ADULT PLASTICITY OF A
BINOCULAR INTEGRATION MECHANISM

A Thesis in
Psychology
by
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ABSTRACT

Although the visual system’s susceptibility to plasticity early in development is especially pronounced (Hubel and Wiesel, 1965, 1970), research has shown that plasticity occurs in adult visual processing as well (Gilbert, 1992; Heinen & Skavenski, 1991). Previous research (Hollins & Hudnell, 1980; Klink, Brascamp, Blake, & Van Wezel, 2010) has proposed that inducing adult plasticity is possible through visual adaptation to dichoptically incongruent spatial gratings, so that each eye sees an independent image. This type of viewing produces a perceptual phenomenon called binocular rivalry. The visual system’s incapability of focusing on both images simultaneously subjects the viewer to constant perceptual switching, so that only one image dominates perceptual awareness at a time (Alias & Blake, 2005). Prolonged binocular rivalry may thus impose experience-driven plasticity on the binocular integration system. Persistent viewing of incongruent images weakens an interocular inhibition mechanism that normally suppresses the binocular integration of opposing stimuli, and remains weakened until exposed to normal, congruent binocular vision once more (Hollins & Hudnell, 1980; Klink et al., 2010). Perceptually, the viewer increasingly experiences mixtures of incongruent images or decreasing perceptual exclusivity. The present study extended this paradigm by randomly assigning participants to one of four interocular orientation difference (IOD) groups (90°, 45°, 37.5°, and 30°). It was expected that reducing IOD would also reduce interocular inhibition. The manipulation permits a direct test of the hypothesis that perceptual adaptation stems from weakened interocular inhibition. A significant reduction in perceptual exclusivity was found between the 30° IOD and other IOD conditions, as well as between the 37.5° and 45° IOD conditions. However, the study failed to produce decreased perceptual exclusivity with respect to time for any IOD condition, including the 90° IOD which was intended to replicate experimental conditions utilized in previous research (Hollins & Hudnell, 1980; Klink et al., 2010). The
discrepancy in these findings may stem from a larger (n=60), more diverse, and inexperienced sample of observers. It is also possible that the small IOD conditions fell within a perceptual threshold that begins to elicit stereopsis (Blakemore, Fiorentini, & Maffei, 1972) in observers, despite the lack of adaptation effects.
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I must also thank my lab associates in the Brain Development Lab, Jeremy Fesi, PhD. and Amanda Thomas, for their companionship and insight in personal and professional matters; Alex Dufford and Ricky Groner, undergraduate lab research assistants, for their many dedicated hours in the laboratory to which I am profoundly grateful for; and to the rest of the lab for taking the time out of the busy school year to help lift this project off the ground. And of course, thanks Ma (Quinn Ru) and Emy (Emily Hwang) for everything up to this point in life. Lastly, I owe much of my sanity to my guitar, Alice (named after the many times she has taken my to Wonderland), for providing me an entry to a plane of emotional and spiritual release so that my soul can find solace when reality would not suffice.
Chapter 1

Introduction

Binocular vision can be described in terms of integration of visual input coming from two separate retinal sources, both of which provide spatially overlapping information about the visual field. As a result, humans typically perceive single, stable representations of the visual scene indicating reconciliation of discrepancies due to the slight horizontal difference in spatial position between the two retinas, or otherwise referred to as retinal disparity. Two different perspectives of the visual scene provide the visual system with information about depth; the neural processing of which depends on integrative mechanisms performed by binocular cells in the early visual areas (Blakemore, Fiorentini, & Maffei, 1972; Brodsky, 2002). Furthermore, natural binocular stimulation early in life is essential for the neural architecture responsible for binocular vision to develop normally (Adams, Sincich, & Horton, 2007; Buisseret, Gary-Bobo, & Imbert, 1982; Burchfiel & Duffy, 1981; Crair, Ruthazer, Gillespie, & Stryker, 1997; Fagiolini, Pizzorusso, Berardi, Domenici, & Maffei, 1994; Gordon & Stryker, 1996; Hirsch & Spinelli, 1971; Hubel & Wiesel, 1965, 1970; Lewis & Maurer, 2005; Rauschecker & Singer, 1981; Sengpiel, Gödecke, Stawinski, Hübener, Löwel, & Bonhoeffer, 1998; Sengpiel, Stawinski, & Bonhoeffer, 1999; Tanaka, Ribot, Imamura, & Tani, 2006). This is not to say that the stability of adult binocular vision indicates a loss of cortical plasticity after visual development ends. Recent research suggests that normal adult binocular integration can be disrupted under certain experimental manipulations over a time period of just minutes (Hollins & Hudnell, 1980; Klink et al., 2010). This thesis describes a study designed to examine the time course of binocular integration in a parametric fashion.
The binocular rivalry paradigm

Figure 1: Examples of rivalrous dichoptic patterns (Tong, Meng, & Blake, 2006). Images in the left and right columns are viewed by the left and right eyes, respectively.

When exposed to binocularly rivalrous patterns (Figure 1), individuals typically perceive only one image at a time: while one image is perceptually dominant, the other image becomes absent from observer awareness. Perceptual dominance tends to last for a brief period of time before the opposing image takes precedence with a quick, sweeping transition (Wilson, Blake, & Lee, 2001). The alternations that occur during binocular rivalry appear to reflect the visual system’s inability to process contrasting stimulation simultaneously.

However, during normal viewing conditions, there are systematic discrepancies (i.e. retinal disparity) that provide depth information essential for stereoscopic vision (Figure 2). This indicates that the visual system can integrate somewhat misaligned images—as long as the optical differences are within certain spatial limits (as defined by Panum’s fusional area; Braddick, 1979) and the visual components from each eye exhibit matching features (Blake, 1989). At the neural level, these integration mechanisms appear to operate at the level of the primary visual cortex.
(V1), where binocular neurons are preferentially tuned to detect the spatial differences (Blakemore, Fiorentini, & Maffei, 1972) between corresponding monocular inputs or retinal disparity. Yet, binocular integration mechanisms are unable to resolve vastly incompatible stimuli because inhibitory connections between neurons innervated by different eyes prevent simultaneous visual processing (Blake, 1989). Under these circumstances, perceptual switching occurs apparently as a result of dynamically fluctuating competition between contrasting suppressive forces. Competition between visual inputs can also arise in cases of abnormal visual development.

