not continuously but as a series of discrete frames.

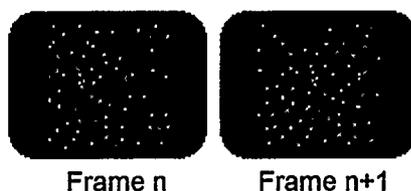


Figure 3. An RDK is a patch of randomly positioned dots. The number of dots can vary from a few dozen to many thousands. At regular time intervals, all the dots are displaced in an experimenter-determined direction. Dots that move past an edge are wrapped around to the opposite edge. When the displacement distance is sufficiently small, smooth global motion is perceived. The RDK can contain any number of frames.

The observer's task in RDK experiments is to determine the global or dominant direction of motion. Apparent motion studies often utilize RDKs in which the dots have been divided into two interspersed groups: signal and noise dots. Signal dots move uniformly in an experimenter-determined direction and the remaining noise dots move in random directions. Except for direction of motion, signal and random dots are indistinguishable. RDKs are ideal stimuli for psychophysical investigation of cooperative-competitive integration since the signal and noise components can be independently

controlled. The proportion of signal dots to the total number of dots is referred to as the RDK's coherence. High coherence RDKs produce strong percepts of uniform motion in the signal direction, whereas, low coherence RDKs produce percepts of local random motions. RDKs contain no discernible edges, have short frame durations, and their dots are too numerous and randomly positioned, to allow observers to infer the global direction of motion by consciously tracking individual dots. As a result, the perception of global RDK motion must rely on the lower-level integration of local dot displacements (Braddick, 1974; Anstis, 1980). High coherence RDKs produce smooth global motion presumably because they stimulate activity concentrated in one directionally-selective channel. Low coherence RDKs stimulate activity across many directionally-selective channels producing little global motion.

Perceived motion coherence is not linearly related to statistical coherence, however, since observers often report RDKs to be more directionally coherent than would be predicted from the RDKs' statistical coherence (eg. Chang and Julesz, 1984; Williams and Sekuler, 1984). The cooperative-competitive network can account for this phenomenon. Examples of competition in motion perception have existed since the early 1970s. In the past decade, support for motion cooperativity has grown as well. Signs of cooperativity typically include disorder-order transitions, bistable states and hysteresis as discussed below.

Levinson and Sekuler (1973, as cited in Sekuler and Levinson, 1974) found that for the detection of rightward motion, a drifting bidirectional left-right sine-wave grating is less effective in adapting motion selective mechanisms than a drifting unidirectional rightward grating of equal contrast. They concluded that the leftward component in the bidirectional stimulus must have reduced the adaptational efficacy of the rightward component by inhibition. Based on this observation, Sekuler and Levinson (1974) proposed that motion detectors tuned to opposite directions inhibit one another.

Lappin and Kottas (1981) found that two superimposed RDKs moving in opposite directions were competitive since increasing the coherence of one RDK reduced the detectability of coherent motion in the second RDK. Later, Chang and Julesz (1984) conducted a study in which adjacent RDK strips were arranged to form a square. They found that strips of low coherence would appear to be moving in the same direction as adjacent strips of higher coherence presumably because of some mechanism favouring coherence. This phenomenon, motion capture, persisted even if the incoherent strips were biased 25% in the direction opposite the direction of the coherent strips.

Williams and Sekuler (1984), Williams and Phillips (1987) and Williams et al. (1986) provided evidence for cooperativity in a study of "motion hysteresis", which is the persistence of a stable percept even after the inducing stimulus has changed. They constructed RDKs in which the dots moved within

a dynamically variable range of directions. If the range of directions was narrow enough, observers reported coherent motion in the mean direction of motion. Williams and his colleagues found that observers would report a normally incoherent wide-range (ie. > 90 deg) RDK to be coherent only if immediately preceded by a narrow-range RDK (ie. < 90 deg). They concluded that some cooperative process was maintaining the percept of coherent motion in time.

Adelson and Movshon (1982) and Snowden (1989) reported that competition occurs not only between opposite directions of motion but also between orthogonal directions of motion as well. Snowden (1989) found that vertical motion can reduce the detectibility of horizontal motion by a factor of one half when vertical and horizontal RDKs were superimposed. He also found that random motion was less effective than coherent vertical motion at suppressing horizontal motion presumably because noise activates many competing channels which will also mutually inhibit each other.

Snowden and Braddick (1989a,b, 1990) report that as the number of frames in an RDK increases, observers' ability to judge the true direction of motion correctly improves in a sigmoidal fashion. Snowden and Braddick suggest that nonlinear gains in sensitivity are mediated by long-lived interactions between motion-detectors. Based on this finding and previous

research by others, they formulated the cooperative-competitive network model.

RDKs were originally used to demonstrate two types of apparent motion: long-range and short-range (Braddick, 1974). Long-range apparent motion is believed to be mediated by high level cognitive processes and is involved in the perception of object displacements greater than 15 min arc or temporal intervals greater than 100 ms. Short-range apparent motion is a low-level process believed to be directly mediated by specialized motion-detecting neurons. Short-range apparent motion is limited to dot displacements of 15 min arc or less and temporal intervals less than 100 ms. The motion cooperativity studies cited above involved short-range apparent motion; experiments involving long-range apparent motion fail to demonstrate cooperativity (Williams and Phillips, 1987). As a result, motion cooperativity is believed to be mediated at the very early stages of motion detection in visual cortex (Braddick, 1974).

Physiology of Motion Processing and Directionally-Selective Neurons

Motion-detecting neurons have been identified at all levels of the visual system from retinal ganglion cells in rabbits (Barlow and Levick, 1965) to extrastriate cortex in macaque monkeys (eg. Baker and Cynader, 1986). Although motion-related information is conveyed to subcortical structures such as the superior colliculus, striate and extrastriate cortex are primarily

such as the superior colliculus, striate and extrastriate cortex are primarily responsible for processing object motion in humans and other primates.

Due to ethical considerations, physiological experimentation in humans is limited. Physiological correlates of motion perception are sought in closely related primates such as the macaque monkey which has a visual system that closely parallels the human visual system (van Essen, 1985). Since much cortical work has been conducted using cats, consideration of the feline visual system is also useful. Visual cortex is divided into numerous retinotopically-organized areas. Several appear to be specialized for processing particular visual submodalities such as texture, color or motion. Directionally-selective (DS) cells have been identified in layer 4B of striate cortex (V1) and these project to extrastriate area MT, the medial temporal area (Lund, 1988; see Figure 4).

In cat and monkey, cells in the LGN lack orientation-selectivity and direction-selectivity but V1 cells exhibit both properties (Schiller et al., 1976). This suggests that V1 is the primary site at which directional information is extracted in higher primates. Studying macaque V1, Hubel and Wiesel (1968) found that half the complex cells are directionally-selective since these cells "showed highly asymmetric responses to diametrically opposite directions of movement." Most unidirectional cells were located in layer 4B. Schiller et al. (1976) confirmed Hubel and Wiesel's findings for complex cells but reported

directional-selectivity in macaque simple cells as well. Using a more conservative directional-selectivity criterion, half-maximum response amplitude, De Valois et al. (1982) reported that about one-third of macaque striate cells were unidirectional regardless of simple-complex groupings. Striate cortex clearly contains a large concentration of motion-sensitive neurons.

Area MT is a relatively small cortical area- about 33 mm² in area or 3% the size of V1 (van Essen, 1985); it is buried deep within the superior temporal sulcus in primate parietal cortex. Area MT receives its major input from V1. Area MT cells differ from V1 cells primarily in that they have larger receptive fields (van Essen, 1985). This suggests that MT neurons integrate the outputs of many V1 neurons. Area MT has been identified in all primates studied and is assumed to have an analog in humans. Mikami et al. (1986) report that about 50% of area MT neurons are directionally-selective. Psychophysicists have associated area MT with motion perception and lesions to the putative human area MT reduce patients' ability to discriminate stimuli moving in different directions (Newsome and Pare, 1988). Adjacent to area MT are the medial superior temporal (MST) and ventral intraparietal (VIP) areas. Both receive major input from area MT but their functions are not well understood.

Physiological Support for Cooperative-Competitive Motion Integration

If the cooperative-competitive model is correct, motion in the nonpreferred direction should suppress a neuron's spontaneous firing rate by competitive inhibition. Hubel and Wiesel (1968) found that movement in nonpreferred directions did not suppress spontaneous activity in V1 neurons and often evoked a small increase in activity. However, Schiller et al. (1976) report the opposite: movement in the nonpreferred direction produces a small degree of inhibition in many V1 cells. Mikami et al (1986) report findings similar to Schiller et al. (1976) for area MT neurons. These and similar studies typically involve unidirectional stimuli. To study motion integration as conceptualized in the cooperative-competitive model, however, it would be necessary to stimulate with multidirectional motion stimuli.

