Neural Mechanisms of Binocular Disparity and Perceptual Learning Effects

Authors: Wang Getong, Xi Jie, Chen Nihong, Huang Changbing, Xi Jie, Chen Nihong

Date: 2020-08-15T00:00:00+00:00

Abstract

The interpupillary distance results in slight positional differences in the retinal images of a spatial object between the left and right eyes. This difference is known as binocular disparity, which constitutes an important source of information for stereoscopic visual perception. Psychophysical research on binocular disparity originated in the early eighteenth century and has a history spanning nearly two hundred years. In recent years, research on binocular disparity has primarily concentrated on two aspects. The first involves investigating the modular representation of binocular disparity in the dorsal and ventral visual pathways using electrophysiological and brain imaging techniques, with the neural representations reflecting the hierarchical and parallel processing principles of the visual system. The second entails employing perceptual learning paradigms to examine the plasticity of binocular disparity. Future research should integrate brain imaging and neuromodulation techniques to investigate the neural mechanisms underlying binocular disparity and its learning effects, including the information integration and interaction between binocular disparity and various depth cues. In terms of applications, training paradigms can be optimized by incorporating virtual reality and other technologies to achieve the rehabilitation and enhancement of stereoscopic vision.

Full Text

Binocular Disparity: Neural Mechanisms and Perceptual Learning Effects

WANG Getong[1],[2], **XI Jie**[1],[2], **CHEN Nihong**[3],[4], **HUANG Changbing**[1],[2]

[1] CAS Key Laboratory of Behavioral Science, Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, China

[2] Department of Psychology, University of Chinese Academy of Sciences, Beijing 100049, China
[3] Department of Psychology, Tsinghua University
[4] IDG/McGovern Institute for Brain Research at Tsinghua University, Beijing 100084, China

Abstract

Binocular disparity refers to the small positional differences between the images of an object projected onto the retinas of the two eyes, arising from the interocular separation. This disparity serves as a critical information source for stereoscopic vision. Psychophysical studies of binocular disparity began in the early 18th century, spanning nearly two hundred years of research history. Recent investigations have focused on two main aspects. First, electrophysiological and brain imaging techniques have been employed to examine the modular representation of binocular disparity in the dorsal and ventral visual pathways, revealing hierarchical and parallel processing principles within the visual system. Second, perceptual learning paradigms have been applied to study the plasticity of binocular disparity processing. Future research should integrate brain imaging and neuromodulation techniques to investigate the neural mechanisms underlying binocular disparity and its learning effects, including the integration and interaction between binocular disparity and multiple depth cues. In terms of applications, training paradigms can be optimized by combining virtual reality technologies to achieve rehabilitation and enhancement of stereoscopic vision.

Keywords: binocular disparity; stereopsis; neural mechanism; perceptual learning; plasticity

1. Introduction

In 1838, the renowned British physicist Charles Wheatstone invented the stereoscope and first proposed the concept of binocular disparity. Using the stereoscope, two images of the same object with a certain horizontal displacement could be projected separately to each eye. After binocular fusion, these images produced a clear sense of depth, demonstrating that binocular disparity is an effective cue for inducing stereoscopic vision (Wheatstone, 1838). Early researchers proposed that disparity processing involved two stages: monocular and binocular. The brain first needed to identify the two-dimensional shape of an object in monocular pathways, then integrate this information binocularly and extract disparity to obtain three-dimensional shape information. In the mid-20th century, Julesz (1960) used modern computer technology to design random-dot stereograms (RDS, [Figure 1: see original paper]), stimuli composed of random dots without any two-dimensional shape information. Observers could only perceive three-dimensional shapes defined by disparity after integrating binocular information (Julesz, 1960, 1971). The finding that observers could extract three-dimensional shape information from random-dot stereograms proved that depth perception could be formed using binocular disparity alone. Since then, RDS has become the most important stimulus material for stereopsis research. Julesz also proposed the famous "correspondence problem" in binocular vision—how to match corresponding features between left and right eye images to reconstruct three-dimensional representations. When the contrast information of random dots in the two eyes is reversed, the resulting anti-correlated random-dot stereograms (aRDS) disrupt the correspondence between left and right eye images, preventing depth perception from forming ([Figure 1: see original paper]).

Figure 1. Schematic diagrams of cRDS and aRDS. Panel A shows a correlated random-dot stereogram (cRDS), where corresponding positions in the left and right eye images have the same contrast, enabling depth perception after binocular fusion. Panel B shows an anti-correlated random-dot stereogram (aRDS), where corresponding positions have opposite contrast. Although aRDS contains disparity information, the disrupted correspondence prevents depth perception.

2. Types of Binocular Disparity

2.1 Absolute and Relative Disparity

Based on the relationship with the fixation point, binocular disparity can be divided into absolute disparity and relative disparity (Anzai & DeAngelis, 2010; Erkelens & Collewijn, 1985; Orban, 2011; Westheimer, 1979). Absolute disparity refers to the absolute difference between the images of an object in the two eyes, representing the relative distance between object P and fixation point F, with a disparity value of α - β ([Figure 2: see original paper]A). When eye movements occur, absolute disparity changes because the fixation point moves. Relative disparity refers to the difference in absolute disparity between two objects P1 and P2, calculated as β_2 - β_1 ([Figure 2: see original paper]B). Unlike absolute disparity, the magnitude of relative disparity is independent of the fixation point position and remains constant during eye movements. Similar to how object spatial structure representation relies more on relative luminance information (i.e., contrast) rather than absolute luminance, depth representation primarily depends on relative rather than absolute disparity computation. The threshold for relative disparity is substantially lower than that for absolute disparity, approximately one-fifth of the absolute disparity threshold (Brookes & Stevens, 1989; Cumming & Parker, 1999; Erkelens & Collewijn, 1985; Rogers & Graham, 1982; Westheimer, 1979).

Figure 2. Schematic illustration of binocular disparity. Binocular disparity is the horizontal difference between the images of an object P projected onto the left eye (LE) and right eye (RE) retinas. Panel A shows absolute disparity, where F is the fixation point, α is the angle between the visual axes at fixation point F, β is the angle at object P, and absolute disparity d_{abs} is (α - β), which depends on the position of fixation point F. Panel B shows relative disparity, where F is the fixation point, α is the angle at fixation point F, and β_1 and β_2 are the angles at objects P1 and P2 respectively. Relative disparity

d_{rel} is (β_2 - β_1), which is independent of fixation point F position.

2.2 Crossed and Uncrossed Disparity

Based on the relative position between an object and the fixation point in three-dimensional space, binocular disparity can be classified as crossed disparity or uncrossed disparity. As shown in [Figure 2: see original paper]B, when we fixate on point F in space, the fixation point falls on the fovea with zero binocular disparity. For objects nearer than fixation point F (such as P1), the disparity is called crossed disparity (near disparity), with a value of α - β_1. For objects farther than fixation point F (such as P2), the disparity is called uncrossed disparity (far disparity), with a value of α - β_2.

2.3 Zero-, First-, and Second-Order Disparity

According to depth structure, disparity can be categorized as zero-order, first-order, or second-order disparity ([Figure 3: see original paper]). Absolute disparity forms zero-order disparity, representing the distance of a surface relative to the fixation point (depth), providing both qualitative near-far information and quantitative distance information. Relative disparity can form first-order and second-order disparity. First-order disparity has a linear disparity gradient, described by two parameters—tilt (slope) and slant (intercept)—representing three-dimensional orientation. Second-order disparity has a curvature-based gradient, defined by three parameters: orientation, sign (near/far), and degree of curvature. Consequently, zero-order disparity forms three-dimensional planes, first-order disparity forms three-dimensional slanted surfaces, and second-order disparity forms three-dimensional curved surfaces (Anzai & DeAngelis, 2010; Janssen et al., 2000b; Orban, 2011).