Figure 2: Retinal disparity between the two eyes yields different perspectives of the same three-dimensional image (Blakemore, Fiorentini, & Maffei, 1972).

**Interocular inhibition mechanisms**

Amblyopia, a visual disorder that occurs when sensory stimulation to one eye is deficient during development, demonstrates the negative effects of interocular inhibition. Amblyopia is caused by either strabismus (eye misalignment) or anisometropia (unequal optical properties; Kiorpes & McKee, 1999). It usually results in poor visual acuity in one eye (the amblyopic eye). The visual system accommodates for defective input from the amblyopic eye by relying heavily upon stimulation from the non-amblyopic eye. In doing so, inputs from the amblyopic eye are
strongly inhibited, and, unless intervention (e.g., patching) is performed at an early age, these compensatory adaptations alter cortical processing permanently (Lewis & Maurer, 2005).

Inhibition demonstrated in amblyopia is interocular. This implies that activity in binocular neurons partial to one eye suppress others that shares retinal fields innervated by the opposing eye.

**Figure 3:** Physically swapping monocular images do not disturb subjective experience of perceptual dominance (Logothetis, Leopold, & Sheinberg, 1996).

**Figure 4:** Complementary, patch-worked pairs demonstrate equivalent durations of eye-of-origin and holistic percepts (Kovács, Paphathomas, Yang, & Fehér, 1996).

However, interocular inhibition at lower-levels of visual processing does not explain image suppression during binocular rivalry in non-amblyopic observers: swapping of monocular stimuli during rivalrous dichoptic presentation does not disturb perceptual dominance (Figure 3; Logothetis, Leopold, & Sheinberg, 1996), and complementary, patch-worked dichoptic pairs yield equal occurrences of holistic and eye-of-origin percepts (Figure 4; Kovács, Paphathomas,
Yang, & Fehér, 1996). Additionally, electrode recordings in monkeys experiencing binocular rivalry do not demonstrate perceptually related modulations in V1 and V2 (Leopold & Logothetis, 1996). Thus, the neural locus of binocular rivalry in observers with normal vision occurs at higher levels of perceptual processing than the inhibition previously described in amblyopic individuals. Accordingly, a hierarchical model of binocular processing may be necessary to explain binocular rivalry in normal observers.

The hierarchical model and state-space transition

Diverging evidence underscores the uncertainty of the neural locus associated with conscious perceptual awareness during binocular rivalry (Blake, 1989; Lee & Blake, 2002; Leopold & Logothetis, 1996; Logothetis, 1998; Lumer & Rees, 1999; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). For example, modulations of activity during perceptual switching in strictly V1 has been observed only inconsistently (Brown & Norcia, 1997; Lee & Blake, 2002; Logothetis, 1998; Polonsky et al., 2000; Tong & Engel, 2001). This supports the notion that neural activity associated with binocular rivalry arises at multiple stages of visual processing. Current models of binocular rivalry focus on a hierarchical approach (Figure 5; Tong, Meng, & Blake, 2006) that includes two representations of rivalry: eye and percept rivalry. Eye rivalry refers to binocular competition from bottom-up processing pathways, primarily the lateral geniculate nucleus (LGN; Wunderlich & Schneider, 2005) and primary visual cortex (V1; Blake, 1989). This type of rivalry is thought to arise from inhibitory connections between conflicting retinal inputs, due to the ocular segregation of visual processing present at these earlier cortical stages. Percept rivalry describes competing perceptual representations resolved at higher-order areas (Kóvacs et al., 1996; Logothetis, Leopold, & Sheinberg, 1996; Logothetis, 1998); for example, visual processing along the dorsal and ventral visual pathways (Ungerleider
& Mishkin, 1982; Goodale & Milner, 1992). It is hypothesized that higher-order perceptual representations provide feedback to bottom-up integration mechanisms (Tong, Meng, & Blake, 2006). Supposedly, perceptual dominance transpires during binocular rivalry because of interactions between multiple loci of neural competition, and it is important to make note that physically presented images (bottom-up stimuli) are not necessarily synonymous with internal perceptual representations.

Figure 5: Schematic of multi-level interactions during binocular rivalry (Tong et al., 2006).

Figure 6: Energy model diagram depicting bistability.

Another conceptual framework describes binocular rivalry using concepts from nonlinear dynamics. The lower-level feedforward system can be represented in a bistable state space
(Lehky, 1988) containing attractors associated with neural configurations responsible for processing either one or the other monocular image (Figure 6). State transitions between attractors occur due to the unstable nature of the neural architecture under an abnormal binocular sensory context, which has been described to exhibit stochastic, non-linear dynamics (Fox & Herrmann, 1967). During high-energy transitional periods (e.g. perceptual switching), the neural network briefly assumes an intermediate processing arrangement; incongruent information received from both eyes is simultaneously propagated forward and produces mixed visual characteristics. The perceptual consequence consists of an amalgamation of both dichoptic images in either a “piecemeal” (groupings from different images dominate certain spatial zones; Blake & Logothetis, 2002; Klink et al., 2010; Kovács et al., 1996; Wilson, 2010) or superimposed (complete overlay of the two images; Klink et al., 2010) fashion (Figure 7). Therefore, reported occurrences (Blake, O’Shea, & Mueller, 1992) of transient mixed percepts during binocular rivalry exhibit a phenomenon of the visual system that might normally integrate congruent dichoptic information, but will otherwise perceptually combine physically independent stimuli under abnormal sensory contexts.

