



Organisation of signals involved in binocular perception and vergence control

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Abstract

A novel type of dynamic random-dot stereogram (DRS) was used to study vergence movements and depth detection in response to temporal modulations of interocular correlation. Each DRS consisted of the repeated presentation of a pair of correlated images alternated by the presentation of a pair of uncorrelated images. The intervals of high (T_c) and low (T_u) correlation varied from 14 to 224 ms in steps of 14 ms. Depth detection and vergence responses behaved very different from each other as functions of T_c and T_u . The different behaviours suggest that depth and vergence most likely result from independent streams of disparity processing. It is speculated that magnocellular layers process disparities that drive vergence and that a parvocellular stream of disparity processing is involved in depth perception. This suggestion is discussed in relation to recent findings on binocularly perceived direction and depth. The discussion leads to suggesting a headcentric organisation of signals involved in binocular perception and a retinal organisation of signals involved in vergence control. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Binocular vision is a capacity that man shares with many animal species. Stereopsis, however, which is the ability to extract a stereoscopic percept from two correlated retinal images, is present only in man and a few animal species. In the course of evolution three specialized neural systems have developed which form the foundation of stereopsis: (1) a detection system of interocular correlation. A great number of cells in the visual cortex, called disparity detectors, are sensitive to specific disparities between interocularly correlated image features (Barlow, Blakemore, & Pettigrew, 1967; Pettigrew, Nikara, & Bishop, 1968; Hubel & Wiesel, 1970; Poggio & Fischer, 1977). Together these neurons have to solve the problem of determining which features in one retinal image correspond to which features in the other (the correspondence problem). (2) A disparity-driven control system of vergence eye movements (Rashbass & Westheimer, 1961; Erkelens &

Collewijn, 1985). Vergence is the oculomotor system that reduces disparities by moving the eyes in opposite directions. Disparities have to be reduced because perception of depth is based on small disparities, particularly in the fovea (Ogle, 1952). (3) A perceptual system. If the correspondence problem has been solved successfully and disparities have been reduced to a minimum, this system interprets the remaining disparities in combination with other signals in terms of distance and depth. The input signals of this system are local horizontal disparities, global vertical disparity and eye position signals (Rogers & Bradshaw, 1995; Bradshaw, Glennerster, & Rogers, 1996; Erkelens & van Ee, 1998; Backus, Banks, van Ee, & Crowell, 1999).

Disparity detectors, measured in area V1 of alert monkeys, have been classified into six types of neurons (Poggio, 1991). Vision scientists have speculated about the role of these different neurons in stereopsis (Poggio, 1991; Howard & Rogers, 1995) and related the classification of disparity-selective neurons to different types of stereoanomaly (Richards, 1971). Another explanation for the existence of different classes of neurons is that certain classes of neurons are involved in stereopsis

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(the tuned cells) and others in vergence (the reciprocal cells). It is clear from behavioural as well as neurophysiological studies that disparity detectors are involved differently in stereopsis and vergence. Several studies have shown that disparity can induce vergence eye movements without concomitant stereopsis. Ongoing vergence movements have been induced by highly correlated image pairs of stereograms, oscillating in counterphase at such high speeds that the stereograms remained rivalrous (Erkelens & Collewijn, 1985). Transient vergence responses have been induced by stimuli that were not the same shape and could not be fused to a single object (Westheimer & Mitchell, 1969; Jones & Kerr, 1972; Jones, 1980; Semmlow, Hung, & Ciuffreda, 1986). Transient vergence responses have been induced by large disparities that could not be reduced in open-loop viewing conditions (Erkelens, 1987). Anti-correlated image pairs of dense stereograms also induced transient vergence responses but did not give rise to depth (Cumming & Parker, 1997; Masson, Bussetini, & Miles, 1997). Cumming and Parker (1997) further showed that disparity-selective neurons in V1 responded to these stimuli, indicating that V1 is directly involved in vergence control but not in depth perception. Recently, Cumming and Parker (1999) showed that the responses of most V1 neurons were consistent with encoding of absolute disparity, whereas they found no V1 neurons whose responses were consistent with encoding of relative disparity.