Figure 3. Schematic diagrams of RDS stimuli for zero-, first-, and second-order disparity. When viewed with red-green glasses, each red-green image produces the corresponding depth perception shown below. Zero-order disparity represents the near-far relationship between an object and the fixation point. First-order disparity creates three-dimensional slanted surfaces with disparity gradients. Second-order disparity creates three-dimensional shapes with both disparity gradients and curvature. Red dots in the stereograms represent fixation points.

2.4 Fine and Coarse Stereopsis

Based on disparity magnitude, stereopsis can be divided into fine and coarse stereopsis. When disparity is smaller than 20-30 arcminutes, the binocular images fuse into a single image, and the resulting stereopsis is called fine stereopsis, providing high-resolution three-dimensional information (Panum, 1940). When disparity is too large for image fusion, diplopia occurs. People typically do not perceive obvious diplopia because binocular convergence rapidly reduces absolute disparity near the fixation point, keeping disparity within the fusion range. In fact, diplopia can also provide stable depth perception, known as coarse stereopsis (Helmholtz, 1909; Ogle, 1952). Coarse stereopsis provides only near-far information without precise disparity magnitude calculation, generally serving as a backup system for fine stereopsis. Its significance is manifested in three aspects: First, when binocular disparity is too large causing diplopia, or when images cannot fuse due to differences in brightness or contrast, it provides coarse depth information for the visual system. Second, before the fine stereopsis system matures, it provides coarse depth information for infants along with monocular cues. Coarse stereopsis reaches adult levels by approximately age 4, while fine stereopsis processing, limited by immature spatial frequency/contrast processing and response capabilities, remains significantly different from adults until school age (Chino et al., 1997; Ciner et al., 1989; Cooper et al., 1979; Fox et al., 1986; Giaschi et al., 2013; Leat et al., 2001; Maruko et al., 2008; Romano et al., 1975; Simons, 1981; Tomac & Altay, 2000). Third, it provides coarse depth information for individuals with impaired fine stereopsis. Since earlier-developing brain structures and functions are less vulnerable to damage, even patients with abnormal stereopsis or stereoblindness may retain the ability to perceive coarse depth information.

It should be noted that common clinical stereopsis tests such as Rand Dot Stereotest™ (Alexander, 1979) and Frisby (Sasieni, 1978) can only measure fine stereopsis thresholds. Most stimuli used in previous laboratory studies also fall within the fine stereopsis range. However, tests including the fly figure in Titmus (Feinberg & Reuel, 1961), the Butterfly stereotest (Chopin et al., 2019), and the *Stereoscopic Vision Test Chart (3rd Edition)* developed by Yan Shaoming (2016) include coarse stereopsis assessment. Additionally, Lang' s horizontal two-pencil test can be used for coarse stereopsis examination (Nongpiur & Sharma, 2010).

3. Psychophysical Studies of Binocular Disparity

Research on binocular disparity commonly employs psychophysical, electrophysiological, and brain imaging methods, with results from different approaches complementing each other to form a theoretical framework for stereopsis processing mechanisms. Early psychophysical studies of binocular disparity yielded several important hypotheses and conclusions.

As mentioned above, Julesz (1960) used computer-generated RDS and discovered that stereoscopic perception could be induced by binocular disparity alone, proposing the "correspondence problem."Subsequently, Julesz (1971, 1978, 1986) introduced the concepts of local stereopsis and global stereopsis: stereopsis induced by RDS is global stereopsis, requiring the brain to evaluate all possible matches between random dots in the two eyes, eliminate false matches, and retain correct correspondence information; traditional stereopsis with contours, texture, and shading cues is called local stereopsis. Julesz (1978) proposed that stereoscopic vision involves two independent processing mechanisms: fine/global and coarse/local (see also Hou, 1995). Single-cell experiments by Poggio et al. (1985) supported this hypothesis, finding neurons in V1 and V2 that responded separately to local and global stereopsis information.

Another important hypothesis about binocular disparity was proposed by Richards (1970, 1971), who found through stereopsis testing that approximately one-third of observers were insensitive to either near or far disparity, suggesting separate mechanisms for processing far and near disparities. Some studies found that observers required shorter stimulus presentation times to identify near disparity stimuli compared to far disparity stimuli (Finlay et al., 1989; Manning et al., 1987). This hypothesis received support from electrophysiological (Cumming & Parker, 1999; Poggio et al., 1988) and brain imaging studies (Goncalves et al., 2015). However, some researchers argued that this separation might be related to testing methods. When stimulus presentation time was extended, stereo-anomalous patients could identify both near and far disparities in random-dot stereograms, suggesting that stereo anomaly might not result from a missing detection mechanism for certain disparities but rather from differential time courses for processing far and near disparities in the brain (Patterson & Fox, 1984). This hypothesis has not gained widespread acceptance.

Stereopsis formation includes two stages: disparity detection and depth perception (Hou, 1995; Marr, 1982). Therefore, besides binocular disparity, other factors may affect stereopsis perception. For example, Bradshaw and Glennerster (2006) found a negative correlation between observers' stereopsis thresholds and stimulus presentation distance, with higher thresholds for near stimuli. However, many studies have shown that stereopsis thresholds are unaffected by presentation distance (Jameson & Hurvich, 1959; Ogle, 1958; Wong et al., 2002), making this conclusion controversial. This controversy may arise from differences in stimulus presentation distance and stimulus type across studies.

In summary, early psychophysical studies provided reasonable model hypotheses for binocular disparity processing mechanisms. However, different studies often reached different or even opposite conclusions due to variations in experimental conditions. To validate these models, conclusions must be tested and refined through replication experiments, and corroborated by electrophysiological and brain imaging results to establish a complete theoretical framework.

4. Neural Mechanisms of Binocular Disparity

4.1 Early Visual Cortex

Research on the neural mechanisms of binocular disparity began with single-cell recording experiments in cats by Barlow et al. (1967) and Nikara et al. (1968), who found disparity-sensitive neurons in the primary visual cortex (area 17). Subsequently, researchers discovered neurons encoding binocular disparity information in the macaque primary visual cortex (V1) (Poggio & Fischer, 1977; Poggio et al., 1988). Damage to V1 significantly impairs stereoscopic acuity in monkeys (Cowey & Wilkinson, 1991; Nienborg & Cumming, 2006), indicating V1' s important role in disparity processing.

V1 is the first site for binocular information fusion. Hubel and Wiesel (1962) classified V1 neurons into simple cells and complex cells. The classic disparity energy model proposed by Ohzawa et al. (1990) suggests that some complex cells in V1 can detect binocular disparity by integrating inputs from simple cells. This model can explain disparity selectivity in V1 of cats (Ohzawa et al., 1997), monkeys (Cumming & Parker, 1997), and mice (Scholl et al., 2013), and can also account for some human psychophysical data (Neri et al., 1999; Tanabe et al., 2008). Subsequently, Haefner and Cumming (2008) proposed a generalized disparity energy model that effectively explains responses to anti-correlated random-dot stereograms and neuronal adaptation in primary visual cortex.

V1 primarily encodes absolute disparity rather than relative disparity (Cumming & Parker, 1999). Cumming and Parker (1997) compared activation patterns of V1 neurons in monkeys viewing RDS and aRDS, finding similar activation patterns for both stimuli. Since the visual system must solve the "correspondence problem" to form depth perception, and contrast-reversed aRDS stimuli cannot induce depth perception, the dissociation between V1 neural activity and depth perception suggests that the "correspondence problem" is not resolved in V1 (Tanabe et al., 2008).

Disparity information is further processed in the secondary visual cortex V2. V2 responds to both absolute and relative disparity, particularly at boundaries with depth differences (relative disparity), with responses related to receptive field location and showing orientation selectivity (Bredfeldt & Cumming, 2006; Von Der Heydt et al., 2000). Like V1, V2 damage significantly impairs stereoscopic acuity (Cowey & Wilkinson, 1991), and V2 neuronal activation correlates significantly with depth discrimination task performance (Nienborg & Cumming, 2006). Neurons selective for near or far disparity form functional columns in V2 (Chen et al., 2008), but V2 still fails to solve the "correspondence problem" (Allouni et al., 2005). Overall, V1 and V2 provide preliminary representation of disparity information, with final depth perception requiring further processing in higher visual pathway areas.