Even though some psychophysical researchers have proposed area MT as the site of motion cooperativity (eg. Snowden and Braddick, 1989a), empirical support for this hypothesis is weak. Support for cooperativity and competition between neurons in striate cortex is stronger. Inhibitory interactions occur in striate cortex between orientation detectors tuned to different orientations (Blakemore and Tobin, 1972, Matsubara and Cynader, 1983). Blakemore and Tobin (1972) found that by stimulating a cell with an optimally oriented bar, varying the orientation of a background grating reduced the cells' responsiveness when the background grating orientation

differed from the bar orientation by less than 90 degrees. Blakemore and Tobin (1972) suggested that inhibition among cells in neighbouring columns serves to sharpen a cell's tuning curve and may be a fundamental property of sensory cortex.

Hubel and Wiesel (1962) and De Valois et al. (1982) propose that V1 neurons' orientation specificities derive from inhibitory interactions between cells rather than simple summation of excitatory inputs. In addition to supporting the Snowden and Braddick model of motion-processing, this may explain why inhibition is typically not observed when a nonpreferred stimulus is presented alone. De Valois et al. (1982) suggest that broadly tuned cells provide inhibitory input to narrowly-tuned orientation-detecting cells in order to further narrow orientation tuning. GABA antagonists, which block intracortical inhibition, are known to reduce neural orientation selectivity (eg. Pettigrew and Daniels, 1973). This data supports the role of inhibition in sharpening neural tuning. The cooperative-competitive model suggests that inhibitory mechanisms improve directional tuning in motion perception.

Ts'o et al. (as cited in Gilbert, 1985) found intrinsic facilitatory connections among cells with similar receptive field properties. These were short-range horizontal connections which may mediate interaction among similarly tuned cells. The lengths of the connections were typically one hypercolumn wide suggesting links connecting neighbouring hypercolumns.

Based on similar data, Mitchenson and Crick (1982) proposed a physiological pattern processing model similar to Snowden and Braddick's motion cooperativity model. Specifically, Mitchenson and Crick propose that striate cortex's facilitatory and inhibitory interconnections sharpen orientation tuning. When Berkeley and Bush (1983) attempted to interrupt such connections in V1, they found a reduction in orientation tuning.

Area MT's intrinsic connectivity is not well investigated. Weller et al. (1984) report area MT columns that exchange intrinsic connections but the functions of those connections was not investigated. Conceivably, the connections could be similar to striate cortex's facilitatory and inhibitory connections.

It was suggested above that investigating cooperative-competitive motion integration at the cellular level requires stimulation with multidirectional stimuli. In a study reminiscent of Snowden (1988), Kaji and Kawabata (1985) found that two superimposed RDKs moving in opposite directions evoked less activity in cat V1 neurons than did one RDK moving in the preferred direction even though the bidirectional stimulus contained twice the number of dots. A linear summation of the responses obtained with each direction alone was larger than the response elicited by the two RDKs superimposed. Presumably, the RDK moving in the nonpreferred direction inhibited the cells' responses to an RDK moving in the preferred direction.

This inhibition could not be a center-surround receptive field effect since the RDKs were completely superimposed. Similar results were obtained with superimposed gratings and RDKs. Interestingly, nonpreferred directions do produce some excitation of the cells when presented alone but also inhibit the same cells when the preferred direction is present. Kaji and Kawabata (1985) suggest that inhibition may originate from cells excited by the inhibited cell's nonpreferred direction; this suggestion is entirely consistent with the cooperative-competitive model of motion integration.

The body of physiological data cited above supports the existence of excitatory interactions between similarly tuned visual neurons and inhibitory interactions between dissimilarly-tuned neurons.

Motion Adaptation and Cooperative-Competitive Integration

Sensory adaptation is a state of reduced sensitivity to a specific stimulus induced by prolonged exposure to similar stimuli. It is a general phenomenon having been reported in many modalities including luminance, contrast, color, spatial frequency, color, pain, touch, olfaction and hearing. Direction-specific motion adaptation is induced by prolonged exposure to a uniformly moving stimulus.

The primary effects of motion adaptation are reduced directional sensitivity, perceived shifts of direction, and motion aftereffects. Reduced sensitivity is reflected in higher detection thresholds for motion in the adapted

direction (Raymond, 1993). Observers also perceive motion to be shifted away from the adapted direction when the direction of motion is moderately different from the adapted direction (Levinson and Sekuler, 1976). Motion aftereffects are illusory percepts of motion opposite the adapted direction even though the test stimulus is stationary (Raymond, 1993). Interestingly, motion adaptation has been found to reduce perceived coherence as well (Movshon et al., 1985). Thus motion adaptation may prove to be a useful tool in studying cooperative-competitive integration.

Various hypotheses of how adaptation reduces sensitivity exist but the dominant themes are based upon theories of neural fatigue or upon evidence for elevation of detection thresholds. Theories of neural fatigue assume that prolonged activation fatigues neurons (Dealy and Tolhurst, 1974; Anstis and Duncan, 1983). Empirical data, however, indicate that neurons with high maximal firing rates often do not adapt while less active neurons do adapt (Sclar, Lennie and DePriest, 1989). Petersen et al. (1985) were able to show adaptation in MT cells, even though the cells had relatively low firing rates. In fact, neural firing rates after adaptation are not dramatically reduced relative to the unadapted state - often by just a few percent (Sclar et al., 1989; Hammond et al., 1986). Movshon et al. (1980, as reported in Petersen et al., 1985) demonstrated contrast adaptation in cortical cells but not in corresponding LGN cells; this suggests that not all classes of cell are prone to

adaptation. When properly stimulated, cells in cortical layers 1 to 3 tend to habituate but cells in layers 4 to 6 generally do not (Hubel and Wiesel, 1968). Thus physiological support for the phenomenon of motion adaptation based on neural fatigue is, at best, inconclusive.

Threshold elevation models propose that an adapted channel's detection threshold is elevated relative to the unadapted state by some high order perceptual process (Ellis, 1972). That is, a channel's activity must reach a higher than normal level to evoked conscious awareness. However, this would not adequately explain motion aftereffects. In the typical motion aftereffect, observers perceive a stationary stimulus to be moving in the direction opposite the adapting direction. If the adapted direction's threshold is elevated, then the probability of perceiving the opposite direction should not be altered and should certainly not be enhanced.

It is possible that adaptation reduces sensitivity by suppressing the cooperative-competitive network so that dominant directions are not amplified. Adaptation may be a property of the cooperative-competitive network rather than individual neurons. In this scheme, the improvements in coherence attributed to cooperative-competitive integration would cease for the adapted direction and thus reduce its activity relative to the unadapted state. An efficient motion-detection system must be optimized to detect change and, as a result, should not indefinitely enhance the detectability of

long-lived stimuli. This model parsimoniously explains both aftereffects and reduction in firing rates. After-effects may be due to a reduction of inhibition of the unadapted directional channels by the adapted channel; the illusory motion opposite the adapting direction may reflect postinhibitory rebound.

Prior to the development of channel-based theories of motion perception, motion-detecting neurons were believed to be organized into mutually opponent pairs (opponent-process theories; Mather, 1980). One member of the pair would detect one direction and the other member would detect the opposite direction but each would, when stimulated, inhibit the other's activity. The relative activity among the population of pairs would determine the perceived direction of motion. Channel theories, however, assumed that neurons responsible for opposite directions are independent. The cooperative-competitive model is, in essence, a modified channel theory. If it is correct, adaptation in one direction should alleviate inhibition on competing directions resulting in an enhancement of activity in unadapted neurons. Such results have been reported by Petersen, Baker and Allman (1985). As expected, they found that when MT neurons are adapted to motion in the preferred direction, responsiveness to the preferred direction is reduced. However, when adapted to the opposite direction, the neurons' responsiveness to the preferred direction is enhanced. Enhancement and suppression effects tended to be equally strong. Cells that were not directionally-selective did not

adapt or exhibit either effect. Presumably, the adapting stimulus was adapting neurons tuned to its direction and thus reducing their ability to inhibit competing neurons. Although Petersen et al. (1985) did not interpret their results in the context of a cooperative-competitive model, they did suggest that enhancement could be due to habituation of an inhibitory input tuned to the adapting direction. Hammond et al. (1985) found that bidirectional cells, regardless of adapting direction, showed depressed activity for motion in the same direction but enhancement for motion in the opposite direction. Von der Heydt et al. (1978 as cited in Hammond et al., 1985) report preferred-direction depression and slight null-direction enhancement after motion adaptation.

Motion Visual Evoked Potentials

Measuring visual function electrophysiologically in humans is limited to noninvasive measures such as the visual evoked potential (VEP). VEPs are electric potentials measured from the scalp and represent the combined synaptic activity of millions of cortical cells in response to a visual stimulus. As a result, VEPs are suitable for studying the global integration of localized visual events.

VEPs are recorded with electrodes applied to the scalp overlying visual cortex and referenced to an electrically indifferent site such as an earlobe. The microvolt-range signals must be amplified hundreds of thousands of times

to produce appreciable recordings. The cortical response to a visual stimulus is small relative to the noisy background EEG activity. As a result, tens of VEP responses are summed to average out noise and extract an appreciable and reliable response.