Figure 7: Examples of mixed percepts: superimposition (left) and piecemeal (right; Wilson, 2010).
Adaptation effects on perceptual exclusivity

Previous research has suggested that prolonged exposure to rivalrous dichoptic conditions increases occurrence of mixed perception or, conversely, decreases exclusive perception of monocular images (Figure 8). Hollins and Hudnell (1980) initially attributed these behavioral findings as fatigue to a binocular suppression system; while Klink and colleagues (2010) suggested that interocular inhibition mechanisms – purportedly responsible for segregating exclusive perceptual experiences – are being attenuated due to extensive adaptation to incongruent neuronal input. Only when re-exposed to normal binocular conditions (as opposed to solely monocular or blindfolded conditions) during recovery periods (Figure 8) did participants reveal that exclusive perception returned to baseline levels, suggesting a preservation of weakened interocular inhibition mechanisms only when the visual system was denied simultaneous and congruent sensory input (Klink et al., 2010).

Figure 8: Adaptation and recovery results from Klink et al. (2010). The ordinate depicts the fraction of exclusive monocular perception, or perceptual exclusivity, within each trial’s total duration. The trend lines depict changes in perceptual exclusivity ratios across trials. During recovery periods, three conditions were designated: free-viewing, normal binocular vision (“Binocular”), monocular stimulation (“Monocular”), or no visual stimulation (“Gray”; Wilson, 2010).
The findings from Klink and colleagues (2010) suggest the possibility that prolonged adaptation to binocular rivalry induces experience-driven plasticity in the adult visual system. Specifically, adaptation causes interocular inhibition mechanisms to weaken. This reduces the effectiveness with which interocular inhibition mechanism segregate incongruent binocular input, possibly because synaptic strength associated with these neural mechanisms (Blake, 1989) is reduced due to continuously discordant neuronal activity (Klink et al., 2010; Wilson, 2010). The perceptual outcome is a reported decline of successfully discriminating between one and the other visual image (i.e. exclusive perception). Moreover, Klink and colleagues (2010) find that return to baseline levels of exclusive perception is contingent on receiving normal, convergent binocular input (Figure 8). The persistence of reduced perceptual exclusivity ratios when recovery periods consisted of normal viewing to only one eye or lack of normal viewing entirely (gray screen) suggests that the convergence of binocular afferents composed of natural visual input is a necessary component for interocular inhibition to appropriately segregate rivalrous information once more. Without purported sensory recalibration between both monocular channels, the adult visual processing systems may experience functional reorganization, or in other words, experience-driven plasticity. These findings are particularly interesting because they contradict research (Hubel & Weisel, 1965, 1970) demonstrating the ineffectiveness of perceptual adaptation in eliciting cortical plasticity beyond a sensitive period of visual development (unless under more invasive measures; Gilbert, 1992; Heinen & Skavenski, 1992; Schmid, Rosa, Calford, & Ambler, 1996).

The current study was modeled closely after the Klink and colleagues (2010) in order to replicate its findings of reduced perceptual exclusivity across repeated exposures, and to revisit the hypothesis that weakened interocular inhibition mechanisms account for changes in perception over adaptation time. This line of research should provide stronger evidence about the
extent of experience-driven plasticity in adults who are exposed to prolonged abnormal viewing, and it may reveal the degree to which the functional manipulation of neural mechanisms are responsible for changes in perception.

**Study aims**

This study replicates the adaptation paradigm used by Klink and colleagues (2010) under multiple interocular orientation discrepancies (IODs). These manipulations serve three purposes: 1) test the hypothesis that weakened interocular inhibition explains the decrease in perceptual exclusivity, 2) evaluate adaptation effects with a larger sample size collected of purely novice observers, 3) test the effect asking observers to directly report mixed states (as opposed to inferring mixed states from no-press durations; Hollins & Hudnell, 1980; Klink et al., 2010). The manipulation of IOD should assess the extent to which interocular inhibition is responsible for exclusive perception of monocular images. Assuming that smaller IOD conditions demonstrate a larger overlap in (Table 1), adaptation effects in smaller IOD conditions should be larger (Figure 9). Levels of interocular inhibition between monocular channels are intrinsically lower for dichoptic presentations with greater luminance level correlations. As a result, the rate of attenuation by interocular inhibition should be greater for less discordant patterns (Figure 9).

**Table 1:** Experimental conditions expressed as either interocular orientation difference or as a correlation coefficient.

<table>
<thead>
<tr>
<th>Interoocular Orientation Disparity (IOD)</th>
<th>90°</th>
<th>45°</th>
<th>37.5°</th>
<th>30°</th>
</tr>
</thead>
<tbody>
<tr>
<td>Correlation Coefficient ($r$)</td>
<td>-7.1667 × 10^-17</td>
<td>0.0014972</td>
<td>0.010164</td>
<td>0.051041</td>
</tr>
</tbody>
</table>
Figure 9: Predicted results. Interpretation of predicted perceptual exclusivity profiles for selected IOD conditions. Predicted perceptual exclusivity profile for the 45° IOD condition differs according to either dichoptic correlation (a) or IOD (b).
Chapter 2

Methods

Participants

Participants were undergraduate students (n=60; female = 49) at Pennsylvania State University with normal or corrected-to-normal visual acuity and normal stereoacuity as measured by the Snellen chart and Stereo Butterfly SO-005, respectively. Participant inclusion required the ability to demonstrate considerable perceptual switching (within the order of one switch every few seconds) and relatively equal ocular dominance, as measured by the proportion of time they reported experiencing left or right eye images. Seven participants were excluded from the study. All participants remained naïve to the objectives of the experiment, and were new to the experimental procedure.

Apparatus and displays

Dichoptic displays (Figure 10) were shown on two halves of a CRT monitor (Philips Business 107B33) at a resolution of 1024 x 768 and a refresh rate of 85 Hz. The displays were presented by a MacBook using Matlab (v7.10.0) and the Psychtoolbox (v3.0.8) extensions (Brainard, 1997). Viewing distance was 67 cm. Participants were tested in a soundproof chamber with the lights turned off. Displays were viewed through binoculars adjusted to sufficiently segregate the two halves of the stimulus display that were mounted to a chin-rest. All stimuli were 5.5 x 5.5º in size and presented on a uniform gray background. Stimuli and background had an average luminance of 37.7 cd/m². Luminance contrasts were adjusted to 45%.
A pair of black alignment rings (26.6 cd/m²) surrounded dichoptic stimulus presentation to promote binocular fusion. Stimuli consisted of sine-wave gratings with a spatial frequency of 0.260509975 cyc/deg. Spatial gratings for the four experimental conditions were presented at +45° and -45° (90° IOD), +22.5° and -22.5° (45° IOD), +18.75° and -18.75° (37.5° IOD), and +15° and -15° (30° IOD) from the vertical meridian. IODs less than 30° (±15°) were observed to produce binocular fusion that was far too consistent for the purposes of the study.