4.2 Ventral Pathway

Visual information is processed along two separate pathways in the cerebral cortex. The ventral pathway, also known as the "what" pathway, runs from V1 through V2 to V4 and the inferior temporal cortex (IT), primarily responsible for object recognition and sensitive to object shape and color (DiCarlo et al., 2013; Goodale & Milner, 1992).

V4 is an intermediate area in the ventral pathway that receives input from early visual areas such as V1 and V2. Studies show that neurons selective for near or far disparity form functional columns in V4 (Watanabe et al., 2002). V4 neurons show stronger selectivity for relative disparity than early visual cortex. Umeda et al. (2007) used RDS composed of a central disk and surrounding annulus as stimuli and found that when the annulus disparity changed, the tuning curves of V4 neurons for the central disk shifted, with greater shift magnitude than in V2 neurons. Brain lesion studies show that extrastriate cortex including V4 impairs monkeys' relative disparity judgment (Cowey & Porter, 1979). Notably, the "correspondence problem" begins to be resolved in V4: most V4 neurons respond more weakly to aRDS than to correlated RDS (cRDS) (Tanabe et al., 2004). V4 shows specific responses not only to zero-order disparity but also to first- and second-order disparity. Electrophysiological studies demonstrate that macaque V4 neurons respond specifically to the slant direction of planes in three-dimensional space (first-order disparity), and this response remains stable when absolute disparity and stimulus location change (Hinkle & Connor, 2002). V4 neurons also show selective responses to convex or concave curved surfaces (second-order disparity), though these responses are modulated by absolute disparity (Hegdé & Van Essen, 2005). These results indicate that V4 begins to represent first- and second-order disparity but has not yet achieved invariant representation of three-dimensional objects.

Furthermore, binocular disparity information is transmitted to the temporal lobe for complex object recognition. TEO (temporal-occipital area) and TE (the superior temporal sulcus) are located in the posterior inferior temporal lobe and are high-level areas in the ventral pathway responsible for object processing (Janssen et al., 1999, 2000a). Studies show that TE neuronal activity correlates highly with monkeys' relative disparity discrimination behavior (Uka et al., 2005); TEO lesions impair performance on second-order disparity stereopsis tasks (Cowey & Porter, 1979) and significantly reduce stereoscopic acuity (Cowey & Wilkinson, 1991). TE neurons respond only to cRDS and not to aRDS (Janssen et al., 2003), indicating that the "correspondence problem" is fully resolved in TE.

TE neurons show selective responses to three-dimensional curved surfaces and maintain selectivity for relative disparity when absolute disparity changes (Janssen et al., 1999; Uka et al., 2000). TE neurons can finely represent object depth differences and are highly sensitive to local surface convexity and concavity (Janssen et al., 2000b; Yamane et al., 2008), which form the basis of complex three-dimensional shapes in the real world. In addition to binocular disparity, TE can integrate shape, texture, shading, and other monocular depth cues to represent three-dimensional shape (Liu et al., 2004; Sereno et al., 2002; Tanaka et al., 2001; Yamane et al., 2008). These findings demonstrate that binocular disparity and other visual information are integrated in high-level ventral pathway areas, ultimately achieving three-dimensional object recognition.

4.3 Dorsal Pathway

The other visual pathway is the dorsal pathway, also known as the "where" pathway. It runs from V1 through V2 to V3A, V5/MT (middle temporal area), V7, MST (middle superior temporal area), and ultimately projects to the intraparietal sulcus (IPS). Binocular disparity is also represented and processed in these areas, enabling functions such as distance estimation, object tracking, object manipulation, limb movement, and eye movement control in three-dimensional space (Verhoef et al., 2016).

V3A is an early area in the dorsal pathway that further processes absolute disparity information. Anzai et al. (2011) used center-surround RDS as stimuli, recording tuning curves of V3A neurons for absolute and relative disparity by changing the disparity of the central disk and surrounding annulus. They found that V3A disparity sensitivity did not differ significantly from other primary and intermediate visual areas, with V3A primarily encoding absolute disparity.

The MT/V5 area receives input from multiple upstream areas (V1, V2, V3, V3A), with major input from V1 (Born & Bradley, 2005). Uka and DeAngelis (2006) applied microstimulation to monkey MT neurons and found that it affected performance only on absolute disparity depth discrimination tasks, not relative disparity tasks, indicating that MT primarily encodes absolute rather than relative disparity. In MT, neurons with consistent disparity selectivity preferences are clustered in functional columns (DeAngelis & Newsome, 1999). Some studies also found that MT neurons can encode the slant direction of planes in three-dimensional space (first-order disparity) independently of the mean depth (absolute disparity) of the stimulus (Nguyenkim & DeAngelis, 2003), suggesting some selectivity for relative disparity in MT. However, MT neurons respond to both aRDS and cRDS stimuli, indicating that MT does not solve the "correspondence problem" (Dodd et al., 2001).

MST receives input from MT. Over 90% of neurons in MST are sensitive to binocular disparity, and among these disparity-sensitive neurons, 95% are near-disparity or far-disparity neurons. Since the disparity range used in this study (1-3°) exceeded the fine stereopsis range, this area appears more suited for processing coarse rather than fine stereopsis (Roy et al., 1992). Additionally, MST neuronal activity correlates with eye movements, and MST neurons still respond to both cRDS and aRDS, indicating that the "correspondence problem" remains unsolved in MST (Takemura et al., 2001).

IPS is a high-level area in the dorsal pathway, selective for three-dimensional shape, two-dimensional shape, and spatial location. IPS can be divided into several major subregions: MIP (medial intraparietal area) is related to reaching movements (Andersen & Buneo, 2002; Snyder et al., 1997); AIP (anterior intraparietal area) (Gallese et al., 1994; Sakata et al., 1995; Taira et al., 1990) and CIP (caudal intraparietal area) (Grefkes & Fink, 2005; Sakata, 2003) are responsible for grasping movements; and LIP (lateral intraparietal area) is related to eye movements (Grefkes & Fink, 2005). In the three-dimensional world, these subregion functions require binocular disparity computation. Current research on the relationship between IPS subregions and binocular disparity is limited. Studies have found that CIP neurons show selective responses to the slant direction of three-dimensional surfaces defined by disparity (Tsutsui et al., 2001) and to three-dimensional curved surfaces (Katsuyama et al., 2010). AIP shows selective responses to first- and second-order disparity that are unaffected by absolute disparity, with most neurons responding selectively to three-dimensional curved surfaces within 70 ms after visual stimulus onset, while TE requires 130 ms. This suggests that the dorsal pathway has characteristics of rapidity, metric coding, and coarseness in disparity representation compared to the ventral pathway (Srivastava et al., 2009).

5. Brain Imaging Studies of Binocular Disparity

Electrophysiological studies can finely describe neuronal-level activity but cannot examine activity across multiple brain areas at a global scale. In contrast, fMRI (functional magnetic resonance imaging) is more suitable for studying functional area-level response patterns. Tsao et al. (2003) used fMRI to compare neural representations of binocular disparity in humans and monkeys, finding that checkerboard stimuli defined by disparity information activated monkey V3, V3A, and CIPS (caudal intraparietal sulcus) areas, and human V3A, V7, V4d-topo, and some posterior parietal regions. V3A showed significant activation in both species. Some studies suggest that V3A activation is closely related to disparity representation (Backus et al., 2001), with cortical response strength modulated by disparity magnitude: when absolute disparity is 0-15 arcmin, cortical activation increases with disparity; when absolute disparity exceeds 30 arcmin, activation decreases with increasing disparity. These changes correlate with disparity perception thresholds, with the trend becoming progressively stronger from V1 to extrastriate cortex, most significantly in V3A.