In the time domain, VEPs are represented as voltage fluctuations as a function of time. Component peaks and troughs along the waveforms vary with stimulus properties such as spatial frequency or contrast. To quantify VEP waveforms, peak to peak voltage differences or peak latencies are determined. Figure 4 illustrates a typical VEP evoked by a moving stimulus.

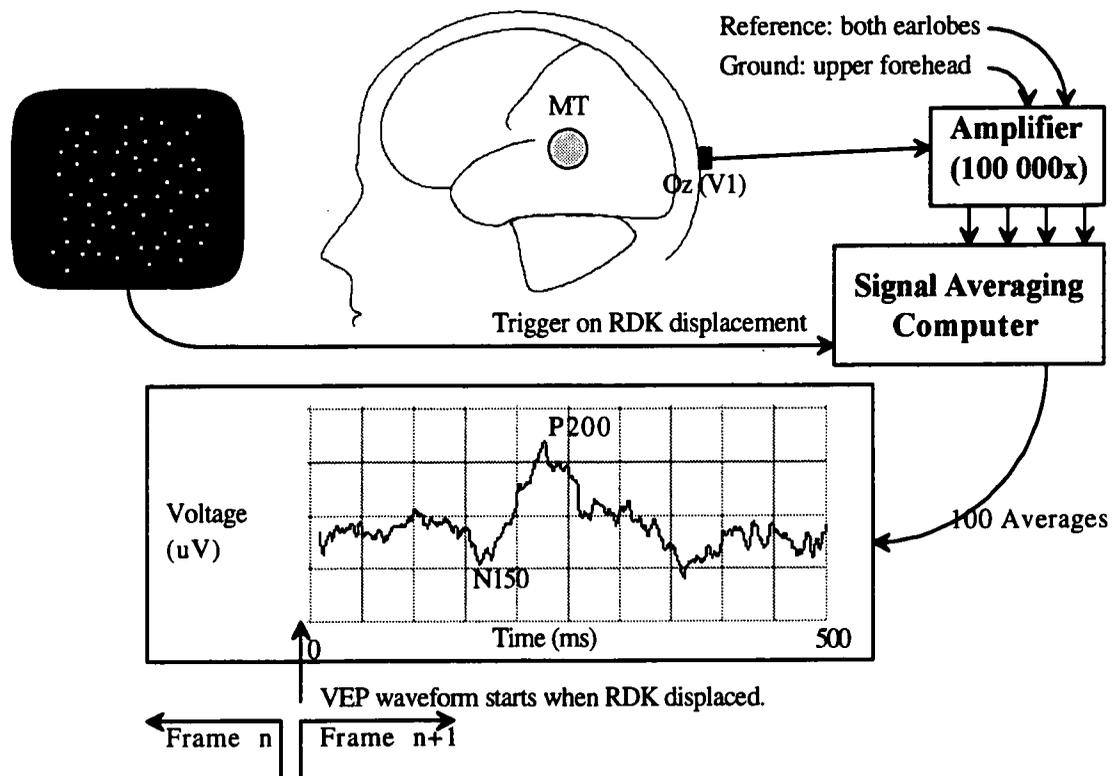


Figure 4. Motion VEPs are recorded from the scalp overlying visual cortex. Recording of each VEP response is initiated by RDK displacement

and continues for 500 ms. 100 such responses are averaged to cancel out noise and extract a clean motion VEP. Motion VEPs typically have two prominent components: a negative peak at 150 ms post-stimulus and a positive peak 200 ms post-stimulus.

Stimuli typically used to evoke motion VEPs include drifting checkerboards, gratings or RDKs. One problem encountered with motion VEPs is the possible intrusion of luminance and pattern-processing components that are unrelated to the motion of the stimuli. These cannot be completely avoided since all visible stimuli must contain some contrast, but they can be minimized by careful stimulus design. It is thus necessary to distinguish genuine motion VEPs (mVEPs) from pattern VEPs. De Valois et al. (1982) reported that small moving spots were often very effective in driving cortical cells. Thus for the purposes of mVEP recording, RDKs may be ideal orientation-free motion stimuli.

Directionally-selective motion VEP have been recorded from human occipital lobes (eg. Clarke, 1973). Researchers have identified two different waveforms evoked by moving checkerboards and gratings: a motion-onset response and a motion-offset response. These two responses differ in waveform and scalp topology. Apparent motion stimuli produce mVEPs with characteristics of both responses. As illustrated in Figure 4, motion-sensitive mVEP components include a negative trough about 150 ms post stimulus onset (N150) and a positive peak about 200 ms post stimulus onset (P200). These

latencies and amplitudes of these components vary with, among other variables, adaptation, stimulus size, eccentricity, displacement size and contrast (Clarke, 1973, Gopfer et al., 1990; Muller et al., 1990; Kuba and Kubova, 1992).

There are presently no reported mVEP studies in which statistical motion coherence was varied. Manning et al. (1991) did compare mVEPs recorded during periods of perceived coherence and periods of motion breakdown and found that periods of coherence result in mVEPs with negative components of smaller amplitude than in mVEPs recorded during periods of perceived breakdown. Unfortunately, this technique does not alter RDK coherence. Instead, the subject views a unidirectional (ie. 100% coherent) RDK and reports periods of perceived coherence and breakdown. Thus the independent variable relies on an alteration of perception rather than stimulation and could involve any stage along the motion-processing pathway. Furthermore, the time required for breakdown of coherence is sufficient to induce motion adaptation.

To determine if mVEPs are influenced by statistical RDK coherence, I conducted a pilot study in which mVEPs to RDKs of 0%, 50% and 100% coherence were recorded. The results revealed that the amplitude of a positive-going (P200) component, 150 to 180 ms post-displacement, varied with statistical RDK coherence. On the basis of that pilot study, formal

experiments were conducted to characterize the relationship between the motion VEP and RDK coherence further. An additional study investigated motion adaptation. The methodology and results of these experiments follow.

General Methods

Subjects

Seven experimentally naive subjects and the author participated as observers in five experiments. The subjects (6 male, 2 female) ranged in age from 16 to 35 years. None had any known visual deficits other than corrected myopia. Three observers (AA, MA and TL) were well experienced in psychophysical motion tasks.

All subjects participated as unpaid volunteers and were given the option to withdraw at any time. Informed consent was obtained from each observer prior to participation in accordance with the University of Calgary's Conjoint Medical Bioethics Committee standards.

Stimuli and Apparatus

The stimuli were RDKs produced by an IBM PC/AT compatible computer equipped with a 512 kilobyte Trident 9000 video adapter (Trident Systems, Mountainview, California) driving a 14 inch Primax Spectrum II (Primax Computer Systems, Toronto) color VGA monitor. The screen resolution was 640 horizontal pixels (picture elements) by 480 vertical pixels. When viewed from a distance of 100 cm, the diameter of individual dots was approximately 1.25 min arc. Dot luminance was set to 10 cd/m² white as

measured by a Hagen Universal Photometer Model S2 (Optikon, Waterloo, Ontario); background luminance was less than 0.1 cd/m². The vertical refresh rate of the video system was 72 Hz or 13.9 ms per frame.

The computer equipment was placed on a desk and adjusted so that the center of the screen would be at eye-level for a seated observer. A computer-generated red fixation point was centered within the RDK stimuli to facilitate steady and prolonged fixation. A chinrest was provided to minimize head movements.

Each RDK stimulus consisted of 4000 single-pixel dots randomly positioned within a 480 by 480 pixel square region centered on the computer screen (10 deg by 10 deg at 100 cm viewing distance). All RDK dots were simultaneously displaced 10 min arc (8 pixels) from frame to frame. The dots could move in any of the four primary directions (up, down, left or right). Each RDK series consisted of 105 displacements (106 frames) of which the last 100 triggered recording of a mVEP response. The dots designated as signal moved along the same trajectory for all 105 displacements. Noise dots were randomly assigned a new direction (up, down, left or right) on each displacement. Dots that passed an RDK boundary were wrapped around to the opposite side of the stimulus.

Since each display frame required a 256 KB memory buffer, two frames could be simultaneously held by the 512 KB video adapter. As one frame was

displayed, the next frame was updated. Every 1100 ms during the display's vertical retrace interval, the two frames were switched to produce a discrete displacement. Switching during the retrace interval ensured near-instantaneous and smooth frame transitions.

Motion VEP responses were recorded by a Cadwell Excel evoked potential recorder (Cadwell Laboratories, Kennewick, Washington). Two replications of one hundred 500 ms-long mVEP responses were recorded and averaged for each stimulus condition. Amplifier gain was 100 000x and frequency bandpass was 1.0 Hz to 100 Hz. In order to discard responses contaminated by muscle artifacts or eye-movements, automatic artifact rejection was enabled for voltage fluctuations greater than 50mV. Motion VEP recording was initiated upon RDK displacement onset (ie. during frame switching). The trigger signal was sent through the computer's parallel printer port to the Excel's trigger-in port.