The picture that emerges from these behavioural and neurophysiological results is that the disparity-selective neurons in V1 involved in stereopsis are a subset of those involved in vergence. In this view all disparity-selective V1 neurons, probably via other cortical areas, project to neurons involved specifically in the control of vergence lying in the mesencephalic reticular formation of the midbrain (Mays, 1984; Judge & Cumming, 1986; Mays, Porter, Gamlin, & Tello, 1986). A subset of these V1 neurons projects to V2 and higher visual cortical areas of which it is speculated that these are involved in depth perception. The subset idea was also suggested from experiments in which vergence responses and judgements of interocular correlation were measured by presenting dynamic random-dot stereograms (DRS) in which the levels of contrast and interocular correlation were varied (Cormack, Stevenson, & Schor, 1991; Stevenson, Cormack, & Schor, 1994). Comparison of vergence responses and perceptual judgements indicated that the signals driving vergence were derived according to the same combination rules as the signals that gave rise to the perception of surfaces (Stevenson et al., 1994). A limitation of the experiments of Stevenson et al. was that vergence and depth were measured in response to constant levels of interocular correlation.

Another explanation for the various types of vergence responses without stereopsis could be that dispar-

ity is processed in two streams, one subserving vergence and the other subserving stereopsis. It is interesting to test the validity of this explanation because recent findings suggest that for the purpose of perception, retinal and oculomotor signals are first combined within monocular streams (Erkelens, 2000). Such a combination of signals seems highly unlikely for disparity driven vergence, because the purpose of vergence is to optimise retinal correspondence. If there are two streams, the transient vergence responses without stereopsis suggest that disparity-selective neurons involved in stereopsis and vergence may have different temporal properties. The purpose of this research is to investigate these temporal properties.

In order to study the temporal properties of disparity signals involved in stereopsis and vergence, one could measure depth detection and vergence gains in response to transient stimuli. Unfortunately, however, these responses are so different from each other that it may be difficult to draw conclusions from the results. Depth detection is a judgement based on the momentary disparity signal. The vergence response is sluggish and depends on feedback. Thus, vergence may simply not have sufficient time to use feedback to show a measurable response, while the same signal may be sufficient to indicate depth for a brief moment and yield a correct response. To overcome this problem I used a novel type of DRS in which the disparity signals were brief (between 14 and 224 ms), but which induced sustained depth and vergence responses (between 1 and 10 s). It seems reasonable to assume that by using these stimuli the results show properties of the disparity processing system rather than those of the two different response systems.

2. Methods

2.1. Subjects

Three subjects participated in the experiments (ages between 26 and 48 years). None of them showed any visual or oculomotor pathologies other than refraction anomalies. The subjects had normal or corrected-to-normal visual acuity. They were checked for normal stereopsis by means of partially decorrelated random-dot test stereograms (Julesz, 1971).

2.2. Stimulus presentation

The stimulus presentation technique was inspired by the dynamic random-dot displays used in previous experiments (Cormack, Stevenson, & Schor, 1991; Stevenson, Cormack, & Schor, 1994). Large DRS subtending $45^\circ \times 30^\circ$ were generated at a frequency of 70 Hz by a HP 750 graphics computer and back-projected on a

fronto-parallel translucent screen by a projection TV (Barco Data 800). Red and green filters were used to make each image visible exclusively to one of the eyes. Each image pair consisted of randomly distributed bright dots (10 arcmin diameter, density 50%) on a black background. Each DRS consisted of the repeated presentation of a pair of correlated images alternated by the presentation of a pair of uncorrelated images (Fig. 1). The correlated image pair contained a square ($10^\circ \times 10^\circ$) floating in front of the background, hidden on either the left or the right side of the stereogram. The disparity of the square relative to the background was 30 arcmin. The presentation time of each DRS was set to 10 s. The patterns and the display times of the correlated (T_c) and uncorrelated (T_u) image pairs were fixed in each single DRS. Different DRS contained different random-dot patterns and T_c and T_u were randomly selected from values between 14 and 224 ms (by steps of 14 ms).

2.3. Psychophysical test of depth detection

In a forced choice procedure, the three subjects were asked to indicate whether the square appeared on the left side of the DRS. This task appeared to be relatively easy. For most combinations of T_c and T_u the subjects were very confident about the presence or absence of the depth stimulus. To get a first indication of depth detection, each combination of T_c and T_u was presented twice (512 trials) in a random order. Measurement of psychometrical functions was not useful because there were too few combinations of T_c and T_u where the scores were different from zero and 100% correct. Decreasing the step interval for T_c and T_u to obtain more relevant measurements was not possible because the interval was limited by the frame rate of the monitor. To get reliable estimates of depth detection, the combi-

nations of T_c and T_u near the transition from absent to detected depth were presented 20 times in a random order. A level of 75% correct answers was used as the criterion for reliable depth detection. The rationale of measuring the detectability of the square was that it indicated whether correlation between the left and right eye's images was picked up by the stereoscopic system. Similarly, the rationale of measuring vergence responses was that it indicated whether correlation was picked up by the oculomotor system.