Primate electrophysiological studies found that lower and intermediate areas in the dorsal pathway are more sensitive to absolute disparity, a phenomenon confirmed by human fMRI studies. Neri et al. (2004) used fMRI adaptation to examine brain areas processing absolute and relative disparity, finding that lower and intermediate dorsal pathway areas (V3A, V7, and MT+) showed adaptation only to absolute disparity, indicating greater reliance on absolute disparity information. The high-level dorsal pathway area IPS can encode relative disparity (Katsuyama et al., 2010; Murata et al., 2000; Tsutsui et al., 2001).

Some fMRI studies found that V3A also shows selective responses to relative disparity (Cottereau et al., 2011; Georgieva et al., 2009; Tsao et al., 2003). One possible reason is that V3A selectively responds to figure-ground segmentation information. Studies show substantial overlap in V3A activation regions for figures defined by illusory contours and figures defined by disparity (Mendola et al., 1999). Relative disparity creates depth planes that induce perception of figure boundaries, similar to figure boundaries defined by monocular contour information, thus activating V3A (Anzai et al., 2011).

Different areas in the dorsal pathway show selective representations for planes (zero-order disparity), slanted surfaces (first-order disparity), curved surfaces (second-order disparity), and three-dimensional structures (containing both first- and second-order disparity information). Georgieva et al. (2009) used three-dimensional objects with second-order curvature and found that second-order disparity caused widespread activation in visual areas, including occipital regions V3A, V3B, and V3, various IPS subregions, and ITG (inferior temporal gyrus). Durand et al. (2007, 2009) compared activation in human and monkey parietal areas to three-dimensional objects. They found that monkey CIP, MIP, and PIP areas, corresponding to human VIPS (ventral IPS region), were activated by both three-dimensional structure and three-dimensional plane stimuli. Areas sensitive only to three-dimensional structure stimuli were monkey AIP and parts of LIP, corresponding to human DIPSA (dorsal IPS anterior region) and DIPSM (dorsal IPS medial region).

Relatively speaking, the dorsal pathway is more sensitive to absolute disparity to guide movement, while the ventral pathway is more sensitive to relative disparity to guide object recognition (Verhoef et al., 2016). Chang et al. (2014) used rTMS (repetitive transcranial magnetic stimulation) and found that suppressing LOC (lateral occipital cortex) in the ventral pathway during stereopsis processing significantly decreased fine discrimination task performance, proving that LOC is responsible for fine discrimination of relative disparity. However, some brain imaging studies found that hV4 and V8 in the ventral pathway showed strong adaptation to both absolute and relative disparity, indicating that the ventral pathway can process both types of disparity simultaneously (Neri et al., 2004).

High-field MRI technology enables investigation of binocular disparity neural mechanisms with higher spatial resolution and signal-to-noise ratio. A 7T fMRI study of absolute disparity revealed that human dorsal visual cortex has specialized organizational structures for disparity processing (Goncalves et al., 2015). Specifically, neurons with similar disparity preferences are clustered in functional columns, and there is a positive correlation between the width of single-voxel tuning curves and their preferred disparity magnitude. Another 7T fMRI study systematically explained the coding patterns of color and binocular disparity in human visual cortex (Tootell & Nasr, 2017): V2 and V3 contain spatially segregated color and disparity functional columns; V3A at the start of the dorsal pathway lacks color functional columns and primarily processes disparity information; V4 in the ventral pathway contains segregated color and disparity preference functional columns; compared to V2, color- or disparity-selective neurons form larger clusters in V4.

The above electrophysiological and brain imaging results demonstrate both universal and specialized aspects of binocular disparity processing mechanisms. The universal aspect is that activation in specific areas has a functional relationship with the physical properties of stimuli, with disparity information processed hierarchically from lower to higher cortical areas. The specialized aspect is that there is no single pathway "responsible" for stereopsis processing; compared to other visual features, disparity activation is widely distributed across cortical areas from primary visual cortex to various levels of ventral and dorsal pathways, ultimately achieving the two major goals of object recognition and movement guidance. [Figure 4: see original paper] integrates electrophysiological and brain imaging findings to illustrate disparity processing in human and monkey cerebral cortex.

Figure 4. Neural representation of binocular disparity. Arrows indicate information flow direction. White-background areas primarily process absolute disparity; orange-background areas primarily process relative disparity. Green boxes indicate activated human cortical areas; blue boxes indicate activated monkey cortical areas; red boxes indicate areas activated in both species. MT+: middle temporal complex; VIPS: ventral IPS area; CIP: caudal intraparietal area; DIPSM: dorsal IPS medial area; LIP: lateral intraparietal area; DIPSA: dorsal IPS anterior area; AIP: anterior intraparietal area; PIP: posterior intraparietal area; MIP: medial intraparietal area; TE: superior temporal sulcus; TEO: temporal-occipital area.

6. Perceptual Learning of Binocular Disparity

6.1 Basic Research on Perceptual Learning

Perceptual learning refers to the phenomenon where perceptual abilities improve through training (Lu et al., 2011). This improvement is thought to reflect changes in the activity of neuronal populations encoding specific visual features (Tsodyks & Gilbert, 2004). Due to the widespread distribution and hierarchical processing characteristics of disparity processing in visual cortex, different types of stimuli and tasks may be accompanied by changes in corresponding cortical sites, providing a powerful tool for understanding the neural mechanisms of binocular disparity. Julesz (1971) first discovered that repeated viewing of random-dot stereograms significantly reduced the time required to perceive depth, a finding supported by subsequent studies (Frisby & Clatworthy, 1975; Ramachandran, 1976; Ramachandran & Braddick, 1973). In addition to reducing reaction time, perceptual learning can also lower stereopsis thresholds based on binocular disparity. Untrained observers have relative disparity discrimination thresholds around 30 arcseconds, which can be reduced to approximately 4-8 arcseconds after training (Fendick & Westheimer, 1983; Gantz et al., 2007; Schmitt et al., 2002; Wilcox & Allison, 2009).

Some studies have inferred the neural sites of disparity processing through the specificity of perceptual learning. Several studies found that disparity perceptual learning exhibits retinal location specificity (Ramachandran, 1976; O' Toole & Kersten, 1992), orientation specificity (Ramachandran & Braddick, 1973), and spatial frequency specificity (Long, 1982), with learning effects failing to transfer to untrained locations or stimulus features. This specificity led researchers to propose that disparity perceptual learning may occur in primary visual cortex. However, Sowden et al. (1996) asked observers to judge the relative depth of two square planes with zero-order disparity and found that disparity perceptual learning showed transfer across retinal locations, suggesting that previously found specificity might result from spatial selective attention mechanisms.

Why do different perceptual learning experiments produce inconsistent transfer effects? As discussed earlier, different types of disparity are encoded at different levels of visual processing, and the encoding characteristics of neurons in these brain areas likely explain differences in behavioral transfer. For example, some studies used zero-order disparity planes (Long, 1982; Ramachandran & Braddick, 1973) or judged the shape of zero-order disparity planes (O' Toole & Kersten, 1992; Ramachandran, 1976). Such stimuli involve absolute disparity processing, whose representation is located in early visual pathways, with primary visual cortex showing selective responses to absolute disparity stimuli (Cumming & Parker, 1999). Therefore, the response properties of primary visual cortex neurons to external stimuli may affect absolute disparity processing, making absolute disparity perceptual learning specific. In contrast, Sowden et al. (1996) used a relative disparity task requiring judgments of relative depth positions of two zero-order disparity planes. Relative disparity processing occurs later than absolute disparity, with early visual cortex showing almost no selective activation for relative disparity (Cumming & Parker, 1999). Its processing mainly occurs in intermediate and high-level visual pathway areas, particularly second-order disparity computation, which is completed only at the ends of ventral and dorsal pathways. These high-level areas have larger receptive fields and are less sensitive to stimulus location, making relative disparity learning potentially transferable. Therefore, different conclusions about transferability in early studies likely stem from different categories of disparity processing. Future research should compare learning effects induced by various stimuli and tasks to comprehensively understand the neural mechanisms and cortical plasticity of stereopsis.