Gold-cup surface electrodes were placed at Oz, O1, and O2 to record electrical activity from midline, left and right primary visual cortex. All three electrodes were referenced to linked ears which have been shown inert to visual motion stimuli (Manning and Mazzucchelli, 1992). The ground electrode was placed on the upper-right forehead. To monitor eye-movements, a pair of electrooculogram electrodes were occasionally applied to the right nasal and temporal canthi of four subjects.

Procedure

All recordings were conducted in a dark room. Observers were seated so that the distance from their zygomatic arch (temple) to the computer screen was 100 cm. They were dark adapted for five minutes prior to each recording session. The observers were made as comfortable as possible by adjusting the chinrest and chair. They were instructed to relax and concentrate on the fixation point. They were also encouraged to resist eye-movements and eye-blinks. If needed, subjects could pause the session and were allowed to terminate participation at any time; no subject withdrew prematurely.

Two replicable averages consisting of 100 mVEPs responses were obtained for each condition in the five experiments presented below. Motion VEP recording commenced after the fifth RDK displacement (sixth frame) of each condition. This was done to avoid unstable initial VEP responses. Each VEP response was evoked by one RDK displacement starting at displacement onset. Excessive eye-movements or blinks during a displacement caused the Excel to reject that VEP response.

The observers' task was to view the stimuli - no behavioural response was required. Each 100-response mVEP average required approximately two minutes to obtain. Total participation time per subject was 2.5 to 3.0 hours. All subjects were tested between 9:00 am and 2:00 pm. The subjects were allowed a minimum two minute break between stimulus conditions to keep

them alert and to avoid motion adaptation. A five minute break between experiments was also provided. An mVEP was obtained for each condition in all experiments before a second replication was attempted. Otherwise, the conditions were presented in random order regardless of experiment.

General Results

Five related experiments were conducted in order to test hypotheses of the cooperative-competitive model of motion integration and to rule out artifacts and misinterpretations. Some general observations are presented first.

General Observations

Although VEP amplitudes and latencies varied considerably across subjects, the waveforms tended to have similar component morphologies. As demonstrated in Figure 5, a 150 ms negative component (N150) and a 200 ms positive component (P200) were especially obvious. A prominent 100 ms positivity (P100) is typically associated with pattern processing but was not

always observed in the present data (Regan, 1989).

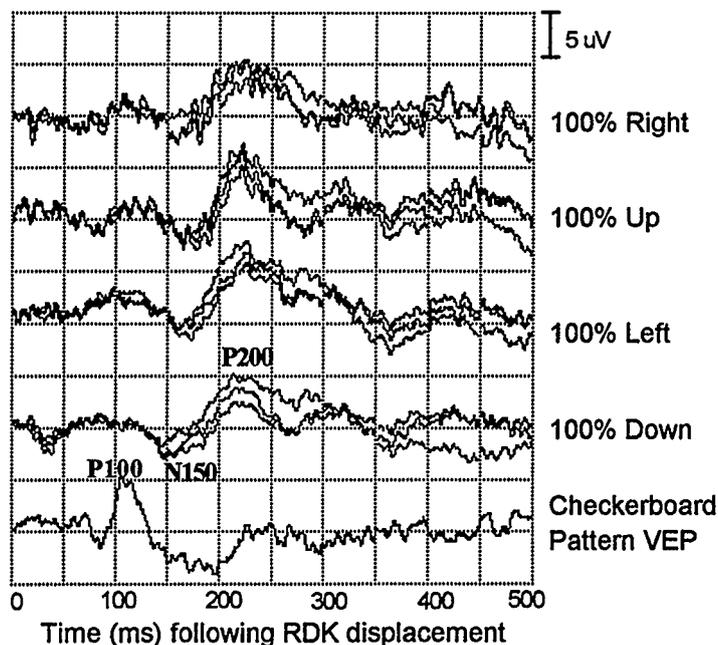


Figure 5. Sample motion VEPs from subject AA evoked in response to unidirectional RDKs moving right, up, left and down (top four traces). Three channels of activity are shown superimposed for each direction: Oz (midline occipital cortex), O1 (left occipital) and O2 (right occipital). The three channels had very similar mVEPs. As expected, these mVEPs had a prominent positive peak at 200 ms post stimulus (P200) and the negative peak at 150 ms post stimulus (N150). The bottom trace is a pattern VEP evoked by an alternating checkerboard pattern. It has a prominent positivity at 100 ms post stimulus (P100). Horizontal scale is 50 ms/division and vertical scale is 5 uV/division.

Due to the small variability between the Oz, O1 and O2 (see Figure 5), only the Oz waveforms were analyzed. The N150-P200 differential amplitude and P200 latency measures were obtained from each waveform after

three-point smoothing. N150-P200 differential amplitude was taken by subtracting the amplitude of the most negative peak in the 100 to 200 ms time interval from the most positive peak in the 150 to 300 ms time interval past RDK displacement. No other characteristics of the waveforms appeared to vary systematically with stimulus type. The amplitude and latency measures obtained from each two replications per stimulus condition per subject were averaged for statistical analysis. Approximately 3% of all mVEP responses were rejected by the VEP recorder due to excessive eye-movement or muscle artifact in those responses.

Exp. 1: How does RDK Coherence Affect mVEP Amplitude?

Rationale

The fundamental premise of the cooperative-competitive model is that motion-detecting neurons sensitive to the same direction of motion facilitate each other's activity but inhibit the activity of neurons tuned to competing directions. Assuming that facilitation and inhibition are directly mediated by excitatory and inhibitory post-synaptic potentials, then the amplitudes of mVEPs recorded in response to RDKs of varying levels of coherence should provide a gross measure of these synaptic interactions. As RDK coherence increases, facilitatory interactions and hence EPSP magnitude should increase. In contrast, as RDK coherence decreases, inhibition and hence IPSP magnitude

should increase. In this experiment, mVEPs were recorded in response to RDKs of varying levels of coherence.

Methods

Eight subjects varying in age from 16 to 35 years participated in this experiment. The stimuli were 10 deg by 10 deg rightward RDKs of 0, 25, 50, 75 and 100% coherence. Percent coherence represents the proportion of signal dots moving rightwards. The remaining dots moved in random directions. Percent coherence was corrected for the proportion of noise dots that move in the signal direction. All other stimulus parameters were the same as described in the general methods.

Results

The N150-P200 amplitude of the obtained mVEPs was found to increase with RDK coherence. The results for a typical subject, AA, are presented in Figure 6. As RDK coherence increased from top to bottom, the mVEP morphology became more definitive especially for the 75% and 100% conditions. The 0% mVEP is barely recognizable but replicates well nonetheless.

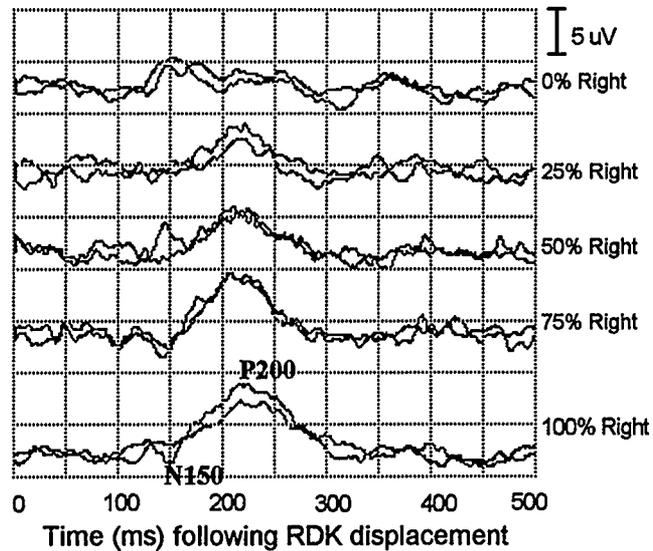


Figure 6. For a typical subject, AA, mVEP N150-P200 amplitude increases with RDK coherence but P200 latency appears to remain relatively constant. Superimposed traces are pairs of replications.

Pooled mVEP data for eight subjects is presented in Figure 7. The plots reveal a direct relationship between mVEP amplitude and RDK coherence. Mean amplitude was 3.1 uV for 0% coherent rightward motion, 4.2 uV for 50% rightward motion, and 7.6 uV for 100% rightward motion. A one-way repeated measures ANOVA revealed significant differences in VEP amplitude, $F(4,28)=16.115$, $p < .0001$. From Figure 7, it appears that the amplitudes obtained in the 0% and 25% coherence conditions differed significantly from the amplitudes obtained in the 75% and 100% coherence conditions.