2.4. Registration of eye movements

The vergence responses were measured in separate trials. For that purpose the positions of both eyes were measured of the three subjects by using the electromagnetic scleral coil technique (Collewijn, van der Mark, & Jansen, 1975). Stimulus presentation was the same as in the experiments in which depth detection was measured with the exception that the entire images were displaced in opposite directions. The images were displaced stepwise by 1° in a rhythm of about 1/s in order to elicit repetitive vergence responses. The precise duration of the intervals between the steps (T_v) was given by $T_v = n \times (T_c + T_u)$, where the integer n was chosen such that T_v was as close to 1 s as possible.

3. Results

DRS consisting of alternating pairs of highly correlated and uncorrelated images was used (Fig. 1). In some DRS, the subjects perceived three luminance levels, judged as black, white and grey, although each pattern contained only two luminance levels. In monocular viewing, the dots looked black and white at those places of the DRS where the luminance of the dots was

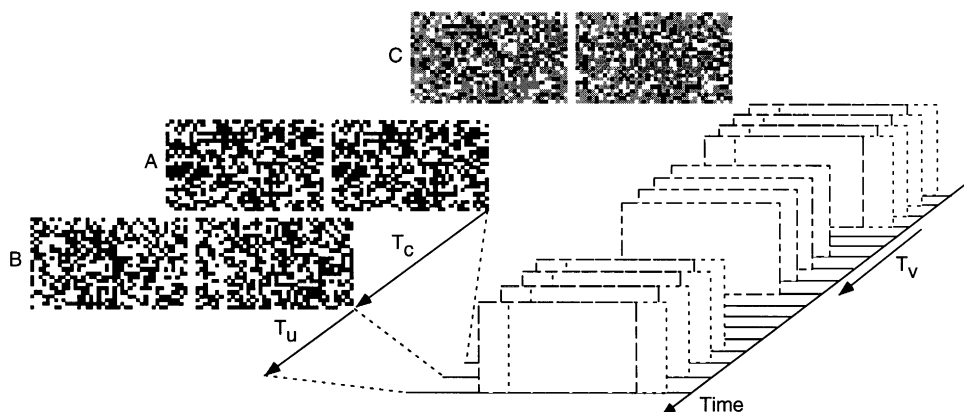


Fig. 1. Stimulus in the depth detection and vergence tasks. A DRS consisting of the repeated presentation of a highly correlated image pair (A) during time interval T_c alternated by the presentation of an uncorrelated image pair (B) during interval T_u . A square floating in front of the background was hidden in the correlated image pair (shown for uncrossed-eye fusion). A static average of A and B is perceived as a rivalrous stereogram (C). The images of each pair are displaced in opposite directions after time intervals of T_v in the vergence task.