![Image](image_url)

**Figure 10**: Example of ±45° stimulus display. Each spatial grating was segregated when viewed through the binocular apparatus.

**Procedure**

Participants reported perceptual states by pressing three keys on a standard keyboard with their right hand, corresponding to either the left, right, or mixed percept. As a percept became dominant, the participant was instructed to hold the corresponding key (left key for left percepts, right key for right percepts, and down key for mixed percepts) for the entire duration of perceptual dominance. Participants were shown a representation of combined of spatial gratings (Figure 7; right) beforehand, so they were aware of the percept corresponding with mixed responses. Verbal instructions were as follows:
“The only keys you will need to use for this experiment are the left, right, and middle arrow keys. Your task is to press and hold the corresponding key associated with whichever image ‘comes to the front’ during perceptual switching. Switching will happen many times, back and forth, throughout a trial. Since all of this is happening individually to only you, we are relying on you to accurately capture each switch and duration length to the best of your ability. Additionally, do not hold down multiple keys. Sometimes the two images may ‘fuse’ together. During these durations, press and hold the middle arrow key. The fused images won’t look the same each time and may disappear quickly. You may also see them between left-to-right and right-to-left swaps. These are usually just transitional phases. If they persist for longer than just a transition, then you should hold the middle arrow key. Otherwise just ignore them and focus on the perceptual switching.”

Before beginning the experimental phase, participants completed preliminary training where images were presented in a monocular fashion and artificially superimposed spatial gratings were presented to both eyes (Figure 11).

Figure 11: Graphical representation of training results. Participants followed alternating monocular images or a binocularly-presented, superimposed mixed image (red) with respective key presses (blue). The abscissa represents left, mixed, or right presentation.
Experimental design and procedure

Participants were randomly assigned to one of the four orientation conditions described previously. The study consisted of two phases. The first phase was a baseline measurement where rivalrous stimuli was presented for 100s then followed by a 100s interstimulus interval (ISI). During the ISI, only the alignment rings were displayed. The baseline procedure repeated four times, so that an initial average fraction of exclusivity proportion was calculated. During the adaptation phase, participants experienced the same procedure as in the baseline portion, except with a reduced ISI of only 10s. There were a total of 16 adaptation trials. Thus, a total of 20 baseline and adaptation rivalry trials were performed for a total duration of 2,560s (approximately 43 minutes). Within each IOD condition, a cumulative perceptual exclusivity ratio was calculated across individuals for each trial, producing an averaged perceptual exclusivity profile within each IOD conditions across the adaptation paradigm.

Data analysis

Perceptual exclusivity for each trial was calculated as the sum of total left and right percept durations divided by total press time (left, right, and mixed)\(^1\). When perceptual exclusivity ratios were not distributed normally a Box-Cox transformation was performed (Appendices A & B). To assess the effects of IOD and Trial on perceptual exclusivity, a repeated

\(^1\) This reporting method differed from previous studies, which divided by total trial time instead of total press time. It was discovered that unreported durations would collect during transitions between left and right key presses. These occurrences accumulated against exclusive perception times, and may have misleadingly attributed to mixed percept duration. Thus, the current study implemented a three-key mapping system where no-key press durations were disregarded in perceptual exclusivity ratio calculations. All participants exhibited press durations for at least 75% of the entire study time.
measures analysis of covariance (ANCOVA) was performed assuming a first-order autoregressive covariance structure (Appendices C & D).
Chapter 3

Results

First, correlation among luminance levels across both spatial gratings in each condition was calculated. Pearson coefficients for these IOD conditions were \(-7.166 \times 10^{-17}, 0.0014972, 0.010164,\) and \(0.051041,\) respectively \((\alpha = .05; \text{Table 1})\). These coefficients reflect the degree of correspondence between dichoptic displays of spatial gratings. Figure 12 demonstrates that dichoptic correlation exponentially increases as IOD decreases.

![Figure 12: Interocular orientation disparity (IOD) expressed in terms of correlation between left and right spatial gratings. IOD conditions were selected to best capture an exponential relationship.](image)

It was assumed that measurements of perceptual exclusivity closely related in time held higher correlations than measurements that were further apart. As a result, a first-order autoregressive structure with homogeneous variances and correlations that declined exponentially with distance in time was used in the analysis. The fit indices for the resulting model \((\text{AIC} = -\)
2155.5, BIC = -2151.3; Appendix E) were not smaller than covariance structures for other models. However, due to the theoretical basis underlying first-order autoregressive structure in characterizing the temporal correspondence across data measurements, the present study maintained calculations with this type of covariance structure. A main effect for IOD was found, $F(3,56)=4.55$, $p=0.0063$. But, there was no significant effect of trial, $F(15,840)=0.80$, $p=0.6734$ and no interaction, $F(45,840)=0.50$, $p=0.9975$.

Results from a one-way ANOVA retaining only IOD as a factor confirmed the significance of IOD on perceptual exclusivity, $F(3,1016)=32.75$, $p<0.0001$, collapsed across adaptation time. Post-hoc, multiple comparison (Tukey-Kramer) tests of factor-level means revealed that the IOD condition of 30º largely determined the significance of this effect, demonstrating a significant difference compared to all other IOD conditions: 37.5º, $t(1016) = -5.63$, $p<0.0001$; 45º, $t(1016) = -9.30$, $p<0.0001$; and 90º, $t(1016) = -7.02$, $p<0.0001$.