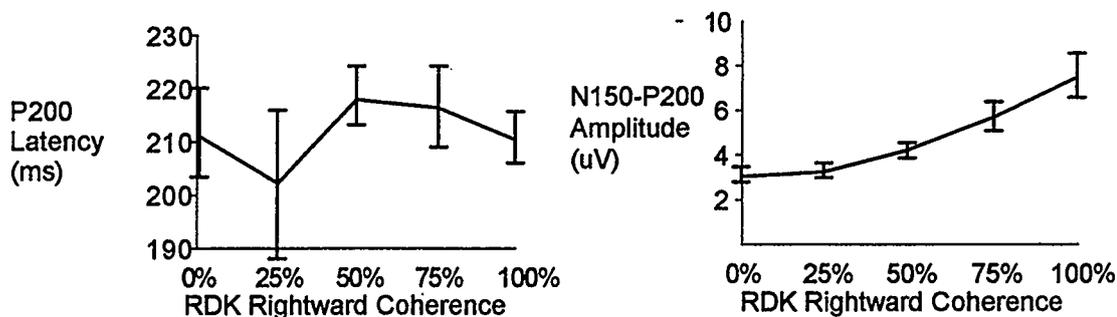


Figure 7. Pooling the data for eight subjects, it becomes clear that mVEP N150-P200 amplitude grows nonlinearly with RDK coherence. The P200 latency is independent of RDK coherence.

Prior VEP studies typically report that VEP peak latency decreases as VEP amplitude increases. However, a one-way ANOVA of the P200 latencies obtained in the current experiment revealed no significant differences in P200 latency regardless of VEP amplitude and, by extension, RDK coherence, $F(4, 28) = .585$, $p = .6763$. The range of latencies extended from 202 ms to 218 ms but no definite trend was obvious as illustrated in Figure 7.

Discussion

Motion VEP N150-P200 differential amplitude increases nonlinearly with RDK coherence. This finding implies differences in how RDKs of varying coherence are processed in primary visual cortex. If motion-integration were linear, then the mVEP amplitude would depend only on the number of dots in the RDK. Motion VEP amplitude does clearly vary with RDK coherence even when the total number of dots remains constant, however. This finding can be explained by the cooperative-competitive model of motion integration if two

alternative explanations are ruled out: different directions producing morphologically dissimilar mVEPs and motion parallel or perpendicular to RDK edges. These two alternatives are explained in the rationales of the next two experiments.

Exp. 2: Do Different Directions of Motion Produce Equivalent mVEPs?

Rationale

If each direction of motion produced a unique mVEP morphology, then the observed effect of RDK coherence on mVEP amplitude could be due to linear summation of morphologically dissimilar mVEP waveforms rather than a cooperative-competitive interaction between motion detectors. When a multidirectional stimulus such as a 0% coherent RDK is used to evoke an mVEP, that resulting mVEP would be expected to have a small amplitude since the component mVEPs could cancel out. It is necessary to compare mVEPs evoked by unidirectional RDKs moving in each direction and ensure they produce mVEPs of similar morphology, amplitude and latency.

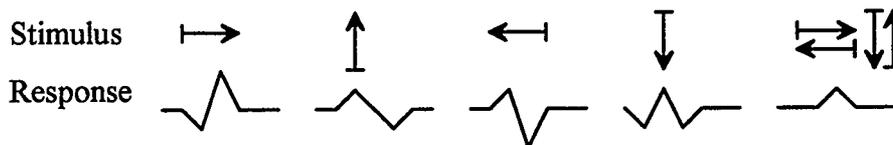


Figure 8. If each direction of motion evoked a morphologically unique mVEP, then an RDK containing multiple directions of motion will evoke an mVEP of relatively small amplitude compared to mVEPs evoked by unidirectional RDKs. This is because components of different latencies,

amplitudes and polarities will attenuate each other during neural integration and produce results similar to those expected from cooperative-competitive integration.

If different directions of motion (stimulus) produce morphologically different mVEP responses, combining directions into a multidirectional stimulus (such as the low coherence RDKs of experiment 1) may produce small amplitude mVEPs regardless of cooperative-competitive integration as illustrated in Figure 8.

Methods

The same eight subjects that participated in experiment 1 served in this experiment. The stimuli consisted of unidirectional - i.e. 100% coherent - 10 deg by 10 deg RDKs moving in each of the four primary directions. The remaining stimulus parameters were unchanged from the general methods.

Results

Motion VEPs evoked by RDKs moving in different directions for a typical subject are presented in Figure 9. For all directions, mVEP did not appear to differ in morphology, latency or polarity.

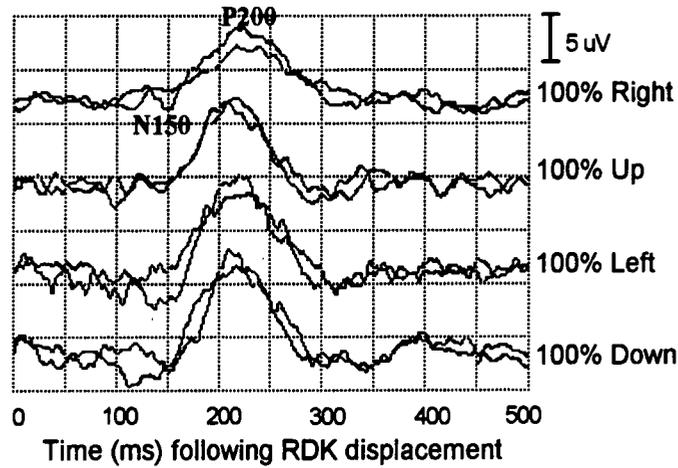


Figure 9. Motion VEPs evoked by unidirectional motion for a typical subject, AA. All four directions of motion produce mVEPs that are similar in morphology, amplitude and latency.

A one-way repeated measures ANOVA conducted on the data of eight subjects revealed no differences in N150-P200 amplitudes with RDK direction, $F(3,21) = .098$, $p = .9604$. These amplitudes for 100% upward, leftward, rightward and downward motion ranged from 7.58 uV to 7.94 uV as shown in Figure 10. In addition, P200 latencies ranged from 207 to 210 ms but were not significantly different for the four directions either, $F(3,21) = .314$, $p = .8150$.

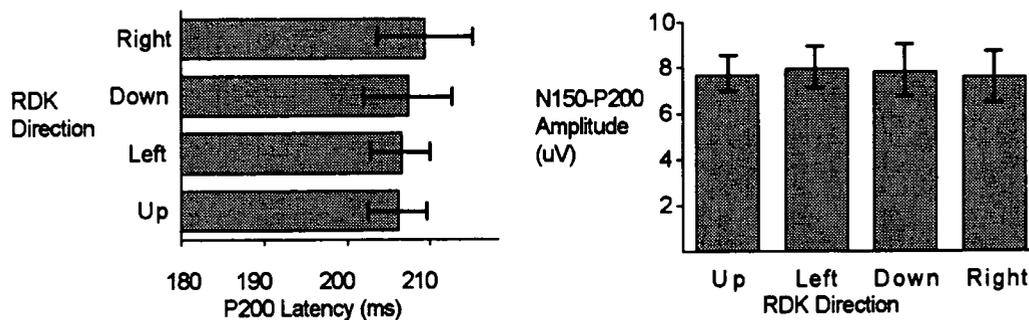


Figure 10. Mean mVEP amplitude and latency as a function of

displacement direction. Both mVEP characteristics were similar for all four directions of unidirectional motion.

Discussion

In light of the amplitude, latency and morphological similarity of mVEPs recorded in response to different directions, the varying amplitudes obtained in the coherence study could not be caused by combining different directions that produce morphologically different mVEPs.

Exp. 3: Does Motion Along or Against an Edge Affect the mVEP?

Rationale

Psychophysical studies reveal that observers are especially sensitive to motion parallel (shear) or perpendicular (compression) to an edge (van Doorn and Koenderink, 1984). Regan (1986) proposed on the basis of adaptation studies that motion parallel and perpendicular to stimulus edges are processed differently. Neurons that are especially sensitive to motion contrast or motion edges have been identified in V1 and MT (Newsome and Pare, 1988).

The relative amount of shear or compression in an RDK can be varied by elongating the RDK. Elongation parallel to the direction of motion amplifies shear while elongation perpendicular to the direction of motion amplifies compression. Even when total stimulus area is held constant, observers are more sensitive to elongated RDKs than to square RDKs (van Door and Koenderink, 1984).

Since shearing and compression motion along an RDK edge increase with RDK coherence, neurons sensitive to this type of motion rather than cooperative-competitive integration could account for the direct relationship between RDK coherence and VEP amplitude. To test this hypothesis, an experiment was conducted using RDKs elongated vertically or horizontally. The resultant mVEPs were compared to mVEPs evoked by square RDKs of equal area.

Methods

Six subjects aged 16 to 35 years took part in this experiment. The stimuli were unidirectional (i.e. 100% coherent) rightward RDKs. The RDKs were of three configurations: 7.0 by 7.0 deg square RDKs, 10.0 by 5.0 deg horizontally elongated RDKs to increase shearing motion, and 5.0 by 10.0 deg vertically elongated RDKs to increase compression motion.

These RDKs were half as large as the 10.0 by 10.0 deg RDKs of the previous experiments but dot density was kept constant by halving the number of dots to 2000. The remaining stimulus parameters were unchanged from the general methods.

Results

As demonstrated in Figure 11 for a typical subject, mVEPs recorded in response to horizontally or vertically elongated RDKs are similar to mVEPs evoked by square RDKs.