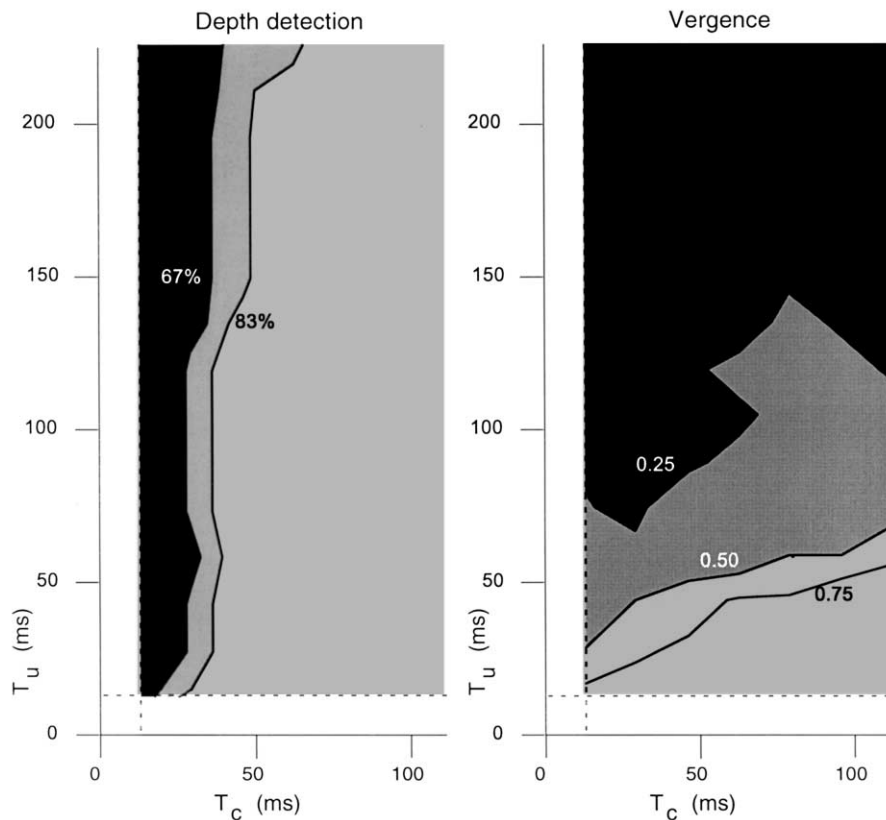


Fig. 2. Performance in the depth detection and vergence tasks. The panels show mean values of the three subjects who showed little individual differences. Detection scores and gains of vergence responses are presented in contour plots as a function of the intervals T_c and T_u . The numbers in the plots indicate the detection levels (a level of 50% indicates chance) and the vergence gains at the contours. The dashed lines indicate the minimum intervals of 14 ms.

the same in the successive images (50% of the dots). The other 50% of the dots looked solid grey when $T_c + T_u < 42$ ms, flickering grey when $42 \text{ ms} < T_c + T_u < 164$ ms, and alternating between black and white when $T_c + T_u > 164$ ms.

Detection of depth depended predominantly on the duration of T_c (Fig. 2). The subjects detected depth in the DRS when $T_c > 42$ ms. Detection of depth was almost independent of T_u . The subjects detected depth in DRS even if T_u was about five times as long as T_c (for instance for the combination $T_c = 42$ ms and $T_u = 192$ ms). A remarkable observation was that the subjects clearly perceived depth in a number of stereograms (for instance the DRS with $T_u = T_c = 56$ ms), whereas they did not experience the textures of the correlated random-dot patterns but rather perceived one of the monocular random-dot patterns (stereogram C of Fig. 1). Since the patterns of the two images were incompatible, this means that the other pattern was suppressed.

Gains of vergence responses ranged from about 0.1 to close to unity (Fig. 2). The fact that vergence gains were very low for a range of T_c and T_u values shows that the borders of the large DRS hardly induced vergence responses. Thus high vergence gains indicated

responses of the vergence system to the correlation in the DRS. Vergence responses showed rather different relationships to T_c and T_u than did depth detection. In a first-order approximation, vergence gains depended predominantly on the duration of T_c , whereas depth detection was better related to T_u . In view of the transient vergence responses in the absence of depth perception that have been reported in the literature, I expected vergence to respond better than depth detection to correlation during short periods of T_c . In particular I expected to find high vergence gains during viewing of those DRS in which the subjects were able to detect depth. Neither of these expectations came true.

The right panel of Fig. 2 shows that vergence responses were small or absent for a large range of T_c and T_u values (the black area), while the left panel shows that depth was easily detected in the majority of these DRS. Depth detection in the absence of vergence responses has not yet been reported in the literature. Fig. 3 shows the four combinations of presence and absence of depth and vergence that were observed in the experiments. Vergence and depth were both absent if periods of T_c were short and periods of T_u were relatively long.

Vergence and depth were both present if periods of T_c were long and periods of T_u were relatively short. Vergence was present and depth was absent if the durations of T_c and T_u were both very short (< 28 ms). Vergence was small or absent and depth was detected if the periods of T_c and T_u were both relatively long (> 50 ms).