6.2 Applications of Disparity Perceptual Learning

The recovery and improvement of stereopsis have important significance. On one hand, depending on diagnostic criteria, the prevalence of stereo anomaly or stereoblindness in the normal population ranges from 3% to 40% (Bohr & Read, 2013; Hess et al., 2015; Richards, 1970, 1971; Wright & Kelly, 1992). Additionally, any adverse factors during visual development, such as strabismus, anisometropia, refractive error, optic nerve damage, cataract, and glaucoma, can cause stereopsis dysfunction or stereoblindness (Hess et al., 2010; Levi et al., 1980; McKee et al., 2003). These patients face numerous inconveniences in daily life and have urgent needs for stereopsis recovery training. On the other hand, many modern professions such as pilots, surgeons, and drivers require good stereopsis function, and increasingly common entertainment forms including VR, AR, 3D television, movies, and video games also demand high stereopsis capabilities, directly affecting people' s work and daily life.

Currently, disparity perceptual learning has achieved some success in restoring impaired stereopsis function and meeting special occupational requirements (Astle et al., 2011; Ding & Levi, 2011; Schoemann et al., 2017; Xi et al., 2014). Research on stereopsis recovery has mainly focused on amblyopic patients. For example, Astle et al. (2011) found that stereopsis perceptual learning could restore adult amblyopic patients' stereoscopic acuity to normal levels, with effects lasting over seven months. Ding and Levi (2011) used sine-wave grating stimuli for stereopsis training in amblyopic patients and found that perceptual learning significantly improved stereopsis function. Xi et al. (2014) used texture images processed with red-green complementary colors as stimuli ([Figure 5: see original paper]A) and found that training normal and amblyopic observers to perform depth detection tasks defined by binocular disparity significantly reduced stereopsis thresholds ([Figure 5: see original paper]B), improved stereoscopic acuity and visual acuity, with improvements maintained for at least five months. Hess et al. (2010) presented dynamic random-dot kinematograms (RDK) separately to the signal and noise portions of amblyopic patients' left and right eyes, training them on motion direction coherence discrimination tasks near threshold, which significantly improved binocular fusion function and consequently stereoscopic acuity. The researchers further transformed this training method into a Tetris game, achieving equally significant perceptual learning effects on iPod as in laboratory training (Hess et al., 2012). Some researchers have also converted random-dot stereogram-based stereopsis training programs into computer game formats for patients who had received traditional treatment, finding that the game effectively improved patients' stereoscopic acuity (Portela-Camino et al., 2018).

Figure 5. Stereopsis training (Xi et al., 2014). Panel A shows training stimuli: the first row displays three texture types, and the second row shows left-eye, right-eye, and fused images using one texture pattern as an example; observers wore red-green glasses during the experiment. Panel B shows individual and average learning curves for 11 amblyopic observers, with training sessions on the horizontal axis and stereopsis thresholds on the vertical axis. The study found that 9 out of 11 amblyopic observers showed significantly reduced stereopsis thresholds after training.

Besides restoring stereopsis function in patients with stereo anomaly or stereoblindness, perceptual learning can also enhance stereopsis function in special occupational personnel. Soccer players showed significantly reduced reaction times after six weeks of dynamic stereopsis training, with effects lasting over six months (Schoemann et al., 2017).

7. Future Directions and Issues

Stereopsis is crucial for organisms living in a three-dimensional world. Although current research has provided relatively clear explanations of the neural mechanisms and perceptual learning effects of stereopsis, many questions remain unresolved. In basic research, although some studies have inferred neural sites of learning based on characteristics of disparity perceptual learning (Ramachandran, 1976; O' Toole & Kersten, 1992; Ramachandran & Braddick, 1973; Long, 1982; Sowden et al., 1996), no brain imaging experiments have directly examined the neural mechanisms of disparity learning. Future research should further explore the perceptual learning characteristics of different types of binocular disparity and combine multiple techniques such as brain imaging (fMRI) and neuromodulation (tDCS, TMS) to investigate the neural mechanisms of stereopsis perceptual learning. Additionally, although binocular disparity is considered one of the most important depth cues, we rarely rely on disparity information alone in daily life, instead integrating multiple cues for depth judgment. Understanding how different depth cues influence disparity processing and investigating the neural mechanisms of information integration and interaction among multiple depth cues are important for understanding disparity and depth perception. fMRI studies show that the V3B/KO area plays an important role in the fusion of disparity and motion depth cues (Ban et al., 2012) and in the fusion of disparity and shading cues (DöVencioglu et al., 2013). However, besides these cues, perspective, accommodation, and convergence are also important depth cues, and their interaction mechanisms with disparity remain unclear and require further investigation.

In practical applications, with the advent of the multimedia interaction era, stereopsis research has broad application prospects. Future research can combine new VR technology developments with more interesting interactive forms to investigate optimal training paradigms, tasks, stimuli, intensities, and intensity distributions to achieve effective rehabilitation of stereopsis in special populations and enhancement in normal populations. However, caution should be exercised in promoting VR-based stereopsis training before clarifying its effects on visual function. On one hand, unlike daily visual experiences, VR technology primarily relies on binocular disparity for depth perception while lacking other depth cues, and prolonged use may negatively affect visual function. Some studies have found that prolonged viewing of stereoscopic motion images induces visual fatigue due to conflict between accommodation and convergence cues (Ukai & Howarth, 2008). This occurs because when viewing stereoscopic images, accommodation is fixed at the screen distance while the angle between the two eyes changes rapidly with disparity, causing dissociation between accommodation and convergence and resulting in visual fatigue. On the other hand, the causes of stereopsis deficits are diverse, including strabismus, anisometropia, refractive error, optic nerve damage, cataract, and glaucoma (Hess et al., 2010; Levi et al., 1980; McKee et al., 2003), but the underlying mechanisms of different types of stereopsis anomalies remain unclear. Additionally, visual motion information when viewing stereoscopic images conflicts with vestibular information, causing visually induced motion sickness (VIMS) with symptoms such as dizziness (Howarth, 2008). Solimini (2013) showed that watching 3D movies can cause nausea and disorientation, particularly in women with sensitive visual-vestibular systems. Therefore, individual differences among users should be considered when using VR technologies.

Finally, some studies show that certain genes are associated with specific stereopsis abilities and development (Bosten et al., 2015; Mazziotti et al., 2017). However, the exact evolutionary advantages, molecular basis, and physiological significance of stereopsis have not been fully elucidated. Research using genomewide association studies (GWAS) and gene targeting technologies, based on behavioral and brain imaging measurements, is urgently needed to understand the functional mechanisms and physiological significance of stereopsis from gene-brain-behavior perspectives.

References

Hou, C. (1995). The mechanism and detection of stereoscopic vision. *Chinese Journal of Strabismus & Pediatric Ophthalmology*, 3, 141-144.

Yan, S. M. (2006). *Stereoscopic vision test chart* (3rd ed.). Beijing: People' s Medical Publishing House.

Alexander, J. A. (1979). A new clinical test of stereopsis: Theoretical evaluation. *The Australian Journal of Optometry*, 62(5), 191-193.

Allouni, A. K., Thomas, O., Solomon, S. G., Krug, K., & Parker, A. (2005). Local and global binocular matching in V2 of the awake macaque (abstract). *Society for Neuroscience Abstracts*, 510.8.

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, 25(1), 189-220.

Anzai, A., Chowdhury, S. A., & DeAngelis, G. C. (2011). Coding of stereoscopic depth information in visual areas V3 and V3A. *The Journal of Neuroscience*, 31(28), 10270-10282.

Anzai, A., & DeAngelis, G. C. (2010). Neural computations underlying depth perception. *Current Opinion in Neurobiology*, 20(3), 367-375.

Astle, A. T., McGraw, P. V., & Webb, B. S. (2011). Recovery of stereo acuity in adults with amblyopia. *BMJ Case Reports*, 7-10.

Backus, B. T., Fleet, D. J., Parker, A. J., & Heeger, D. J. (2001). Human cortical activity correlates with stereoscopic depth perception. *Journal of Neurophysiology*, 86(4), 2054-2068.