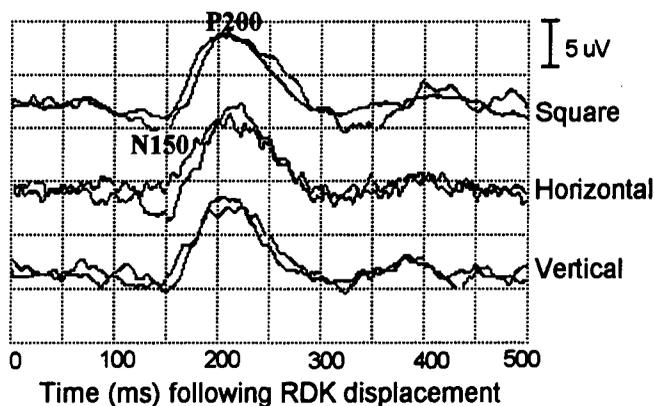


Figure 11. As evident from this data for a typical subject, AA, mVEPs evoked by unidirectional rightward RDKs are similar in waveform regardless of whether or not the RDK are elongated.

After averaging over six subjects, it was found that both types of elongated RDKs evoked slightly larger VEPs than the square RDK (see Figure 12). However, a one-way repeated measures ANOVA failed to reveal any significant differences between the three stimulus types in terms of N150-P200 amplitude, $F(2,10)=1.072$, $p=.3785$. No significant differences in P200 latency were found either, $F(2,10)=.496$, $p=.6233$.

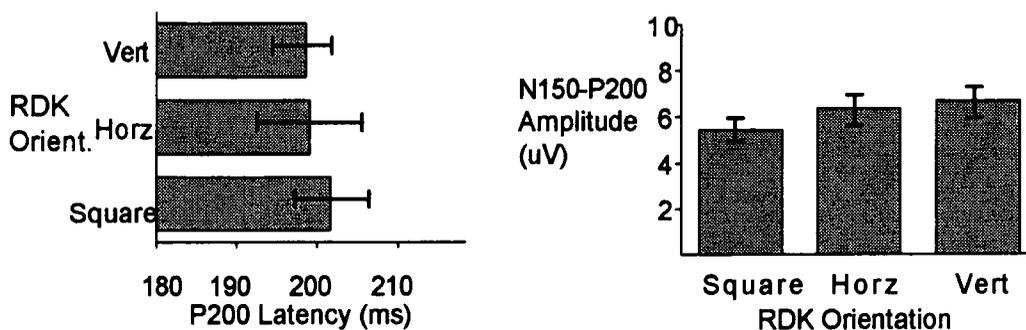


Figure 12. Pooling of the data for six subject revealed no statistically significant difference between elongated or square RDKs in terms of N150-P200 amplitude or P200 latency.

Discussion

These findings suggest that differences in the processing of shearing or compression motion are not manifested in the mVEP as amplitude or latency changes. Based on the psychophysical findings of van Doorn and Koenderink (1984), elongated RDKs would be expected to produce larger mVEPs than square RDKs of the same area. Thus even though the extent of shear and compression grows with RDK coherence, shear and compression cannot account for the direct relationship between mVEP amplitude and RDK coherence observed in Experiment 1.

Exp. 4: Are Orthogonal Directions of Motion Mutually Inhibitory?

Rationale

The square condition RDKs in experiment 3 contained 2000 rightward-moving dots; whereas, the 50% coherent RDKs in experiment 1 contained 2000 rightward-moving dots and 2000 randomly-moving dots but evoked mVEPs of smaller amplitude than the square condition of experiment 3 (4.2 uV vs 5.4 uV; $t(6)=2.57$, $p<.05$). The addition of noise dots attenuates mVEP amplitude - presumably by mutual inhibition among motion detectors tuned to competing directions.

Opponent-motion models of motion perception typically assume that motion-detectors tuned to opposite directions of motion are mutually inhibitory. However, the cooperative-competitive network model assumes that

competition between motion-detectors encompasses not only detectors tuned to opposite directions, but detectors tuned to orthogonal directions as well. This assumption has received support in the work of Snowden (1989). To investigate the competitiveness of orthogonal directions relative to opposite directions using an mVEP methodology, it was necessary to implement RDKs in which the noise dots were restricted to moving opposite or orthogonal to the signal direction.

Methods:

Six subjects aged 16 to 32 participated in this experiment. The stimuli consisted of 10 by 10 deg RDKs of 50% rightward coherence. In the "opposite" condition, the noise dots moved left; in the "orthogonal" condition, the noise dots moved either up or down; and in the "all" condition, the noise dots moved up, down and left. This last condition was the same as the 50% condition in experiment 1. The RDKs contained 4000 dots as in the general methods.

Results:

For subject AA, RDKs involving noise dots that moved orthogonal to the signal direction produced mVEPs similar to the mVEPs produced by RDKs in which noise dots moved opposite the signal direction (see Figure 13). This consistency was maintained after averaging the data for six subjects (see Figure 14). The opposite, orthogonal and all conditions produced equivalent

mVEPs. One-way repeated measures ANOVAs revealed no significant differences among the conditions in terms of N150-P200 amplitude, $F(2,12) = .702$, $p = .5148$, or P200 latency, $F(2,12) = 2.158$, $p = .1583$.

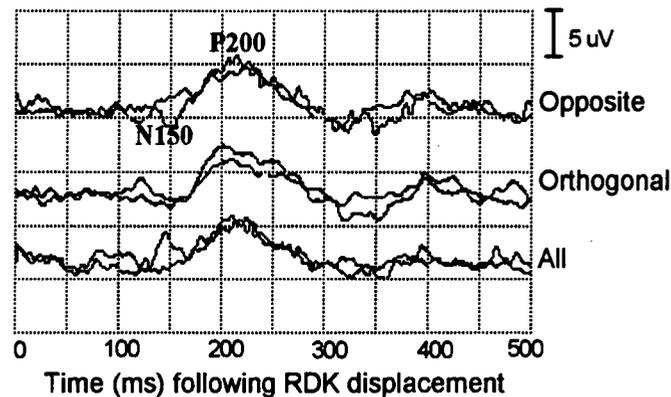


Figure 13. As evident for this typical subject, AA, mVEPs were similar regardless of whether the noise in a 50% coherent RDK was moving opposite or orthogonal to the signal direction.

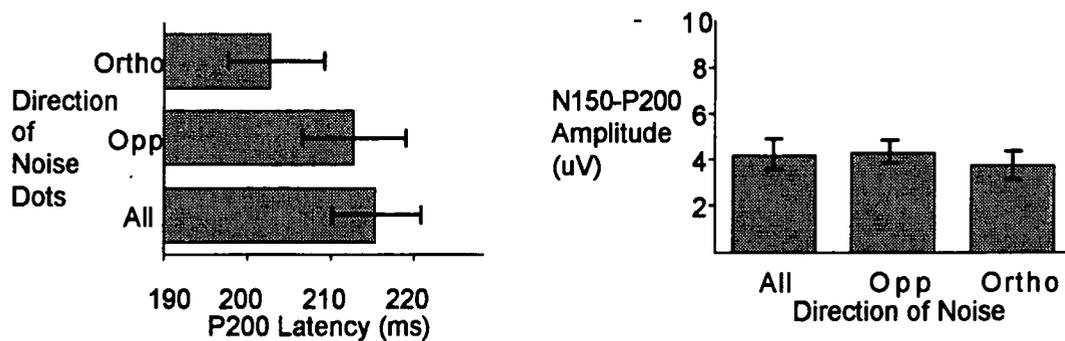


Figure 14. Rightward RDKs of 50% coherence in which noise was opposite the signal direction, orthogonal to it or both were used to evoke motion VEPs. After pooling the data of six subjects, the resultant VEPs did not differ significantly in amplitude or latency suggesting that orthogonal directions are just as mutually inhibitory as opposite directions.

Discussion

Orthogonal directions appear to be as mutually competitive as opposite directions as is assumed in the cooperative-competitive model of motion integration and demonstrated in the work of Snowden (1989). These data do not support traditional opponent-process models of motion-perception because such models limit mutual inhibition to motion-detectors tuned to opposite directions. Opponent-process models would predict mutual inhibition between opposite directions of motion (eg. left and right) but not orthogonal directions of motion (eg. up and right).

Exp. 5: Does Motion Adaptation Produce Disinhibition of Competing Directions?

Rationale:

Motion adaptation is assumed to reduce an observer's sensitivity to the adapted direction by reducing the responsiveness of neurons tuned to that direction. Furthermore, motion adaptation often enhances sensitivity to the unadapted directions (Petersen et. al., 1985). In light of the cooperative-competitive model of motion integration, enhancement effects may reflect disinhibition from the adapted directions. To test this hypothesis physiologically, mVEPs to RDKs of different directions were recorded prior to and after adaptation to one direction.

Methods:

Four subjects aged 16 to 26 participated in this experiment. Prior to mVEP recording, the subjects were preadapted for 90 seconds to either a unidirectional rightward RDK or a stationary "RDK". The adapting stimulus was a unidirectional 10 by 10 deg RDKs moving 10 min arc to the right every 114 ms. This short time interval between displacements was necessary to quickly induce strong adaptation. Motion VEPs to similar unidirectional RDKs moving up, left or right were recorded immediately after the adaptation period. Otherwise, the RDK parameters described in the general methods were implemented. The unadapted mVEPs were actually the same subjects' data from experiment 2.