4. Discussion

4.1. Dissociation of disparity signals related to vergence and stereopsis

A novel type of DRS was used to study vergence movements and depth perception in response to temporal modulations of interocular correlation. With the help of these stimuli I investigated whether disparity processing subserving stereopsis can be regarded as a part of disparity processing subserving vergence. The answer appears to be negative. Scores of depth detection and vergence gains were so different from each other as functions of T_c and T_u that depth- and vergence-related disparities are most likely processed independently. Of course, it cannot be ruled out that at an early stage of disparity processing all the correlation was detected that appeared to be detected by either the perceptual or the oculomotor system. However, it has to be assumed then that for one reason or another certain detected correlations are not used for depth detection, whereas others are not used for vergence. More straightforward is the suggestion that depth and vergence follow from independent streams of disparity processing. In view of this suggestion, the recent findings of Cumming and Parker (1999) may be interpreted as follows: certain classes of disparity-selective neurons of V1 are exclusively involved in the control of vergence, whereas others are exclusively involved in depth perception. Magnocellular layers of V1 connecting to area MT may be involved in vergence because, based on electrophysiological recordings in the cat, it has been

speculated that MT and MST neurons discharge with vergence (Leigh & Zee, 1999). Depth perception may result from a parvocellular stream of disparity processing including V1, V2, V3 and V3a (Livingstone, 1996). This hypothesis is corroborated by LGN lesions studies (Schiller, Logothetis, & Charles, 1990a,b) which showed loss of stereopsis after lesions to parvocellular layers and no deficits after lesions to the magnocellular layers. This dissociation between parvocellular and magnocellular disparity processing fits in nicely with recent evidence that for the purpose of perception, signals carrying retinal and oculomotor information are first combined within monocular streams (Erkelens, 2000), whereas vergence is more likely controlled by retinal signals alone. The consequence of this organisation of signals is that depth perception is based on headcentric disparities and vergence on retinal disparities (Erkelens & van Ee, 1998).

4.2. Organisation of binocular signals

It is clear from psychophysical studies that retinal and oculomotor signals are used in binocular perception of depth (Rogers & Bradshaw, 1995; Bradshaw, Glennerster, & Rogers, 1996; Backus, Banks, van Ee, & Crowell, 1999) and direction (Hering, 1879/1942; Ono, 1991). From neurophysiological studies, little is known about how and where these signals are combined in the binocular visual system (DeAngelis, 2000). I suggest an organisation of retinal and oculomotor signals (Fig. 4) that is based on insight coming from three areas of research, namely from research on binocular perception of depth, binocular perception of direction and control of binocular eye movements.

Up to now the general belief was that the oculomotor signals of the two eyes are first pooled before they become available for perception of depth and direction. In this sense the eyes were believed to act together as one unit known as the cyclopean eye. Very recently, it was found that the cyclopean illusion was absent during monocular viewing in daylight conditions (Erkelens,

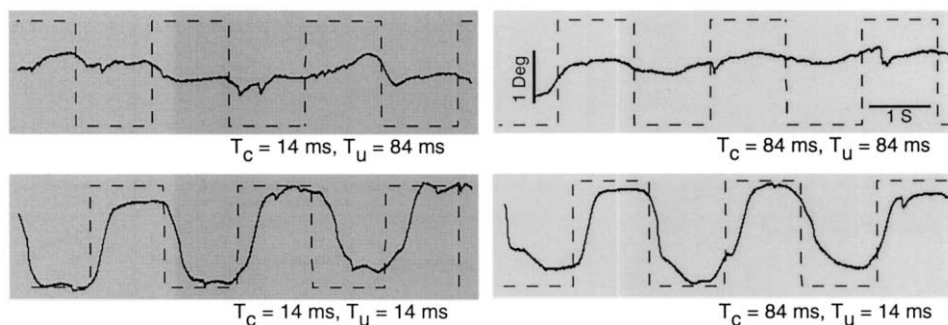


Fig. 3. Vergence responses with four combinations of T_c and T_u . Vergence eye movements (continuous lines) in response to stepwise displacements of the left and right eye's images of the stereograms (dashed lines) in counterphase. Detection of the depth stimulus is indicated by the dark (no depth) and light (depth) backgrounds.

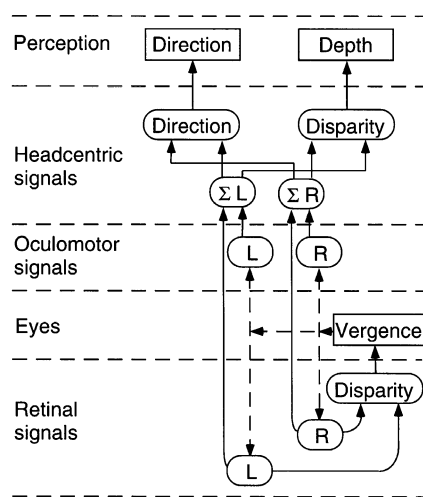


Fig. 4. Flow diagram of signals involved in binocular vision and vergence. Signals are indicated by boxes with round corners and continuous lines. Their effect (perception, vergence) is indicated by rectangular boxes. Dashed lines indicate the effect of eye positions on signals.