Additionally, 37.5º yielded a significant difference in perceptual exclusivity compared to the 45º IOD condition, $t(1016) = -3.52$, $p=0.0005$. According to an interaction plot between conditions (Figure 13), the direction of these significant findings was that smaller IODs exhibited lower levels of perceptual exclusivity.
Individual-level perceptual exclusivity profiles reveal a degree of individual variability (Appendix F). Although it is possible that averaging perceptual exclusivity ratios across participants may have negated any adaptation effects, the individual-level perceptual exclusivity profiles do not demonstrate overall trends in adaptation time—many of which consist of constant or increasing slopes. Linear regressions were performed on each individual’s perceptual exclusivity profile, and a t-test was performed on each slope coefficient to evaluate its significance from zero. A contingency table consisting of results from these t-tests was constructed (Table 2), such that count data classifying significantly negative slopes, significantly positive slopes, or slopes not significantly different from zero was tallied for each IOD condition. A Fisher-Freeman-Halton Exact test determined that there was no significant dependence across rows or columns in the contingency table ($p = 0.8318$).
Additionally, Figure 14 shows an individual-specific (910419ryla; 30° IOD condition) stem-plot of cumulative press duration (left, right, and mixed) across trial time for each 100s trial. This finer-grained analysis – examining an individual’s time course of perceptual durations within each trial – might uncover effects of adaptation that were not initially observed when computing cumulative trial ratios alone. However, that analysis is beyond the scope of this paper.

Table 2: 3-x-4 contingency table depicting the number of individuals that demonstrated a negative, zero, or positive slope in a linear regression performed on perceptual exclusivity ratios across trials.

<table>
<thead>
<tr>
<th></th>
<th>90°</th>
<th>45°</th>
<th>37.5°</th>
<th>30°</th>
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</thead>
<tbody>
<tr>
<td>β² &lt; 0</td>
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<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>β² = 0</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td>8</td>
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Figure 14: Individual-level stem-plot for subject, 910419ryla, in the 30° IOD condition. The plot demonstrates cumulative reported durations for left (black), right (magenta), and mixed (cyan) percepts as a function of within trial time (100 s total) and for each discrete trial (1-16).
Chapter 4

Discussion

Participants who viewed grating pairs with 30 and 37.5 deg of interocular difference showed lower levels of perceptual exclusivity – more frequent mixed percepts – than did participants in the 45 or 90º IOD conditions. However, no group showed increases in mixed percepts across trials. Thus, the current study did not replicate findings from previous reports demonstrating a decrease to perceptual exclusivity after adaptation to the binocular rivalry paradigm. Specifically, participants who viewed dichoptic spatial gratings of 90º IOD over the course of approximately 45 minutes of adaptation – an experimental paradigm similar to that of previous research (Hollins & Hudnell, 1980; Klink et al., 2010) – did not exhibit any change in the frequency of mixed percepts. In addition, predicted adaptation effects on perceptual exclusivity ratios were not revealed in any other IOD conditions. However, an analysis examining perceptual exclusivity ratios at the individual-level demonstrated that some participants exhibited a decreasing perceptual exclusivity profiles.

There are several reasons why this study failed to replicate the change in perceptual exclusivity across time found by Klink et al. (2010) and others. First, the reporting methodology exhibited by Hollins and Hudnell (1980) and Klink and colleagues (2010) did not account for gaps between key pressing, which may have resulted in an inappropriate measure for mixed perception that biased the results toward larger and increasing levels of mixed responses. Second, the occurrence of perceptual switching has been shown to be subject to voluntary control (van Ee, van Dam, & Brouwer, 2005; Chong & Blake, 2006), which suggests that top-down modulatory
effects of attention may extend to mixed perception, and that subjective experience may greatly impact degrees of perceptual exclusivity. I discuss each of these issues in turn.

In previous experimental paradigms (Hollins & Hudnell, 1980; Klink et al., 2010), perceptual exclusivity for each trial was calculated as the duration of left and right key presses divided by entire trial time (100 s). The duration of mixed perceptual states was inferred based on the total trial time not spent in one of the two states of perceptual exclusivity. In contrast, the current study implemented a three-key mapping system in which participants had to explicitly report the duration of both exclusive and mixed perceptual states. There are unavoidable gaps between key presses. In previous studies, the durations of these gaps were summed to calculate the duration of mixed percepts. The measure of mixed percept duration used in previous studies (e.g., Klink et al. 2010) does not discriminate between key-press gaps with the duration of true mixed perceptual states. Response-gaps turn out to be especially problematic when successive key press durations are short. This results in inflated no-press times due to a rapid series of alternating key presses. Klink and colleagues (2010) reported that no-press durations – interpreted as mixed perceptual periods – increased over adaptation trials and decreased across recovery times (Figure 15). Consequently, Klink et al. (2010) may have observed increases in mixed percepts across trials not because of increased frequency and duration of mixed perceptual states, but because participants reported shorter and more frequent shifts between perceptually exclusive state—ultimately, resulting in greater no-press durations and decreased perceptual exclusivity ratios.
Additionally, there are limitations to the neural processing of mixed afferents; the free energy model and evidence of interocular suppression (Alias & Blake, 2005; Blake, 1989) suggest that low level processing rarely involves simultaneous binocular input during rivalrous conditions. The bistability of the system results because little amounts of activation energy are required to shift the system into a resting state associated with exclusive monocular perception. Furthermore, perceptual switching occurs rapidly (between one and two seconds), the neural mechanism of which – at least in earlier stages of visual processing – entails recurrent disinhibition (Wilson, 2001) across ocular dominance (OD) columns in V1 and thalamic neural networks (Rinzel, 1998). When interocular inhibition is overcome, a given neuron will rapidly facilitate activity throughout an integrated neural network responsive to the same monocular input (Malach, Amir, Harel, & Grinvald, 1993). This network-wide propagation is thought to travel along lateral projections that ensure processing performed by monocular afferents is functionally coupled (Malach et al., 1993; Das & Gilbert, 1995). Therefore, wave-like transitions (Wilson, 2001; Lee, Blake, & Heeger, 2007), visible during perceptual switching, illustrate an aggregate neurobiological subsystem experiencing highly interlaced (albeit delayed) innervation.