Ban, H., Preston, T. J., Meeson, A., & Welchman, A. E. (2012). The integration of motion and disparity cues to depth in dorsal visual cortex. *Nature Neuroscience*, 15(4), 636-643.

Barlow, H. B., Blakemore, C., & Pettigrewt, J. D. (1967). The neural mechanism of binocular depth discrimination. *The Journal of Physiology*, 193(2), 327-342.

Bohr, I., & Read, J. C. (2013). Stereoacuity with Frisby and revised FD2 stereo tests. *PLoS One*, 8(12), e82999.

Born, R. T., & Bradley, D. C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience*, 28(1), 157-189.

Bosten, J. M., Goodbourn, P. T., Lawrance-Owen, A. J., Bargary, G., Hogg, R. E., & Mollon, J. D. (2015). A population study of binocular function. *Vision Research*, 110, 34-50.

Bradshaw, M. F. & Glennerster, A. (2006). Stereoscopic acuity and observation distance. *Spatial Vision*, 19, 21-36.

Bredfeldt, C. E., & Cumming, B. G. (2006). A simple account of cyclopean edge responses in macaque V2. *The Journal of Neuroscience*, 26(29), 7581-7596.

Brookes, A., & Stevens, K. A. (1989). The analogy between stereo depth and brightness. *Perception*, 18(5), 601-614.

Chang, D. F., Mevorach, C., Kourtzi, Z., & Welchman, A. (2014). Training transfers the limits on perception from parietal to ventral cortex. *Current Biology*, 24(20), 2445-2450.

Chen, G., Lu, H. D., & Roe, A. W. (2008). A map for horizontal disparity in monkey V2. *Neuron*, 58(3), 442-450.

Chino, Y. M., Smith, E. L., Hatta, S., & Cheng, H. (1997). Postnatal development of binocular disparity sensitivity in neurons of the primate visual cortex. *The Journal of Neuroscience*, 17(1), 296-307.

Chopin, A., Bavelier, D., & Levi, D. M. (2019). The prevalence and diagnosis of 'stereoblindness' in adults less than 60 years of age: A best evidence synthesis. *Ophthalmic and Physiological Optics*, 39(2), 66-85.

Ciner, E. B., Scheiman, M. M., Schanel-Klitsch, E., & Weil, L. (1989). Stereopsis testing in 18- to 35-month old children using operant preferential looking. *Optometry & Vision Science*, 66(11), 782-787.

Cooper, J., Feldman, J., & Medlin, D. (1979). Comparing stereoscopic performance of children using the Titmus, TNO, and randot stereo tests. *Journal of the American Optometric Association*, 50(7), 821-825.

Cottereau, B. R., McKee, S. P., Ales, J. M., & Norcia, A. M. (2011). Disparity-tuned population responses from human visual cortex. *The Journal of Neuroscience*, 31(3), 954-965.

Cowey, A., & Porter, J. (1979). Brain damage and global stereopsis. *Proceedings of the Royal Society B: Biological Sciences*, 204(1157), 399-407.

Cowey, A., & Wilkinson, F. (1991). The role of the corpus callosum and extra striate visual areas in stereoacuity in macaque monkeys. *Neuropsychologia*, 29(6), 465-479.

Cumming, B. G., & Parker, A. J. (1997). Responses of primary visual cortical neurons to binocular disparity without depth perception. *Nature*, 389(6648), 280-283.

Cumming, B. G., & Parker, A. J. (1999). Binocular neurons in V1 of awake monkeys are selective for absolute, not relative, disparity. *The Journal of Neuroscience*, 19(13), 5602-5618.

DeAngelis, G. C., & Newsome, W. T. (1999). Organization of disparity-selective neurons in macaque area MT. *The Journal of Neuroscience*, 19(4), 1398-1415.

DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2013). How does the brain solve visual object recognition?. *Neuron*, 73(3), 415-434.

Ding, J., & Levi, D. M. (2011). Recovery of stereopsis through perceptual learning in human adults with abnormal binocular vision. *Proceedings of the National Academy of Sciences of the United States of America*, 108(37), E733-E741.

DoVencioglu, D., Ban, H., Schofield, A. J., & Welchman, A. E. (2013). Perceptual integration for qualitatively different 3D cues in the human brain. *Journal of Cognitive Neuroscience*, 25(9), 1527-1541.

Dodd, J. V., Krug, K., Cumming, B. G., & Parker, A. J. (2001). Perceptually bistable three-dimensional figures evoke high choice probabilities in cortical area MT. *The Journal of Neuroscience*, 21(13), 4809.

Durand, J. B., Nelissen, K., Joly, O., Wardak, C., Todd, J. T., Norman, J. F., . . . Orban, G. A. (2007). Anterior regions of monkey parietal cortex process visual 3D shape. *Neuron*, 55(3), 493-505.

Durand, J. B., Peeters, R., Norman, J. F., Todd, J. T., & Orban, G. A. (2009). Parietal regions processing visual 3D shape extracted from disparity. *NeuroImage*, 46(4), 1114-1126.

Erkelens, C. J., & Collewijn, H. (1985). Motion perception during dichoptic viewing of moving random-dot stereograms. *Vision Research*, 25(4), 583-588.

Feinberg, R. & Reuel, S. (1961). Device for testing visual acuity. US3011394A.

Fendick, M., & Westheimer, G. (1983). Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. *Vision Research*, 23(2), 145-150.

Finlay, D. C., Manning, M. L., Dunlop, D. P., & Dewis, S. A. M. (1989). Difficulties in the definition of 'stereoscotoma' using temporal detection of thresholds of dynamic random dot stereograms. *Documenta Ophthalmologica*, 72, 161-173.

Fox, R., Patterson, R., & Francis, E. (1986). Stereoacuity in young children. *Investigative Ophthalmology & Visual Science*, 27(4), 598-600.

Frisby, J. P., & Clatworthy, J. L. (1975). Learning to see complex random dot stereograms. *Perception*, 4, 173-178.

Gallese, V., Murata, A., Kaseda, M., Niki, N., & Sakata, H. (1994). Deficit of hand preshaping after muscimol injection in monkey parietal cortex. *Cognitive Neuroscience and Neuropsychology*, 5(12), 1525-1529.

Gantz, L., Patel, S. S., Chung, S. T. L., & Harwerth, R. S. (2007). Mechanisms of perceptual learning of depth discrimination in random dot stereograms. *Vision Research*, 47(16), 2170-2178.

Georgieva, S., Peeters, R., Kolster, H., Todd, J. T., & Orban, G. A. (2009). The processing of three-dimensional shape from disparity in the human brain. *The Journal of Neuroscience*, 29(3), 727-742.

Giaschi, D., Narasimhan, S., Solski, A., Harrison, E., & Wilcox, L. M. (2013). On the typical development of stereopsis: fine and coarse processing. *Vision Research*, 89, 65-71.

Grefkes, C., & Fink, G. R. (2010). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy*, 207, 3-17.

Goncalves, N. R., Ban, H., Sánchez-Panchuelo, R. M., Francis, S. T., Schluppeck, D., & Welchman, A. E. (2015). 7 Tesla fMRI reveals systematic functional organization for binocular disparity in dorsal visual cortex. *The Journal of Neuroscience*, 35(7), 3056-3072.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, 15(1), 20-25.

Haefner, R. M., & Cumming, B. G. (2008). Adaptation to natural binocular disparities in primate V1 explained by a generalized energy model. *Neuron*, 57(1), 147-158.

Hegdé, J., & Van Essen, D. C. (2005). Role of primate visual area V4 in the processing of 3D shape characteristics defined by disparity. *Journal of Neurophysiology*, 94(4), 2856-2866.

Helmholtz, H. V. (1909). *Handbuch der Physiologischen Optik*. New York: Dover.

Hess, R. F., Mansouri, B., & Thompson, B. (2010). A new binocular approach to the treatment of amblyopia in adults well beyond the critical period of visual development. *Restorative Neurology and Neuroscience*, 28(6), 793-802.