2000). Earlier, Enright (1988) reported without giving an explanation that the cyclopean illusion did not appear during monocular viewing of after-images. Both studies showed that the perceived directions of objects are indicated by their retinal locus in combination with the angular position of the viewing eye only, the angular position of the closed eye being irrelevant. This result indicated that in binocular vision the integration of left and right eye signals first occurs after retinal and oculomotor signals have been integrated of each eye separately.

Although these experiments were dealing with perceived direction, the conclusions may also have far reaching consequences for our understanding of the neuronal organisation underlying the binocular perception of depth. The findings put a constraint on how the relevant signals are combined in stereoscopic vision. A likely assumption, not yet invalidated by physiological data, is that the cortical cells involved in binocular perception of depth are also involved in binocular perception of direction. The consequence of this assumption is that the ordering of retinal and oculomotor signals found for processing of direction also holds for the processing of depth. This ordering of signals is at odds with the widely held idea that stereopsis and binocular depth perception are based on retinal disparities (Howard & Rogers, 1995). The concept of retinal disparity implies that retinal signals of the left and right eyes are related directly to each other. The view that depth perception is based on retinal disparity has recently been challenged (Erkelens & van Ee, 1998). Headcentric disparities were defined as the difference between the left and right eye's headcentric directions, which are also the relevant signals for binocular percep-

tion of direction. Erkelens and van Ee (1998) showed that their model based on headcentric disparities describes the psychophysical results related to global disparity transformations and explains why stereoscopic perception remains stable during (inaccurate) eye movements. Furthermore, the model explains why horizontal disparity is a local measure and vertical disparity is a global measure provided that horizontal and vertical disparities are defined relative to the head (or to the screen that is used for the presentations of the stereograms) and not relative to the retinae. Recently experiments were presented large stereograms of which half-images were scaled relative to each other were presented in such a way that the subjects could not see any difference in slant between these stereograms and an unscaled one (Berends & Erkelens, 2001). After a period of 5 min of freely looking around in the scaled stereograms, an after-effect was found in the perceived depth of objects defined by horizontal disparity. From the fact that the subjects were free to fixate anywhere in the stereograms, it was concluded that this adaptation to disparity was better related to headcentric than to retinal disparity.

In the 40 years since Hubel and Wiesel (1959, 1962) discovered that receptive fields of binocular cells occupied corresponding positions in the two eyes, a vast number of physiological studies have reported about the properties of disparity detectors. Most work has been done on the organisation and characteristics of disparity detectors in relation to the properties of visual stimuli (Gonzalez & Perez, 1998). Disparity detectors have been found in cortical visual areas V1, V2, V3, V3a, VP, MT and MST of monkeys. According to their tuning function, these detectors have been grouped into six categories (Poggio, 1991) and inter- and intra-receptive-field offsets (Freeman & Ohzawa, 1990) are believed to be the neural mechanisms of disparity detection. Nevertheless, many fundamental questions are not yet answered. Only little is known about the relationship between disparity detection and visual perception. For instance, one does not know which cortical cells are involved in stereopsis and which in the control of vergence eye movements or in both. Physiological studies did not yet show how retinal and oculomotor signals are combined in binocular vision. With respect to disparity detection it is generally believed that binocular cells are tuned to retinal disparity. However, this belief is more based on constraints in the experimental procedures of physiological studies than on direct evidence. In cat experiments the eye muscles were usually paralysed and in monkey experiments fixation points were used to stabilise the images on the retinae (Howard & Rogers, 1995). Under such conditions the responses of the cells could not provide evidence in favour or against retinal or headcentric representations. In summary, it is not known which

binocular cells are involved in the binocular perception of depth and direction. Nor do we know whether the disparity detectors in the relevant cortical areas are coding for retinal or headcentric disparities. The present results on depth detection and vergence, and the previous findings on the cyclopean illusion question the generally held belief that in binocular vision retinal and oculomotor signals are first pooled within the oculomotor and retinal streams. The results suggest a headcentric organisation of signals involved in binocular perception and a retinal organisation of signals involved in vergence control.

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