Results:

As demonstrated for a typical subject in Figure 15, 90 seconds of motion adaptation to a rightward RDK significantly reduces N150-P200 amplitude relative to adaptation to a stationary RDK. The same amplitudes to leftward and upward stimuli appears little affected.

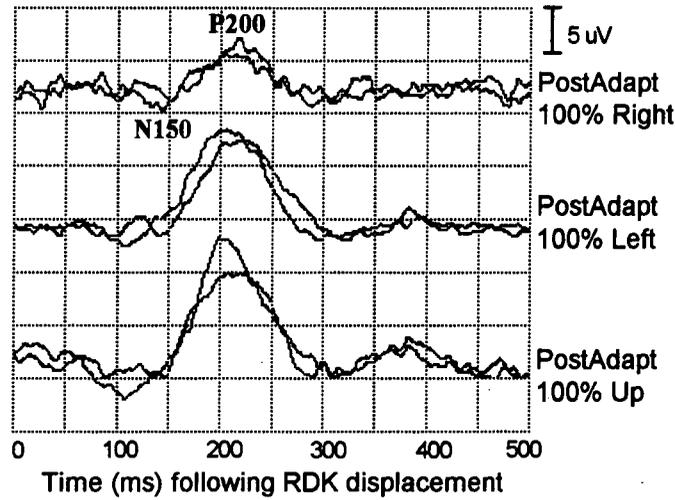


Figure 15. For subject AA, 90 seconds of adaptation to unidirectional rightward motion reduces VEP amplitude dramatically for subsequent rightward motion but leaves upward and leftward mVEPs little changed. These postadaptation mVEPs should be compared to those given in Figure 9 which were recorded without previous motion adaptation.

For all four subjects, the mean reduction of postadaptation rightward-moving RDK N150-P200 amplitude by 4.88 uV is readily appreciated from Figure 16 and is statistically significant $t(3) = 5.925$, $p = .0096$.

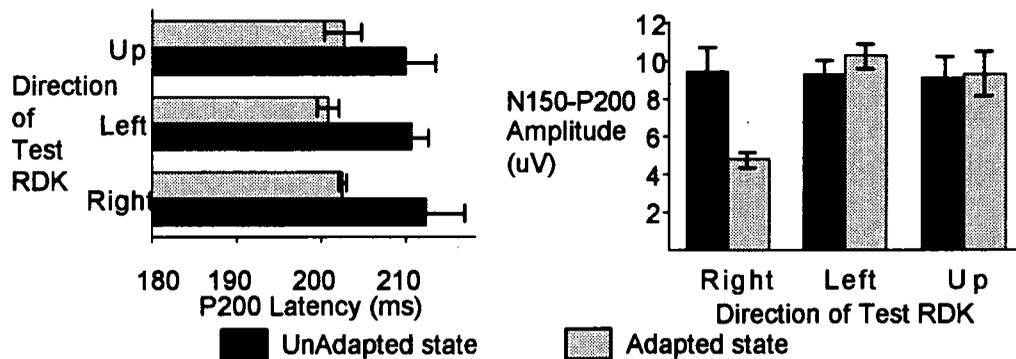


Figure 16. For four subjects, 90 seconds of adaptation to unidirectional rightward motion significantly reduced mVEP amplitude for subsequent

rightward motion but had no significant effect on leftward and upward motion. Adaptation consistently reduces P200 latency.

However prior adaptation to rightward motion does not significantly alter N150-P200 amplitudes in mVEPs evoked by leftward (mean elevation 1.03 uV , $t(3) = -.941$, $p=.4161$) or upward motion (mean elevation 0.21 uV, $t(3)=.446$, $p=.6861$; see Figure 16). A two-way ANOVA revealed that adaptation does significantly reduce P200 latency for all directions, $F(1, 9) = 12.52$, $p < .01$;

Discussion

The findings of this experiment suggest that reduction of inhibition from rightward motion-detectors does not produce an appreciable disinhibition effect in detectors tuned to directions opposite to and orthogonal to the adapted direction. Adaptation does, however, reduce the amplitude of mVEPs evoked by the adapted direction. The latencies of VEP peaks typically increase as amplitude decreases. The opposite effect was observed in this experiment for motion in the adapted direction: P200 latency decreased as N150-P200 amplitude decreased. This finding is unusual and inexplicable.

Discussion

Motion VEP Validity

An important issue in motion VEP experiments concerns the validity of the measured mVEPs as true motion responses. For a moving stimulus to be visible, it must possess some threshold contrast and hence some texture. As a

result, all or part of the measured mVEPs may be caused by pattern rather than motion processing. For example, events that are time-locked to stimulus displacement such as local luminance changes, flicker, blurring and pursuit eye-movements could cause variations in scalp potential that are not attenuated during mVEP response averaging (Regan, 1989). These sources of error must be eliminated in the current experiments in order for the measured VEPs to be considered valid indicators of motion processing.

Smooth unidirectional motion readily elicits involuntary smooth-pursuit eye-movements (eg. Murphy, 1978). Clarke (1972) demonstrated that pursuit eye-movement latencies were uncorrelated with motion VEP component latencies and thus could not be responsible for VEP generation. Nonetheless, two precautions were adopted in the current experiments to minimize the influence of eye-movements. Firstly, a central fixation point - long known to facilitate steady fixation - was provided. Secondly, eye-movements were monitored in four subjects to confirm that eye-movements were not significantly contributing to the resulting VEP. The signal averager's automatic artifact rejection feature was enabled so that EOG responses containing large voltage variations would be discarded. EOG recordings obtained from four subjects revealed that eye-movements occurred in only 3% of all trials regardless of RDK coherence. Moreover, completely random motion cannot consistently elicit pursuit eye-movements, yet, the VEPs

obtained in response to unidirectional RDKs contained the same components as the noise-evoked VEPs. The highly coherent RDKs produced mVEPs that were much larger in amplitude than the low coherence RDKs. This implies that motion VEPs, regardless of stimulus coherence, are generated by a single process not involving eye-movements.

Local luminance changes and blurring during pattern displacement, neither of which are influenced by dot displacement direction, can produce pattern-onset and pattern-offset VEP responses (Regan, 1989). If either were a significant contributor to the motion VEPs, then VEP amplitude should not vary with RDK coherence because the number of dots in the stimulus and hence the extent of blurring and luminance changes remains constant. However, this was not the case since VEP amplitude varied significantly with RDK coherence. Furthermore pattern-related P100 components were rarely observed in the obtained VEPs suggesting that pattern processing was minimal (Regan, 1989). This is not unexpected since RDKs are designed to be as pattern-free as possible.

Screen flicker during frame switching is nondirectional and, as a result, unrelated to RDK coherence. Again, this feature of the stimulus cannot underlie the motion VEPs since VEP amplitudes varied with RDK coherence. Furthermore, frame switching occurred during the screen's vertical retrace interval which is too short to be perceptible (1.2 ms) and hence can be

considered instantaneous. Screen refresh - and hence screen flicker - was time-locked to stimulus displacement; the screen refresh rate was 72 Hz but no 72 Hz frequency component was apparent in the mVEPs.

It is thus reasonable to conclude that the mVEPs obtained by stimulation with RDKs of varying coherence were not caused by eye-movements, local luminance changes or screen flicker and are true motion responses.

The majority of mVEP studies utilize drifting bar gratings, checkerboards or RDKs that reverse direction upon reaching the screen edge (eg. Spekreijse et. al., 1985, Kuba and Kubova, 1992, Manning and Mazzucchelli, 1992). The resulting mVEPs appear time-locked to the motion reversal and often resemble pattern-appearance or pattern-disappearance VEPs. Few studies actually establish the necessary directional selectivity of their mVEPs. The mVEPs presented in experiment 1 can be due only to RDK motion because RDK coherence depends solely on dot direction.

Motion VEPs and Cooperative-Competitive Integration

Motion VEP amplitude was found to increase with RDK coherence. This trend could be due to concomitant factors unrelated to the RDK coherence such as the combination of morphologically dissimilar unidirectional VEPs or activation of neurons specially sensitive to motion along stimulus edges.

Although individual observers often demonstrate some directional bias in overt judgements of RDK direction, psychophysically-measured motion detection thresholds tend to be similar for all four primary directions (Raymond, 1993). The observation that different directions of motion produce indistinguishable VEPs supports the psychophysical findings. There is no physiological evidence to suggest that direction detectors are disparately distributed in terms of numbers or response direction. Assuming that motion integration is linear and given that different directions of motion produce similar VEP responses in striate cortex, a multidirectional stimulus should produce a VEP similar to a unidirectional stimulus as shown in Figure 17. This stems from the superposition principle of systems analysis: the overall response of a linear system is equal to the sum of the individual responses to the individual components of the stimulus. However, the coherence study demonstrated that as RDK coherence decreases, so does the amplitude of the mVEP. Thus the responses to the different directions cannot be linearly summed and must somehow interact during integration. Snowden and Braddick's (1989a,b) cooperative-competitive model in which motion-detectors tuned to dissimilar directions inhibit one another

parsimoniously accounts for these findings.