Hess, R. F., Thompson, B., Black, J. M., Machara, G., Zhang, P., Bobier, W. R., & Cooperstock, J. (2012). An iPod treatment of amblyopia: An updated binocular approach. *Optometry (St. Louis, Mo.)*, 83(2), 87-94.

Hess, R. F., To, L., Zhou, J., Wang, G., & Cooperstock, J. R. (2015). Stereo vision: The haves and have-nots. *i-Perception*, 6(3), 2041669515593028.

Hinkle, D. A., & Connor, C. E. (2002). Three-dimensional orientation tuning in macaque area V4. *Nature Neuroscience*, 5(7), 665-670.

Howarth, P. A. (2008). The adverse health and safety effects of viewing visual images. *Displays*, 29(2), 45-46.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat' s visual cortex. *Journal of Physiology*, 160(1), 106-154.

Jameson, D., & Hurvich, L. M. (1959). Note on factors influencing the relation between stereoscopic acuity and observation distance. *Journal of the Optical Society of America*, 49, 639.

Janssen, P., Vogels, R., Liu, Y., & Orban, G. A. (2003). At least at the level of inferior temporal cortex, the stereo correspondence problem is solved. *Neuron*, 37(4), 693-701.

Janssen, P., Vogels, R., & Orban, G. A. (1999). Macaque inferior temporal neurons are selective for disparity-defined three-dimensional shapes. *Proceedings of the National Academy of Sciences of the United States of America*, 96(14), 8217-8222.

Janssen, P., Vogels, R., & Orban, G. A. (2000a). Selectivity for 3D shape that reveals distinct areas within macaque inferior temporal cortex. *Science*, 288(5473), 2054.

Janssen, P., Vogels, R., & Orban, G. A. (2000b). Three-dimensional shape coding in inferior temporal cortex. *Neuron*, 27(2), 385-397.

Julesz, B. (1960). Binocular depth perception of computer-generated patterns. *Bell System Technical Journal*, 39(5), 1125-1162.

Julesz, B. (1971). *Foundations of cyclopean perception*. Boston: MIT Press.

Julesz, B. (1978). Global stereopsis: Cooperative phenomena in stereoscopic depth perception. In R. Held, H.W. Leibowitz, & H.L. Teuber (Eds) *Perception: Vol. 8: Handbook of Sensory Physiology* (pp. 215) Springer, Berlin, Heidelberg.

Julesz, B. (1986). Stereoscopic vision. *Vision Research*, 26, 1061-2012.

Katsuyama, N., Yamashita, A., Sawada, K., Naganuma, T., Sakata, H., & Taira, M. (2010). Functional and histological properties of caudal intraparietal area of macaque monkey. *Neuroscience*, 167(1), 1-10.

Leat, S. J., St Pierre, J., Hasan-Abadi, S., & Faubert, J. (2001). The moving dynamic random dot stereosize test: Development, age norms, and comparison with the frisby, randot and stereo smile tests. *Journal of Pediatric Ophthalmology & Strabismus*, 38(5), 284-294.

Levi, D. M., Harwerth, R. S., & Smith, E. L. (1980). Binocular interactions in normal and anomalous binocular vision. *Documenta Ophthalmologica*, 49(2), 303-324.

Liu, Y., Vogels, R., & Orban, G. A. (2004). Convergence of depth from texture and depth from disparity in macaque inferior temporal cortex. *The Journal of Neuroscience*, 24(15), 3795.

Long, N. R. (1982). Transfer of learning in transformed random-dot stereostimuli. *Perception*, 11(4), 409-414.

Lu, Z. L., Hua, T., Huang, C. B., Zhou, Y., & Dosher, B. A. (2011). Visual perceptual learning. *Neurobiology of Learning and Memory*, 95(2), 145-151.

Manning, M. L., Finlay, D. C., Neill, R. A., & Frost, B. G. (1987). Detection threshold differences to crossed and uncrossed disparities. *Vision Research*, 27, 1683-1686.

Marr, D. (1982). *Vision*. San Francisco: Freeman.

Maruko, I., Zhang, B., Tao, X., Tong, J., Smith, E. L., & Chino, Y. M. (2008). Postnatal development of disparity sensitivity in visual area 2 (V2) of macaque monkeys. *Journal of Neurophysiology*, 100(5), 2486-2495.

Mazziotti, R., Baroncelli, L., Ceglia, N., Chelini, G., Sala, G. D., Magnan, C., . . . Pizzorusso, T. (2017). Mir-132/212 is required for maturation of binocular matching of orientation preference and depth perception. *Nature Communication*, 8, 15488.

McKee, S. P., Levi, D. M., & Movshon, J. A. (2003). The pattern of visual deficits in amblyopia. *Journal of Vision*, 3(5), 380-405.

Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. H. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *The Journal of Neuroscience*, 19, 8560-8572.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology*, 83, 2580-2601.

Neri, P., Bridge, H., & Heeger, D. J. (2004). Stereoscopic processing of absolute and relative disparity in human visual cortex. *Journal of Neurophysiology*, 92(3), 1880-1891.

Neri, P., Parker, A. J., & Blakemore, C. (1999). Probing the human stereoscopic system with reverse correlation. *Nature*, 401, 695-698.

Nguyenkim, J. D., & DeAngelis, G. C. (2003). Disparity-based coding of three-dimensional surface orientation by macaque middle temporal neurons. *The Journal of Neuroscience*, 23(18), 7117-7128.

Nienborg, H., & Cumming, B. G. (2006). Macaque V2 neurons, but not V1 neurons, show choice-related activity. *The Journal of Neuroscience*, 26(37), 9567-9578.

Nikara, T., Bishop, P. O., & Pettigrew, J. D. (1968). Analysis of retinal correspondence by studying receptive fields of binocular single units in cat striate cortex. *Experimental Brain Research*, 6(4), 353-372.

Nongpiur, M. E. & Sharma, P. (2010). Horizontal Lang two-pencil test as a screening test for stereopsis and binocularity. *Indian Journal of Ophthalmology*, 58(4), 287-290.

O'Toole, A. J., & Kersten, D. J. (1992). Learning to see random-dot stereograms. *Perception*, 21(2), 227-243.

Ogle, K. N. (1952). Disparity limits of stereopsis. *Archives of Ophthalmology*, 48(1), 50-60.

Ogle, K. N. (1958). Note on stereoscopic acuity and observation distance. *Journal of the optical society of America*, 48, 794-798.

Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1990). Stereoscopic depth discrimination in the visual cortex: Neurons ideally suited as disparity detectors. *Science*, 249(4972), 1037-1041.

Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1997). Encoding of binocular disparity by complex cells in the cat' s visual cortex. *Journal of Neurophysiology*, 75(5), 2879-2909.

Orban, G. A. (2011). The extraction of 3D shape in the visual system of human and nonhuman primates. *Annual Review of Neuroscience*, 34(1), 361-388.

Panum, P. L. (1940). *Physiological investigations concerning vision with two eyes* (C. Hubscher, Trans.). Hanover, NH: Dartmouth Eye Institute.

Patterson, R. & Fox, R. (1984). The effect of testing method on stereoanomaly. *Vision Research*, 24(5), 403-408.

Poggio, G. F., & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *Journal of Neurophysiology*, 40(6), 1392-1405.

Poggio, G. F., Motter, B. C., Squatrito, S., & Trotter, Y. (1985). Responses of neurons in visual cortex (V1 and V2) of the alert macaque to dynamic random-dot stereograms. *Vision Research*, 25(3), 397-406.

Poggio, G. F., Gonzalez, F., & Krause, F. (1988). Stereoscopic mechanisms in monkey visual cortex: Binocular correlation and disparity selectivity. *The Journal of Neuroscience*, 8(12), 4531-4550.

Portela-Camino, J. A., Martín-González, S., Ruiz-Alcocer, J., Illarramendi-Mendicute, I., & Garrido-Mercado, R. (2018). A random dot computer video game improves stereopsis. *Optometry and Vision Science*, 95, 1-8.