Figure 15: Average mixed durations (left) and exclusive perceptual durations (right) reported across adaptation time (Klink et al., 2010). A clear trend of decreasing exclusive durations during rivalry suggests increasing pressing alternations, which, according to the behavioral measures, would accumulate key-press gaps that would attribute to mixed perceptual duration.
Although lower level visual processing systems are prone to intermediate functional configurations – where incongruent ocular input from two sources can feedforward to later levels of perceptual processing – neurons embedded in the same OD framework must unsuccessfully propagate or remain unresponsive to disinhibitory signals. Due to tight coupling (Malach et al., 1993), however, disruption of recurrent disinhibition, resulting in the processing of rivalrous input from both eyes, would be difficult. According to the hierarchical model (Tong, Meng, & Blake, 2006), higher-order perceptual representations can selectivity group together, through feedback mechanisms, lower level neuronal interconnectivity even if the grouped neurons are processing incongruent information that originates from separate eyes. Perceptual grouping potentially explains previous findings (Kovács et al., 1996; Logothetis, Leopold, & Sheinberg, 1996) demonstrating that percept rivalry holds precedence over eye rivalry. Consequently, perceptual feedback mechanisms may be capable of stabilizing intermediate states of lower-level heterogeneous ocular processing, while strictly eye rivalry conditions – exclusive of top-down modulation – would conserve bipartisanship of monocular input.

Thus, even though weakening of interocular inhibition mechanisms at lower levels of ocular segregation may prove to be difficult due to tightly coupled intraocular mechanisms (Malach et al., 1993; Das & Gilbert, 1995), it is possible that the previous studies (Hollins & Hudnell, 1980; Klink et al., 2010) were able to achieve integration of visual input in earlier cortical stages due to top-down influences. Possibly, attentional mechanisms facilitate heterogeneous processing of incongruent dichoptic input and, subsequently, manifestations of mixed percepts at higher-order processing pathways. Small sample sizes (n = 2, Hollins & Hudnell, 1980; n = 5, Klink et al., 2010) and experienced observer participation (both studies included authors as participants) suggest that top-down modulatory factors may have impacted results. Thus, previous experience with the binocular rivalry paradigm and underlying knowledge
of research goals should be accounted for especially due to the subjective nature of perceptual reports.

Evidence that top-down modulation of perceptual events, such as voluntary attentional control (Helmholtz, 1925; Ooi, & He, 1999; Meng & Tong, 2004; van Ee, van Dam, Brouwer, 2005; Paffen, Alais, & Verstraten, 2006) and neural interactions from parietal and prefrontal areas on V1 inhibitory mechanisms (Lumer & Rees, 1999) during perceptual bistability signify that perceptual switching is likely susceptible to executive functioning. Accordingly, the notion that experienced observers can conceivably discriminate mixed percepts at lower thresholds and sustain the perceptual experience with less difficulty, intent to manipulate scientific outcomes notwithstanding, needs to be considered. Although weakened interocular inhibition between eye-of-origin afferents may potentially explain decreasing perceptual exclusivity over prolonged exposure to binocular rivalry (Klink et al., 2010), these effects might require proficient perceptual discrimination and active cognitive control. If experienced perceptual reporters solely demonstrate adaptation effects, then it is likely that attention serves as a mediator for not only exclusive perception, but perceptual mixing as well.

Results from the current study demonstrated that novice participants were capable of reporting mixed perception (Figure 13) even if it did not come to dominate their subjective experience. Additionally, preliminary training incorporated in the current study should have reinforced the likelihood of mixed perceptual state reporting: participants were shown artificial representations of mixed percepts (combined spatial gratings; Figure 7) and all participants had to demonstrate mixed percept responding prior to moving on to the full study (Figure 11). Still, the predicted effects (Figure 9) of decreased perceptual exclusivity across repeated exposure trials were not observed, even when consistently high mixed perception were reported.

Attention shifts might also account for the results, but there are questions about its degree of influence on perceptual awareness during binocular rivalry (Alias & Blake, 2005; Tong, Meng,
Blake, 2006). Meng and Tong (2004) found that reversals during binocular rivalry are significantly less susceptible to voluntary control than during Necker Cube ambiguity. Helmholtz (1925) reported that by counting the stripes of a spatial grating of one monocular image was he able to retain an extended perceptual experience of that monocular percept. Ooi and He (1999) demonstrated that attention was capable of both deterring and instigating incidents of perceptual switching, as well as cueing specific dominant percepts. Chong and Blake (2006) expanded upon these higher-order attentional influences on binocular rivalry to feature both exogenous (physical manipulations) and endogenous (predisposed feature detection) effects of attention. In addition, introducing a contrast manipulation (i.e. exogenous cue) negated any endogenous attention effects, which is suggestive of potential interactions of higher-order control on lower-order contrast gain (Chong & Blake, 2006) in order to obtain perceptual salience. Lastly, evidence that voluntary control exhibits changes to the temporal dynamics of perceptual switching (i.e. speeding up and slowing down) exists (van Ee, van Dam, & Brouwer, 2005); however, it was also demonstrated that intentional manipulation of perceptual awareness could not be sustained indefinitely (Helmholtz; 1925; van Ee, van Dam, Brouwer, 2005; Paffen, Alias, Verstraten, 2006).

Top-down modulation via attention poses something of a problem for adaptation methods used in the present research. If perceptual awareness and executive functioning are indeed related, then maintenance of mixed percepts, possibly due to previous experience, can confound an adaptation paradigm. In other words, decreased perceptual exclusivity may not have been influenced strictly by consistent exposure to binocular rivalry, but rather by the studies’ motivations—where the requirement to report mixed perceptual experience during binocular rivalry may have fundamentally biased observers towards perceiving more occurrences of mixed perception. As such, any changes to neural mechanisms during adaptation to rivalrous spatial gratings may hinge upon higher-order factors. This possibility deserves future study because if
sensory experience is yoked to an individual’s conscious awareness, then cortical functioning potentially accommodates for one’s subjective perception.