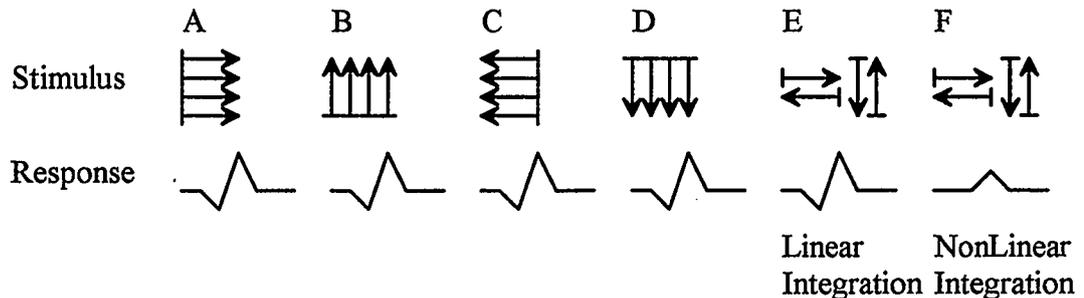


Figure 17. All four directions of motion tested were found to evoke equivalent VEPs (A to D). Combining the four directions into one stimulus should produce a similar response (E) if motion integration is linear since the output of a linear system is equal to the sum of the individual responses. However, the obtained VEP was clearly different (F) suggesting that motion integration is cooperative-competitive.

The direct relationship between RDK coherence and mVEP amplitude could be explained by motion parallel (shear) or perpendicular (compression) to the RDK edges. As RDK coherence increases, shearing and compressing increase as well. Heightened sensitivity to shearing and compression was psychophysically demonstrated by, among others, Van Door and Koenderink's (1984) use of elongated RDKs. Experiment 3 revealed no significant differences between a square RDK, a horizontally elongated RDK, and a vertically elongated RDK of the same area even though the shearing and compression were 50% greater in the elongated RDKs than in the square RDK. Mikami et al. (1986) found that motion-contrast sensitive neurons are predominantly found in area MT. Since the current study did not consider

MT, it is plausible that the heightened sensitivity develops beyond striate cortex and thus could not be detected by occipital mVEPs.

Other possible explanations notwithstanding, direct relationships between motion VEP amplitude and RDK coherence can only be explained by a dependence on RDK coherence. Psychophysicists have long assumed RDK coherence to be related to motion "intensity" and this series of experiments supports that assumption. As discussed above, a linear system of motion integration would produce VEPs with amplitude independent of RDK coherence. This is because all cells would be expected to respond similarly and their outputs linearly summated.

The observed results can be explained only by a cooperative-competitive integrative process involving preferential amplification of activity within directionally-selective channels and/or by mutual inhibition among channels. Snowden and Braddick's (1989a,b) model elegantly meets either or both criteria by positing a neural network in which motion detectors tuned to the same direction of motion mutually enhance each other's activity and inhibit the activity of detectors tuned to competing directions. Alternative models of recurrent enhancement could include Zeki and Shipp's (1988) which involves a series of feedback loops among cortical centres in which higher-levels feedback and amplify lower-levels that are driving them. For example, area MT may assess the dominant direction

evident from the V1 input and feedback onto V1 to amplify the activity of V1 cells responsive to that direction of motion and suppress the activity of detectors tuned to other directions. Zeki and Shipp propose that this mechanism enhances perceptual coherence - much as the cooperative-competitive network does. Such a feedback model could also explain motion-capture or hysteresis and other "cooperative" phenomena in motion perception if the feedback were to persist in time.

It is difficult to assess whether both cooperativity and competition are indeed involved in motion integration. Either mechanism in isolation could produce a direct relationship between RDK coherence and mVEP amplitude. If motion-detecting neurons did not interact, mVEP amplitude would depend only on the number of dots in the RDK and not its coherence. Experiment 4 revealed that both opposite and orthogonal directions are mutually inhibitory. This finding strongly supports the existence of competition between motion detectors. One could argue that the reduced mVEPs in both conditions were due to less cooperativity in the signal direction because of the reduction in signal dots by one-half. However in the absence of competition, cooperativity between noise dots moving in the same direction would be expected to compensate for the reduction in signal-dot cooperativity and hence produce mVEPs comparable to a 100% rightward RDK. The slightly smaller mVEP in

the orthogonal condition may be due to the additional competition between up and down not found in leftward noise.

Disregarding neural fatigue, support for cooperativity may be found in the adaptation study. It would be difficult to explain the reduction of rightward mVEP amplitudes after adaptation to rightward motion solely by competition since the unidirectional test stimulus did not contain any competing directions. According to the model, reduction of the competitive efficacy of one direction by adaptation should be reflected in enhanced sensitivity of unadapted directions due to reduced inhibition. Previous psychophysical and physiological studies have consistently reported same-direction suppression but the occurrence of different-direction enhancement effects is not always observed (eg. Hammond 1982; Raymond, 1993). This may be due to use of stimuli not suited to studying enhancement. For example, exposing a neuron to a 100% coherent test stimulus opposite in direction to the adapting stimulus leaves little, if any, room for enhancement. The adaptation study revealed no disinhibition of nonadapted directions. Conceivably, this could be due to lack of stimulated competing directions: a ceiling effect obtained by using unidirectional test RDKs. Thus there is simply no room for the VEPs to increase in amplitude and any inhibition that might have been induced by stimulation in the adapted direction would be minimal since the test RDKs did not contain any motion in the adapted direction. In

retrospect, 50% coherent test stimuli containing motion in the adapted direction might have proved more powerful sources of disinhibition.

In conclusion, both cooperativity and competition were implicated in the results of Experiment 4. Some researchers have suggested that the input to striate cortex is primarily excitatory but stimulus-tuning is sharpened by intracortical inhibition (eg. De Valois et al., 1982). The present results suggest that intracortical excitation may be involved as well.

Anatomy and Cooperative-Competitive Integration

Since the VEP is largely a measure of synaptic activity, this research suggests that the cooperation is mediated by synaptic excitation and competition by synaptic inhibition. This agrees well with the findings of Blakemore and Tobin (1978).

Snowden and Braddick (1989a), citing the work of Mikami et al. (1986), suggested that this type of integration occurs in area MT. However, the current study, in which VEPs were recorded from occipital cortex, indicates that cooperative-competitive integration occurs as early as primary visual cortex. This is consistent with the greater physiological and anatomical support for cooperative and competitive interactions in V1 as presented in the introduction.

Integration of Non-translational Motion

Translational motion is not the only type of motion to which humans demonstrate acute sensitivity. In fact expanding motion, motion in depth and rotary motion often produces many effects similar to linear motion - such as adaptation and priming - and is assumed to have physiological detectors (Regan, 1986; Longuet-Higgins and Prazdy, 1980). Linear trajectories can be combined to produce, for example, rotational motion (Regan, 1986). The cooperative-competitive model precludes such integrations, however, since a stimulus containing all directions will produce mainly inhibitory interactions and not a percept of rigid rotation. Regan and Beverley (1985 as cited in Regan, 1986), using an adaptation paradigm, found that discrete linear and rotary motion mechanisms can be distinguished based on selective adaptation. This suggests that the perception of rotary motion may be mediated by different channels than translational motion. It would be interesting to conduct an experiment to determine if clockwise and counter-clockwise motion are mutually competitive with each other and with linear motion. Such a study could be extended to the other types of motion cited above.

Figure-Ground Segregation and Cooperative-Competitive Integration

Objects moving against a background are particularly obvious. Well-camouflaged animals are often undetectable until they move. In the laboratory, RDKs can contain subregions in which a shape is defined

exclusively by its relative motion - not luminance, color or texture. When the RDK is stationary, the shape is invisible (Regan, 1986). The objects' boundaries are defined by relative motion: shearing or compression. Noise in the visual system is shown to reduce the coherence of moving objects. The cooperative-competitive network can enhance such boundaries however by amplifying signal (dominant directions) and suppressing noise resulting in better Figure-ground segregation. Regan (1986) suggests that spatial opponency between motion detectors may underlie the crispness associated with motion-defined boundaries. The observed improvement in stimulus contours with motion is not novel; it has been proposed to function in the detection of suprathreshold spatial frequency gratings and random dot stereograms (Levinson and Sekuler, 1976; Poggio, 1982).

Epistemology

The finding that local motion signals are nonlinearly integrated to produce a global percept of motion possibly has implications for sensory research in general. Much as lateral inhibition and center-surround opponency have redefined how the visual system codes contrast, motion cooperativity and opponency reveals that neural systems can take advantage of physical and logical consistencies in the real world to enhance otherwise noisy motion signals. Thus our percepts become faithful representations of the physical world's unitary and persistent objects. Without such active enhancement,

limitations of sensory transduction, transmission and integration might leave us with an incomplete picture.

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