Ramachandran, V. S. (1976). Learning-like phenomena in stereopsis. *Nature*, 262(5567), 382-384.

Ramachandran, V. S., & Braddick, O. (1973). Orientation-specific learning in stereopsis. *Perception*, 2(3), 371-376.

Richards, W. (1970). Stereopsis and stereoblindness. *Experimental Brain Research*, 10(4), 380-388.

Richards, W. (1971). Anomalous stereoscopic depth perception. *Journal of the Optical Society of America*, 61(3), 410-414.

Rogers, B., & Graham, M. (1982). Similarities between motion parallax and stereopsis in human depth perception. *Vision Research*, 22(2), 261-270.

Romano, P. E., Romano, J. A., & Puklin, J. E. (1975). Stereoacuity development in children with normal binocular single vision. *American Journal of Ophthalmology*, 79(6), 966-971.

Roy, J. P., Komatsu, H., & Wurtz, R. H. (1992). Disparity sensitivity of neurons in monkey extrastriate area MST. *The Journal of Neuroscience*, 12(7), 2478-2492.

Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cerebral Cortex*, 5, 429-438.

Sakata, H. (2003). The role of the parietal cortex in grasping. *Advances in Neurology*, 93, 121-139.

Sasieni, L. S. (1978). The frisby stereotest. *Optician*, 176, 7-10.

Schmitt, C., Kromeier, M., Bach, M., & Kommerell, G. (2002). Interindividual variability of learning in stereoacuity. *Graefe' s Archive for Clinical and Experimental Ophthalmology*, 240(9), 704-709.

Schoemann, M. D., Lochmann, M., Paulus, J., & Michelson, G. (2017). Repetitive dynamic stereo test improved processing time in young athletes. *Restorative Neurology and Neuroscience*, 35(2), 413-421.

Scholl, B., Burge, J., & Priebe, N. J. (2013). Binocular integration and disparity selectivity in mouse primary visual cortex. *Journal of Neurophysiology*, 109(12), 3013-3024.

Sereno, M. E., Trinath, T., Augath, M., & Logothetis, N. K. (2002). Three-dimensional shape representation in monkey cortex. *Neuron*, 33(4), 635-652.

Simons, K. (1981). Stereoacuity norms in young children. *Archives of Ophthalmology*, 99(3), 439-445.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature (London)*, 386(6621), 167-170.

Solimini, A. G. (2013). Are there side effects to watching 3D movies? A prospective crossover observational study on visually induced motion sickness. *PLoS ONE*, 8(2), e56160.

Sowden, P., Davies, I., Rose, D., & Kaye, M. (1996). Perceptual learning of stereoacuity. *Perception*, 25(9), 1043-1052.

Srivastava, S., Orban, G. A., De Mazière, P. A., & Janssen, P. (2009). A distinct representation of three-dimensional shape in macaque anterior intraparietal area: Fast, metric, and coarse. *The Journal of Neuroscience*, 29(34), 10613-10626.

Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Experimental Brain Research*, 83(1), 29-36.

Takemura, A., Inoue, Y., Kawano, K., Quaia, C., & Miles, F. A. (2001). Single-unit activity in cortical area MST associated with disparity-vergence eye movements: Evidence for population coding. *Journal of Neurophysiology*, 85(5), 2245-2266.

Tanabe, S., Umeda, K., & Fujita, I. (2004). Rejection of false matches for binocular correspondence in macaque visual cortical area V4. *The Journal of Neuroscience*, 24(37), 8170-8180.

Tanabe, S., Yasuoka, S., & Fujita, I. (2008). Disparity-energy signals in perceived stereoscopic depth. *Journal of Vision*, 8(3), 1-10.

Tanaka, H., Uka, T., Yoshiyama, K., Kato, M., & Fujita, I. (2001). Processing of shape defined by disparity in monkey inferior temporal cortex. *Journal of Neurophysiology*, 85(2), 735-744.

Thomas, O. M., Cumming, B. G., & Parker, A. J. (2002). A specialization for relative disparity in V2. *Nature Neuroscience*, 5(5), 472-478.

Tomac, S., & Altay, Y. (2000). Near stereoacuity: Development in preschool children; Normative values and screening for binocular vision abnormalities; A study of 115 children. *Binocular Vision Strabismus Quarterly*, 15, 221-228.

Tootell, R. B. H., & Nasr, S. (2017). Columnar segregation of magnocellular and parvocellular streams in human extrastriate cortex. *The Journal of Neuroscience*, 37(33), 8014-8032.

Tsao, D. Y., Vanduffel, W., Sasaki, Y., Fize, D., Knutsen, T. A., Mandeville, J. B., . . . Tootell, R. B. H. (2003). Stereopsis activates V3A and caudal intraparietal areas in macaques and humans. *Neuron*, 39(3), 555-568.

Tsodyks, M., & Gilbert, C. (2004). Neural networks and perceptual learning. *Nature*, 431(7010), 775-781.

Tsutsui, K. I., Jiang, M., Yara, K., Sakata, H., & Taira, M. (2001). Integration of perspective and disparity cues in surface-orientation-selective neurons of area CIP. *Journal of Neurophysiology*, 86, 2856-2867.

Uka, T., & DeAngelis, G. C. (2006). Linking neural representation to function in stereoscopic depth perception: Roles of the middle temporal area in coarse versus fine disparity discrimination. *The Journal of Neuroscience*, 26(25), 6791-6802.

Uka, T., Tanabe, S., Watanabe, M., & Fujita, I. (2005). Neural correlates of fine depth discrimination in monkey inferior temporal cortex. *The Journal of Neuroscience*, 25(46), 10796-10802.

Uka, T., Tanaka, H., Yoshiyama, K., Kato, M., & Fujita, I. (2000). Disparity selectivity of neurons in monkey inferior temporal cortex. *Journal of Neurophysiology*, 84(1), 120-132.

Ukai, K., & Howarth, P. A. (2008). Visual fatigue caused by viewing stereoscopic motion images: Background, theories, and observations. *Displays*, 29(2), 106-116.

Umeda, K., Tanabe, S., & Fujita, I. (2007). Representation of stereoscopic depth based on relative disparity in macaque area V4. *Journal of Neurophysiology*, 98(1), 241-252.

Verhoef, B. E., Vogels, R., & Janssen, P. (2016). Binocular depth processing in the ventral visual pathway. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1697), 20150259.

Von Der Heydt, R., Zhou, H., & Friedman, H. S. (2000). Representation of stereoscopic edges in monkey visual cortex. *Vision Research*, 40(15), 1955-1967.

Watanabe, M., Tanaka, H., Uka, T., & Fujita, I. (2002). Disparity-selective neurons in area V4 of macaque monkeys. *Journal of Neurophysiology*, 87(4), 1960-1973.

Westheimer, G. (1979). Cooperative neural processes involved in stereoscopic acuity. *Experimental Brain Research*, 36(3), 585-597.

Wheatstone, C. (1838). On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical transactions - Royal Society*, 53, 371-394.

Wilcox, L. M., & Allison, R. S. (2009). Coarse-fine dichotomies in human stereopsis. *Vision Research*, 49(22), 2653-2665.

Wong, B., Woods, R., & Peli, E. (2002). Stereoacuity at distance and near. *Optometry and Vision Science*, 79(12), 795-800.

Wright, L. A., & Kelly, J. S. (1992). Stereopsis and ageing. *Eye*, 6(5), 473-476.

Xi, J., Jia, W. L., Feng, L. X., Lu, Z. L., & Huang, C. B. (2014). Perceptual learning improves stereoacuity in amblyopia. *Investigative Ophthalmology and Visual Science*, 55(4), 2384-2391.

Yamane, Y., Carlson, E. T., Bowman, K. C., Wang, Z., & Connor, C. E. (2008). A neural code for three-dimensional object shape in macaque inferotemporal cortex. *Nature Neuroscience*, 11(11), 1352-1360.

Note: Figure translations are in progress. See original paper for figures.