If this is the case, then the recovery results from Klink and colleagues (2010) can be potentially explained by attentional mechanisms. To reiterate, normal viewing of only one eye resulted in a lack of recovery to baseline perceptual exclusivity levels (Figure 8). If attention is responsible for decreasing perceptual exclusivity, then a question remains as to why perceptual exclusivity would return to baseline levels—assuming that observers in Klink et al. (2010) were still actively attending for mixed percepts. An explanation may be that contrast adaptation, weakened interocular inhibition, or some undetermined change to neural mechanisms is taking place, but is conditional upon attentional modulation. (In fact, contrast adaptation most likely is occurring in the present study due to the length of experimental exposure to dichoptic presentations.) Thus, it is possible that the perceptual system does experience a change in functional processing, which allows for increased visual awareness of mixed percepts. This functional change – mediated only by higher-order attentional mechanisms – might then facilitate previously unachievable durations of mixed perceptual experience. Therefore, even though the perceptual system for one eye is exposed to normal viewing conditions (Klink et al., 2010), only congruent stimulation to both eyes can revert any functional changes to the perceptual system back to a baseline state. Consequently, the observer is abstained from substantially perceiving rivalrous mixing without inducing adaptation effects once more.

Finally, despite the lack of adaptation effects, the 30º IOD condition demonstrated significantly lower perceptual exclusivity ratios compared to the larger three IOD conditions. The 37.5º IOD condition also exhibited the same trend, but only in contrast with the 45º IOD condition. Taken together, these findings suggest that the parametric manipulation of IOD may have revealed a perceptual threshold, such that smaller orientation differences that fall within a certain IOD yield consistently high amounts of mixed perceptual reports. As previously
mentioned, orientation disparities approximately less than 36º begin to produce three-dimensional percepts (Braddick, 1979) characterized as a stereoscopic slant either toward or away from the observer (Figure 16; Brodsky, 2002). The extent of dichoptic angular difference is defined by Panum’s fusional area, such that presentations beyond this IOD elicit double vision (Braddick, 1979). The 30º IOD condition resides well within this perceptual threshold. Consequently, binocular integration mechanisms (Blakemore, Fiorentini, & Maffei, 1972) are expected to take effect, and stereopsis transpires (Braddick, 1979; Brodsky, 2002). Thus, participants in the 30º IOD condition may have potentially reported mixed perception to a visual experience represented by tilted three-dimensional spatial gratings instead of piecemeal or superimposed mixed percepts. The distinction between mixed perception and stereopsis is difficult to define due to the subjective nature of perceptual reports, but should require consideration in the future, perhaps by manipulating the extent to which rivalrous images have 3D interpretations.

Figure 16: Interocular orientation differences (IODs) produce depth cues (Brodsky, 2002).

If, in fact, participants perceive small dichoptic displays in 3D terms, it is conceivable that dichoptic stimulation in the current study is capable of evoking higher-order perceptual representations. Theoretically, perceptual grouping should be prevalent when stereopsis occurs
due to an emergence of feedback mechanisms that impose neural organization in lower level functional processing (Tong, Meng, & Blake, 2006), such that visual input associated only with the higher-order percept is selectively communicated downstream. If the assumption is valid – stereopsis assumes a higher-order representation in the visual system – then stereoscopic occurrences during binocular rivalry should result in a preservation of functional neural configurations that simultaneously process rivalrous input from both ocular sources. Accordingly, any purported effects of perceptual grouping in concert with significantly lesser degrees of conflicting interocular inhibition should distinguish the 30º IOD condition as optically ideal for adaptation effects to emerge. Nevertheless, the present study does not demonstrate that incidents of stereopsis (assumed to be prevalent in the 30º IOD condition and capable of eliciting substantial perceptual grouping) encourages adaptation over time or potentially plays a role in weakening interocular inhibition mechanisms.

Criticisms of previous research

An alternative account for decreases in perceptual exclusivity is that the sensory system undergoes adaptation to contrast rather than weakened interocular connections. If this were the case, then decreased perceptual exclusivity would occur due to facilitation of binocular mixing because of globally diminished neuronal sensitivity irrespective of the nature of the visual stimuli. Hollins and Hudnell (1980) examined the contrast-adaptation hypothesis by comparing rivalry conditions against alternating monocular stimulation in order to demonstrate that only when rivalrous stimuli are simultaneously presented did perceptual exclusivity wane. After adaptation, the authors report that the rivalry condition significantly exhibited a decrease in exclusive visibility (Figure 17) while physically alternating monocular stimuli did not.
Klink and colleagues (2010) addressed the same alternative hypothesis by intermittently presenting matching dichoptic plaids identical in spatial frequency and orientation as rivalry spatial gratings (Figure 18A), the purpose of which was to reintroduce binocular neural correspondence with identical stimulation across retinal space after adaptation effects have run its course. Subsequently, Klink and colleagues (2010) discovered that perceptual exclusivity returned to baseline immediately after matching plaid presentations – a finding that was suggested to be unlikely if contrast adaptation were responsible for decreased perceptual exclusivity because the matching plaids and rivalry gratings composed of the same luminance properties.

However, a discrepancy in Klink and colleagues’ (2010) examination of contrast adaptation exists due to the degree to which matching plaids returned perceptual exclusivity ratios to baseline levels. According to results in Klink and colleagues (2010; Figure 18B), baseline levels were instantaneously recovered after exposure to matching plaids, but regaining perceptual exclusivity after binocular free viewing was not successful until after many interleaved recovery sessions (Figure 8). Assuming normal binocular input is much more effective at recalibrating
binocular integration systems than matching monocular plaids, an opposite trend of results should surface. The present study’s experimental manipulation provided an alternative method to examine the contrast adaptation hypothesis, in that; different IOD conditions should not have any difference with respect to adaptation to contrast over time. However, if weakened interocular inhibitory mechanisms are responsible for decreased perceptual exclusivity profiles, then a pattern of increasing adaptation rates should be observed in smaller IOD conditions—smaller IOD conditions have exponentially increasing overlap in visual properties (Table 1; Figure 12).

However, due to a lack of adaptation effects, we cannot determine whether contrast adaptation or weakened interocular inhibition is responsible for the phenomenon.

![Image](image_url)

Figure 18: Results from Klink et al. (2010) to examine the effects of exposing participants to binocular displays of matching (A; top) or non-matching plaids (A; bottom) during adaptation periods. Perceptual exclusivity was shown to immediately return to baseline levels when only exposed to matching plaids (B; filled circles) as opposed to non-matching plaids (B; unfilled squares) or monocular images (B; gray asterisks).

Additionally, if weakened inhibitory mechanisms are indeed responsible for increased mixed perception, it is not clear as to what level of binocular rivalry adaptation effects are acting
upon. If previous reports are evaluated in light of the hierarchical model, then rivalrous dichoptic stimulation by spatial gratings alone are more prone to eye rivalry as opposed to higher-order percept rivalry (Klink et al., 2010). This ultimately determines where in the neural framework of binocular rivalry fused perceptual representations takes place. Without evidence demonstrating that adaptation effects are taking place beyond bottom-up processing associated with eye rivalry, then any neural changes occurring during adaptation periods may be equivalent to contrast adaptation, such that only short-term neural habituation – rather than experience-driven plasticity – is in effect.

A state-space account provides another perspective on these issues. Over adaptation periods, a hypothetical dynamic system shifts from a bistable state space to a state space containing three attractors – two low-energy states (i.e. exclusive monocular perception) and an intermediate energy state (i.e. mixed perception) that resembled a high-energy transitional barrier in non-adapted circumstances (Figure 6). The adapted intermediate state cannot constitute as a definite energy minima because mixed percepts do not hold uniform perceptual representations (piecemeal percepts are variable). Thus, adaptation effects would exhibit a general flattening of the transitional barrier between low-energy states as opposed to a substantiation of a local minimum. The neural instantiation could be hypothetically depicted as a broad-scale, unpredictable attenuation to all inhibitory and excitatory connections. Inconstant mixed percepts would not successfully rival against well-defined monocular percepts, and higher-order mixed representations would not effectively produce consistent feedback to feedforward neurons (Figure 5). Therefore, higher-order feedback mechanisms would not generate consistent processing configurations among lower-level afferents. Instead, bottom-up processing configurations would experience spontaneous functional organization, depending on the variability of higher-order, mixed perceptual representations. This would not effectively foster experience-driven plasticity as suggested by Klink and colleagues (2010).
Yet, it is possible that Klink and colleagues (2010) implied that a global weakening of interocular inhibition rather than percept-specific reorganization of binocular processing mechanisms takes place, but this distinction requires elaboration. The former suggests that piecemeal percepts are merely the consequence of indiscriminate eye-of-origin intermixing, and representations of definite mixed percepts at higher levels of the perceptual pathway would hardly persevere. (An exception to non-uniform mixed percepts is when gratings appear superimposed, which represents a distinctly unique higher-order percept. However, perpendicular gratings do not easily facilitate this fused percept, and no distinction between superimposed and piecemeal percepts is made in the previous studies’ behavioral reports; Hollins & Hudnell, 1980; Klink et al., 2010.)

Analogous to the neural effects of contrast adaptation, a decrease in eye-level rivalry – even by means of weakened interocular inhibition – does not necessarily represent experience-driven plasticity. The reports of recovered perceptual exclusivity in response to matching plaids or simultaneous binocular vision (Klink et al., 2010) do not reconcile this uncertainty because recovery to normal perceptual exclusivity may require binocular contrast calibration in the same manner that proper interocular inhibition necessitates binocular correspondence of neuronal innervation. It may be the case that contrast adaptation and weakened interocular inhibition produce similar neural results, such as a temporary desensitization to spatial gratings in early visual processing. Thus, without evidence that higher-order inhibitory mechanisms are prone to visual adaptation and remain stable after abnormal exposure, conclusions that a substantial change to functional processing (i.e. neuroplasticity) should not be drawn.
Conclusions

Adaptation effects demonstrated by previous studies may be contingent on several other factors, and the extent to which adaptation elicits neuroplasticity under the binocular rivalry paradigm requires further elaboration. Neural mechanisms responsible for perceptual awareness extend beyond bottom-up processing mechanisms, and modulations due to higher-order perceptual systems necessitate a hierarchical approach to understanding the visual system. Moreover, these interactions that take place throughout visual processing contribute to the complexity behind the study of functional changes in neural architecture, such as experience-driven plasticity as a result of sensory adaptation. Therefore, the present study’s findings suggest further research is needed to understand the nature of decreased perceptual exclusivity—precisely identifying the neural basis behind this phenomenon and any mediating factors, the extent of these effects throughout the visual pathway, the substantive degree of cortical remapping, and, ultimately, details at the intersection of neurobiological function and subjective psychological experience.
References


Appendix A

Histograms

Histogram of \text{data.biri$PEraw}

Histogram of \text{data.biri$PEtrans}
Appendix B

Quantile-Quantile Plots

Normal Q–Q Plot

Sample Quantiles

Theoretical Quantiles

Normal Q–Q Plot

Sample Quantiles

Theoretical Quantiles
Appendix C

Mixed Model Procedure

### The Mixed Procedure

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### Appendix D

#### Covariance Estimation

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Convergence criteria met.
Appendix E

Fit Indices

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Individual-Level Profiles

Individual Specific Perceptual Exclusivity Profiles (30 deg)

Individual titles include subject name, slope ($\beta_1$), intercept ($\beta_2$), and correlation coefficient ($R$) for linear regression of perceptual exclusivity data across trials.
Individual titles include subject name, slope ($\beta_1$), intercept ($\beta_2$), and correlation coefficient ($r$) for linear regression of perceptual exclusivity data across trials.
Individual Specific Perceptual Exclusivity Profiles (45 deg)

Individual titles include subject name, slope ($\beta_1$), intercept ($\beta_2$), and correlation coefficient ($R$) for linear regression of perceptual exclusivity data across trials.
Individual Specific Perceptual Exclusivity Profiles (90 deg)

Individual titles include subject name, slope ($\beta_1$), intercept ($\beta_2$), and correlation coefficient ($r$) for linear regression of perceptual exclusivity data across trials.